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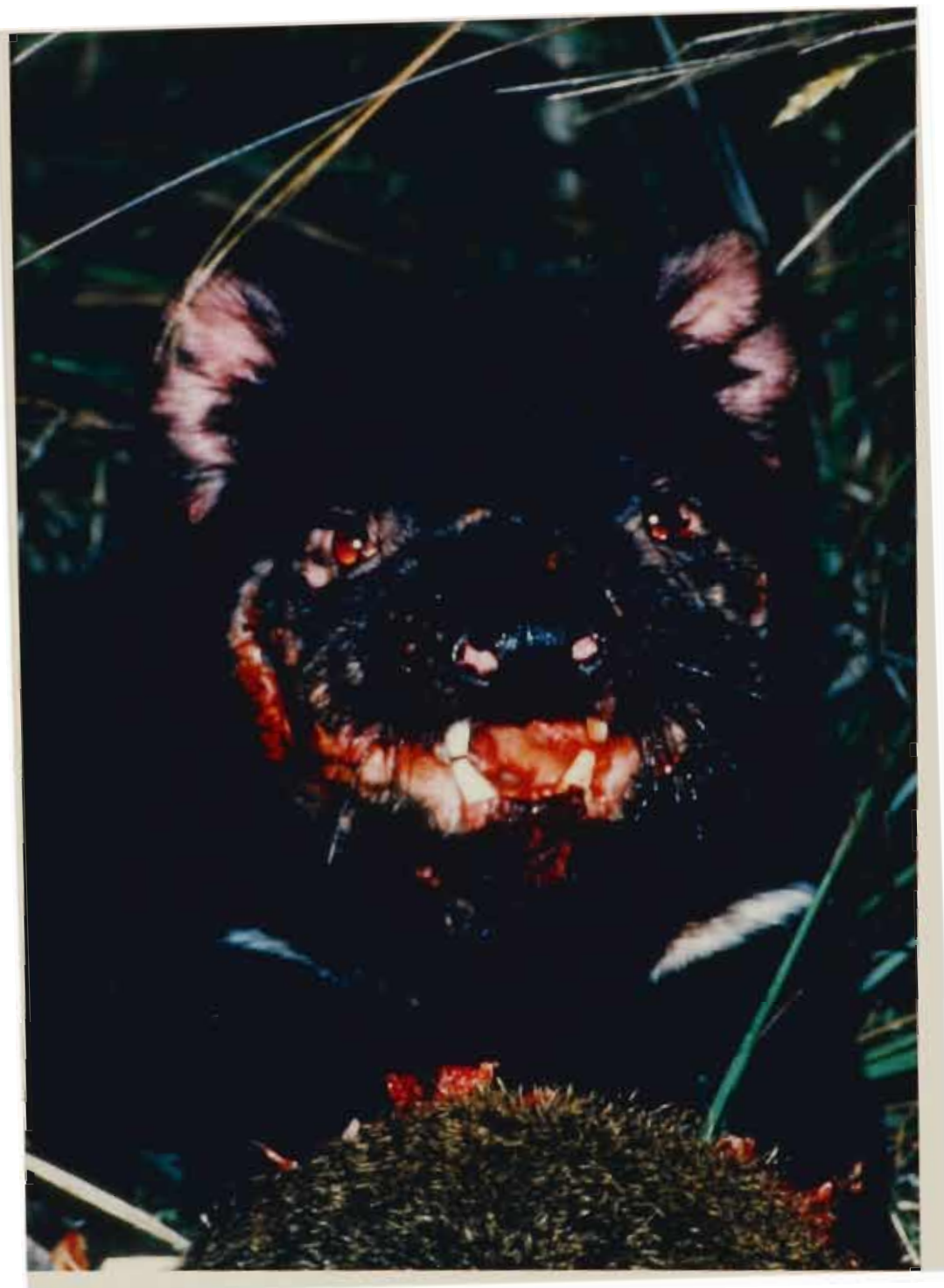

SOCIAL ORGANISATION AND BEHAVIOUR OF THE TASMANIAN DEVIL, *Sarcophilus harrisii*

by

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B. Sc. (Rhodes), Hons (Witwatersrand)

Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

in the Science Faculty, Zoology Department

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HOBART

July 1990

DECLARATION

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

David Pemberton

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ABSTRACT

There are two conflicting views regarding the nature of the social organisation of the Tasmanian Devil *Sarcophilus harrisii*. It has been described either as a polygamous species in which the males hold a dominance hierarchy or a promiscuous species where there is no prolonged association between individuals. It is the aim of this thesis to precisely describe the social organisation and behaviour of the Tasmanian Devil and thereby dispel the confusion.

Many studies of the social organisation of highly social animals have been carried out but relatively few on solitary animals such as the Tasmanian Devil. Notwithstanding this, it is known that the density of devil populations can be high in any one area, that they have a notorious aggressive behaviour towards each other and also an elaborate communicatory repertoire. This suggests that the pattern of relationships between individuals of a population could be highly complex. In order to investigate this, a three year field study was carried out on a population at Mt. William, north-east Tasmania. This study investigates and describes the population demogaphy and size, social behaviour and the dispersion pattern of the devil population.

A trapping preiod of 500 trap nights conducted over a period of ten days was found to be suitable to effectively sample the population. The largest source of error in calculating the population size was the unequal catchability of animals both within and between trap sessions. For this reason, a number of different methods for calculating population size were used and the results evaluated with respect to each other. The population reached a peak of between 200 and 400 animals from summer through to spring after which it declined to between 80 and 100 animals. This trend did not vary between years. The seasonal pattern was the result of an influx of weaned young into the population in January which remained in the area until August when they dispersed. Females were sexually mature in their second year with 81 % carrying on average 2.3 young, of which 73 % survived to weaning. Fertility decreased with age. There was a highly synchronised birth-pulse taking place over a three-week period with April 10 being the median birth date. No breeding was recorded out of season and over the three year period of the study there was no major variation in the median birth date. The females den their young in August and leave the young in the same den each night while foraging. Young were weaned 240 days after birth. There was a male-biased dispersal pattern of juveniles. Those males that remained philopatric to their natal area suffered less mortality than the philopatric females. There were similar numbers of adult male and female residents throughout the year. Male residents remained in the area for the duration

of the study, whilst some females were absent for periods of a year or more. This form of dispersion was termed discontinuous residency. Females that showed a discontinuous residency behaviour had lower fertility rates than the continuous residents.

Telemetry studies of the dispersion pattern of the devils showed that they occupied overlapping home ranges of 13.3 km^2. Devils were tenacious to their dens and used between 2 and 3 dens. Most of the dens were burrows in relict Quaternary dunes. Three foraging strategies were identified with respect to the rate at which the animals traveled through the night: Linear, Exponential and Stepped. The home ranges were located over the habitat containing the highest concentrations of macropods.

Observations of social interactions around food showed that devils used a variety of postures and vocalizations. Communication during agonistic interactions between animals competing for access to food was ritualistic and hence seldom resulted in physical damage. The results of these encounters were related to the length of time that the participants had being feeding and not to any form of hierarchy in the population. The form of these interactions is described with respect to the Resource Holding Potential hypothesis.

The pattern of stress resulting from social interactions in the population manifested itself in an annual variation in steroid and androgen levels. Stress, as indicated by elevated corticosteroid levels, was highest during the period of maximum population size. Males had lower stress levels than females. Female stress levels showed two peaks, associated with the early phase of breeding when sexual encounters take place and the latter half of lactation, when the females are caring for denned young. The testosterone levels of the males were depressed throughout the year but unlike in all other dasyurids studied to date, there was no peak associated with the copulation period. The varying stress levels in the devil are explained in terms of varying social conflict and its duration.

This study has shown that the Tasmanian devil is a solitary, nocturnal predator occupying an overlapping home range with other members of a fluctuating population. Interaction between the members of this population is intense and manifests itself in the lower reproductive potential of those females who are not continuous residents and the latent stress levels in all animals, particularly juveniles, in relation to high population levels. It is this interaction between individuals of the population which, along with the life history pattern of being a facultatively monoestrous species, which dominates the social organisation of the Tasmanian devil resulting in resident animals having a higher

reproductive potential than non-residents. It is hypothesised that the communal feeding habits of the animals and use of communal latrines are highly significant forces.

The various facets of this study are drawn together to give a description of the social organisation of the species and some of the factors which exert a control over it. Hypotheses are made on how the social organisation may vary with different food regimes in different habitats.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to the following people who assisted me during the course of this project:

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CHAPTER 1

GENERAL INTRODUCTION

1.1 BACKGROUND AND AIMS

The Tasmanian devil, *Sarcophilus harrisii* (Boitard), is the largest extant carnivorous marsupial and whilst it was living on the mainland of Australia up to 430 years ago (Archer & Baynes 1972), it is now restricted to Tasmania.

The Tasmanian devil, or more commonly, the devil, is protected by the Tasmanian National Parks and Wildlife Act (1970) but may be culled under Crop Protection permits. The species is distributed throughout Tasmania in a variety of habitats (Fig 1.1). There has been no detailed study of the densities of devils in these habitats, but there is a broad trend for a decrease in densities from the drier warmer areas of the dry sclerophyll habitat through the wet sclerophyll forests to the wetter rain forests and sedge lands and the colder alpine moorland (Dept. Parks Wildlife & Heritage TASPAWS records). There is scanty evidence to suggest that devils have undergone one major population cycle since the arrival of Europeans in Tasmania (Guiler 1982). At present they are widespread and numerous partly as a result of their ability to exploit food sources associated with farming practises.

Whilst there is a vast literature on the biology of many dasyurids, that on the devil is limited both in scope and quantity. Aspects of reproduction have been studied by Roberts (1915), Fleay (1935, 1952), Flynn (1910,1911, 1922), Pearson (1940, 1945), Pearson & de Bavay (1953), Guiler (1970a, b) and Hughes (1976a, b; 1982). There has also been a suite of laboratory based physiological studies which have concentrated on aspects of metabolic rate, body temperature and blood biochemistry (Guiler & Heddle 1970, Heddle & Guiler 1970, Parsons *et al.* 1971a, b, Hulbert & Rose 1972, Sallis *et al.* 1973, Guiler & Heddle 1974, Sallis & Guiler 1977, Nicol 1978, Green & Eberhard 1979, Nicol 1982, Baudinette 1982, Shah *et al.*1986). The ecology and life history of the devil has been studied in the field in a long term trapping study by Guiler (1970 a,b; 1978) and aspects thereof by Lazell (1984), Taylor (1986) and Green (1967). In addition, Guiler has also published work on albinism in devils (1976), temporal and spatial distribution of the species (1982) and on maintenance of the devil in captivity (1971). The distribution and taxonomic status of fossil devils has been investigated and summaries of these findings are presented by Dawson (1982) and Guiler (1982).

Despite these investigations into aspects of the biology of the devil, there is a paucity of data on the social system and life history of the species. Lee & Cockburn

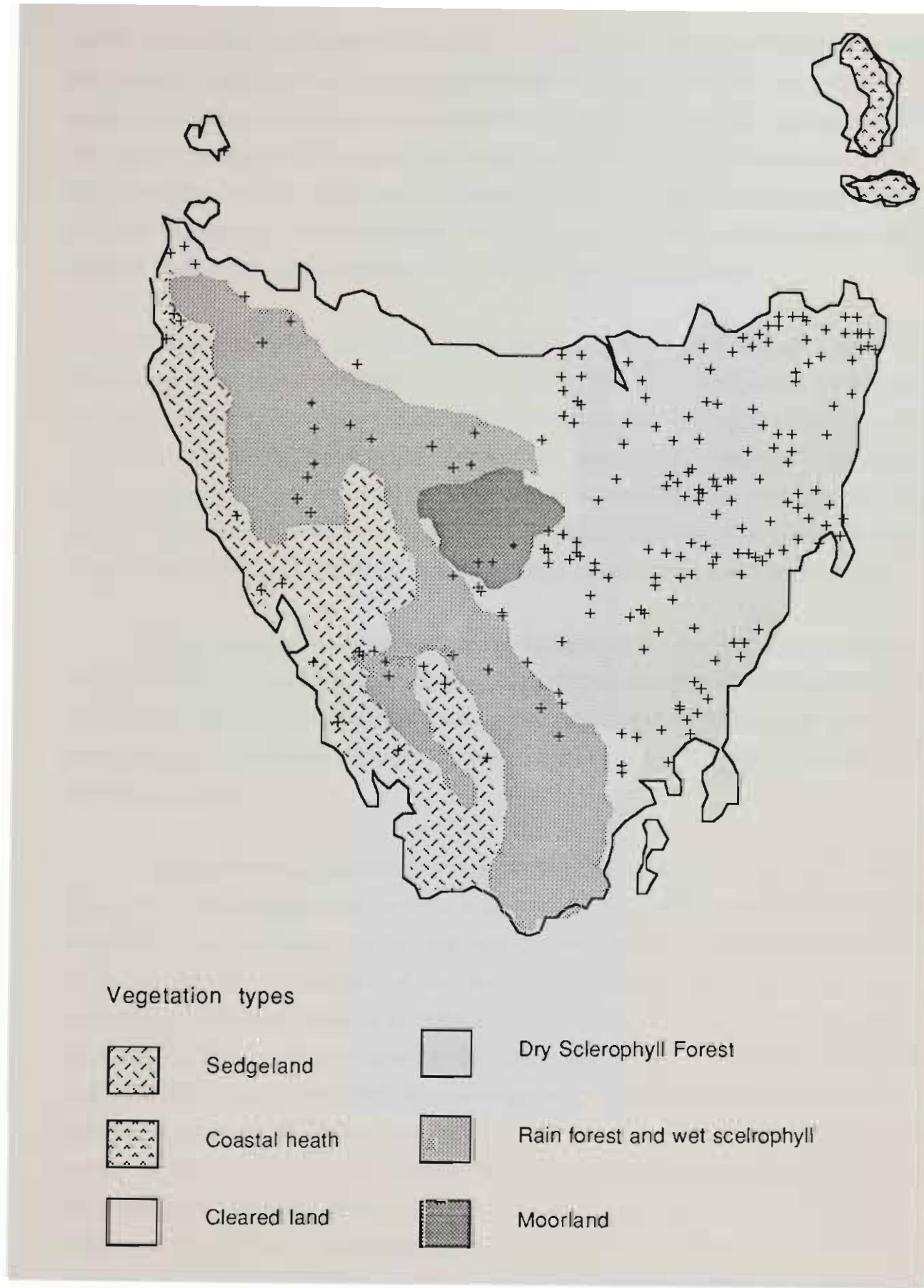


FIGURE 1.1

Map of Tasmania showing the distribution of devils (+) from TASPAWS records and the dominant vegetation types (after Jackson 1965).

(1985) pointed out that the devil remained an enigma with respect to classifications of life history strategies which accommodated all the other dasyurids. In a review of social organisation in marsupials, Russell(1984) pointed out that little is known about the social organisation of the devil, and being the largest extant carnivorous marsupial, such an understanding would contribute significantly to interpretations of the evolution of social organisation. It is the central aim of this thesis to redress this situation via a detailed study of the social organisation and behaviour of the species.

Eisenberg (1981) considered four social phases of a mammals life to be informative with respect to classifying the social organisation of a species, these being the mating system, rearing system, foraging behaviour and refuging phase. Russell (1984), in classifying social organisation in the marsupials, categorised the social relationships concerned with spacing patterns, mating systems and parental care. The present study incorporated the methods of classification of these two authors in order to obtain and synthesize information relating to the social organisation of the devil.

Thus, classification of the social organisation of the devil required information on the following facets of the population: demography, population size and how this varies with time, social behaviour, home range size and distribution with respect to time and space, and the pattern of stress with respect to population size and reproductive stage.

The methods used to assess the age of the devils are presented in Chapter 2. This process was critical to the study as it allowed all the other parameters measured to be related to age and hence incorporated into the description of the social organisation of the population. An analysis of the population size of devils in the study site is presented in Chapter 3. There is a plethora of methods by which to estimate the size of mammal populations. Five methods were used in this study, each with its own biases and attributes. In order to satisfy the assumptions which accompany these methods, exhaustive analyses of the trap response of devils were undertaken. These analyses were essential as much of the subsequent analyses of demography and parameters investigated in this study relied on data collected via an effective sampling regime. Chapter 4 describes various demographic features of the population and, whenever possible, these are discussed in age-related terms. A detailed description of dispersal is included in this chapter. The social behaviour of devils was investigated and is described in Chapter 5. Carcasses were provided in the wild which attracted devils and allowed detailed observations of the behaviour of devils when in contact with conspecifics at feeding sites. In order to assess the dynamics of spatial organisation and foraging, devils were radio tracked as they traversed their range (Chapter 6). The use of radio tracking also facilitated the identification of den sites. The pattern of use of

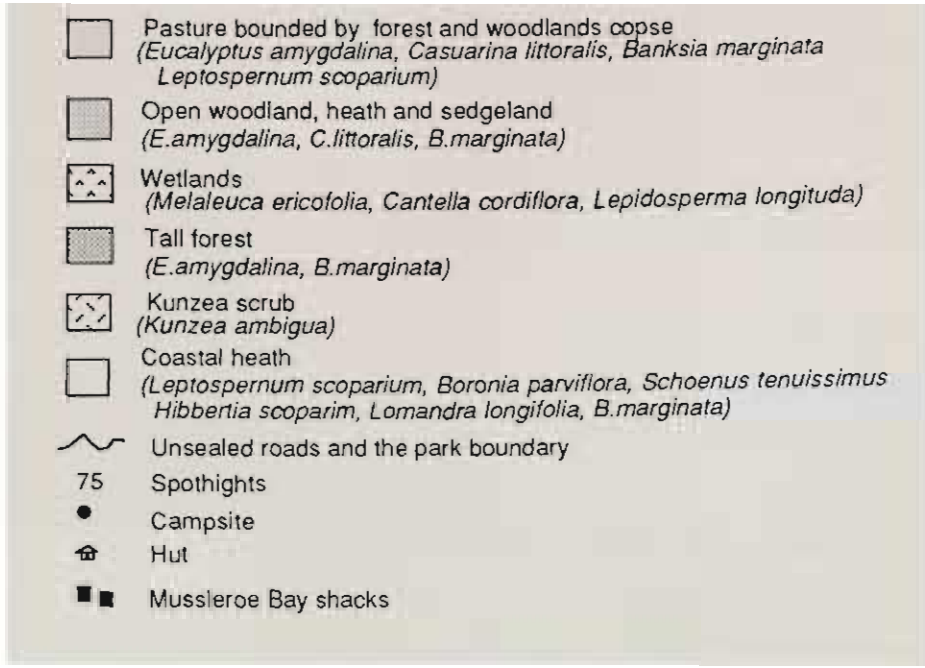
these dens was interpreted with respect to the spatial and temporal constraints on the movements of female devils in particular. A description is also given of the use of latrines by devils. The seasonal pattern of social interactions was investigated by measuring the levels of circulating hormones (Chapter 7). The pattern of these hormone levels was also related to the breeding regime of the devil, and in particular, to the possible affects on male die-off as is recorded for many of the smaller dasyurids. A General Discussion is presented in Chapter 8 where these parameters are synthesized and interpreted in order to provide a comprehensive description of the social organisation and behaviour of the devil.

This information is then examined with the aim of identifying factors which operate in the control of the dynamics of the population density and movements. The distribution of resources such as food and dens is an important determinant of social systems, having a direct effect on dispersion of animals and thereby, indirectly on mating systems. A close relationship between social organisation and distribution of food, and the way in which that food is exploited has been established for many mammals (see for example: Kruuk 1975,1978, 1987; Mills 1982, Macdonald 1983). Two important components of social organisation are group size (or density where groups per se are not formed) and the territory or size of an animals range. These can therefore be expected to be influenced by the dispersion of food. This has led to the development of hypotheses about factors such as food and dens influencing the group size and range sizes of animals (Bradbury & Vehrenkamp 1977, Eisenberg 1981, Macdonald 1983, Kruuk & Macdonald 1985). The relationship between the distribution of food and dens and the dispersion and population density of the devils was also investigated and discussed in this study (Chapter 6 & 8).

1.2 STUDY SITE

The site used for this study was the Mt. William National Park in the north eastern corner of Tasmania. This site was selected as the devil population is undisturbed and protected from "external influences," such as shooting, by the status of the National Park. Further, the topography and habitats were appropriate for radio tracking. The locality of the study site within the Park is shown in Figure 1.2. All land to the west of the Park is used as a sheep station. The Park covers an area of relatively low relief comprised of a tract of granite country which rises from a coastal plain to Mt.William (216 m elevation). The study site is bounded by a coastline of sandy beaches and granite headlands. The northern section of the Park is dominated by relict sand dunes. The habitats, together with dominant flora found within the study site are shown in Figure 1.2. The legend for this Figure also provides a species list of the mammals (other than Chiroptera) found in the park.

MAJOR VEGETATION TYPES



MAMMALS

Macropus giganteus
Macropus rufogriseus
Thylogale billardierii
Bettongia gaimardi
Dasyurus maculatus
Dasyurus viverrinus
Sarcophilus harrisii
Sminthopsis leucopsus
Antechinus minimus
Vombatus ursinus
Trichosurus vulpecula
Pseudocheirus perigrinus
Tachyglossus aculeatus
Isoodon obesulus
Hydromys chrysogaster
Pseudomys novaehollandiae
Rattus lutreolus
Rattus rattus
Mus musculus

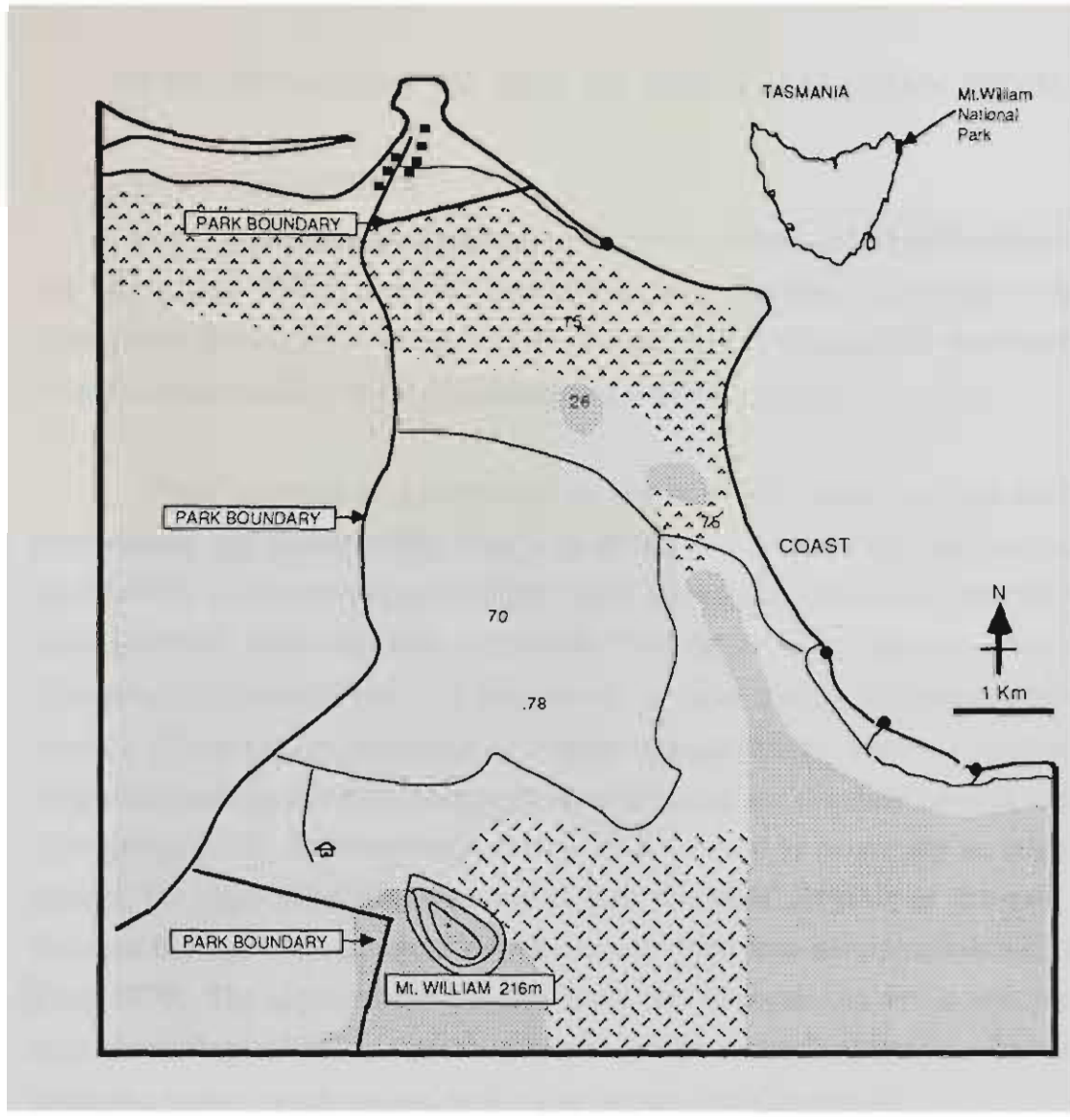


FIGURE 1.2

Location of study site located east of Mt. William National Park boundary.
Distribution of major vegetation types is shown and described opposite.
A list of mammals present in Mt. William National Park also presented opposite

CHAPTER 2

DETERMINATION OF AGE OF THE TASMANIAN DEVIL

2.1 INTRODUCTION

In any population analysis the most useful parameters are often those related to age (Caughley 1977). For the Tasmanian devil, however, there is no published quantitative information on age determination. This is an essential pre-requisite for a detailed understanding of its population and social dynamics.

When material of known-age is not available there are two methods for determining age (King 1979). One is to divide the animals into natural age-classes bounded by characteristic parameters, such as eruption of teeth, irrespective of the chronological intervals they represent. The other is to pre-conceive desirable chronological intervals and to fit the animals to these classes. Differences between age classes of mammals spanning less than a year relate more to season than to chronological age. Hence, classes defined in years are the only natural units of age (Caughley 1977). Further, the chronological method is necessary to identify year-classes for population analyses and is also the more flexible of the two methods because the age-classes can always be sub-divided into natural classes if required (King 1979). The approach used in this study was to divide the devils into year-classes on a chronological basis. April is taken as the first month of the year because this is when the highly synchronized birth pulse occurs (see Chapter 4).

There is a basic distinction between relative age and absolute age (Morris 1972). The former is simply the age of one animal measured relative to the state of development of another. It is a comparative process greatly assisted by having known age material. Absolute age as used in this study describes age in precise measurements: i.e. as months or years. The ages of devils were inferred using various criteria which have been divided between absolute age and relative age.

It has been suggested that, at least in captive devils, the age of dependent young can be estimated using the status of teeth, shank length and body mass (Guiler 1970a). Morris (1972), however, stated that age determination methods based upon the principles of growth patterns and sequences in captive animals will be affected by the artificial conditions. At Mt.William, during the present study, only four devils were caught within the body mass range described by Guiler (1970a) and, therefore, other criteria were used to establish the absolute age of devils.

2.2 METHODS

2.2.1 AGEING CRITERIA FOR ABSOLUTE AGE

The lower molars of all animals captured were checked to assess the stage of eruption. This was done by holding the devil in a sack, grasping the neck in both hands and looking into the mouth. Devils can be easily induced to open their mouths by blowing gently on their faces. The lower molars, rather than the upper molars, were checked as these are more easily seen whilst also restraining the devil. Sharman *et al.* (1964) divided the degree of eruption in the red kangaroo (*Macropus rufus*) into four stages. These stages were modified for use with the devil, to show the sequence of eruption of each cusp (Table 2.1).

2.2.2 AGEING CRITERIA FOR RELATIVE AGE ESTIMATES

In order to establish criteria for relative age estimates, morphometric measurements were taken and growth curves were plotted for all known-age animals, i.e. those animals marked as weaned young of the year and re-trapped and measured through the study. Linear measurements were made of the pes, from the tip of the calcaneum to the tip of the metatarsal. The tibia was measured from the calcaneum to the furthest point on the patella. The width of the head was taken as the widest distance between the zygomatic arches. The length of the head was measured from the tip of the snout to the middle of the occipital. All measurements were made with vernier calipers, accurate to one decimal place. The calipers were held horizontally to standardize the procedure. Body mass was not used in this analysis because large variations in mass (e.g. ± 1 kg within one day) were common.

There are many structures in the body which suffer gradual degradation with time. These time (but not growth) related features were used to help categorize age-classes. Two forms of degradation, tooth wear and facial scarring were assessed as tools for the determination of age of devils.

Tooth wear is conspicuous in devils, particularly on the canines and molars. Canines were not used in the analysis of age because re-trapped individuals showed that these teeth were subject to fracturing and breaking, thereby showing a major change in a short time. The M_1 is bicuspid and the M_2, M_3 and M_4 are tricuspid. Each cusp is pointed in early life, but wears down to the gums at old age. Figure 2.1 shows the wear characteristics used to class the animals. These characteristics are broad and easily distinguishable because they incorporate features such as dentine exposure and presence of cusps, but do not use subjective estimates of tooth height.

Facial scarring in devils takes place primarily around the cheeks and muzzle. The degree of scarring was ranked according to the index described in Table 2.2

TABLE 2.1 Stages of tooth eruption as modified for this study after Sharman et al. (1964)

Stage	Modified index
1	Just below surface
2	One cusp showing
3	Two cusps showing
4	Fully erupted

TABLE 2.2 Description of facial scar index

Scar index	Description of diagnostic features
0	Clean skin and fully furred
1	Loss of fur; localised and superficial scarring
2	Pigmented scars covering cheeks; fresh wounds and calloused scar tissue

TABLE 2.3 Maximum values of parameters used to identify weaned young of the year

Sex	Back leg length mm	Head length mm	Head width mm
Male	< 140	< 110	< 145
Female	< 135	< 98	< 140

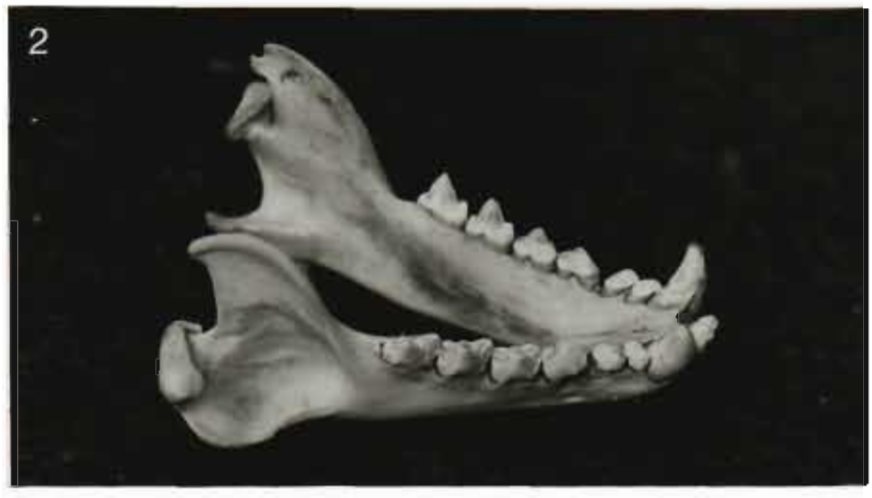
FIGURE 2.1 Wear characteristics of the lower molars used to identify age classes. The wear characteristics were scored on a scale of 0 to 5 which were described as:

0 - no wear
1 - tip worn
2 - dentine showing
3 - all cusps worn but still distinguishable
4 - no distinguishable cusps
5 - flat and worn to gum

The photographs shown here provide examples and display the following wear characteristics:

Photograph	Lower molar			
	1	2	3	4
1	0	0	0	0
2	2	2	0	0
3	3	3	snapped	0
4	4	4	4	1


1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4

2.3 RESULTS

2.3.1 AGEING CRITERIA FOR ABSOLUTE AGE

In this study after the first season of field work devils without a fully erupted M4 could confidently be identified as young of the year. These animals were first trapped in the population in November-December of each year and reached a peak in February and March (Fig. 2.2). All animals in the population had a fully erupted fourth molar by June. The stages of M4 eruption relative to time and the individual variation in time of eruption stages of M4 are shown in Figure 2.3.

2.3.2 AGEING CRITERIA FOR RELATIVE AGE ESTIMATES

2.3.2.1 Growth of known age animals

The growth curves for length of the pes, back leg, head and the width of the head for known age devils (based on initial capture of weaned young from the second year of study: 1984) of both sexes are shown in Figures 2.4 and 2.5. Appendix 1 lists the sample sizes, means and standard errors used to plot these figures. The maximum values of the other morphometric parameters are shown in Table 2.3.

These growth curves (Figs. 2.4 and 2.5) were then used to identify and age young of the year caught in the first year of the study: 1983. The data from the devils which were first caught in 1983, and trapped subsequently during the study, served to increase both the sample size and the age which could be assessed for devils during the three year field study. The growth curves of the morphometric parameters of all devils whose age was known are shown in Figures 2.6 and 2.7. Appendix 2 shows the sample sizes, means and standard errors used in these Figures.

Due to the synchronized breeding season these individuals could then be aged to the month. For example, an individual caught in May with a fully erupted M4 but with morphometric measurements less than those in Table 2.3 is accepted as a weaned young. It is 14 months old having been born during April (month 1) of the previous year.

2.3.2.2 Morphological characters related to time but not growth

Representative examples of the posterior progression of wear along the tooth row and down each tooth with time are shown for five animals in Table 2.4. The degree of wear on each tooth for known age animals shows overlap between ages (Fig. 2.8). There are, however, distinguishing features which help in ageing. The degree of tooth wear of the weaned young of both sexes shows large overlap with the one year olds. The male two year olds can be distinguished from the one year olds by wear class 4 on the M2 and wear classes 2 and 3 on the M3. The female two year olds can be distinguished by wear class 4 on the M2 and wear class 2 on the M3.

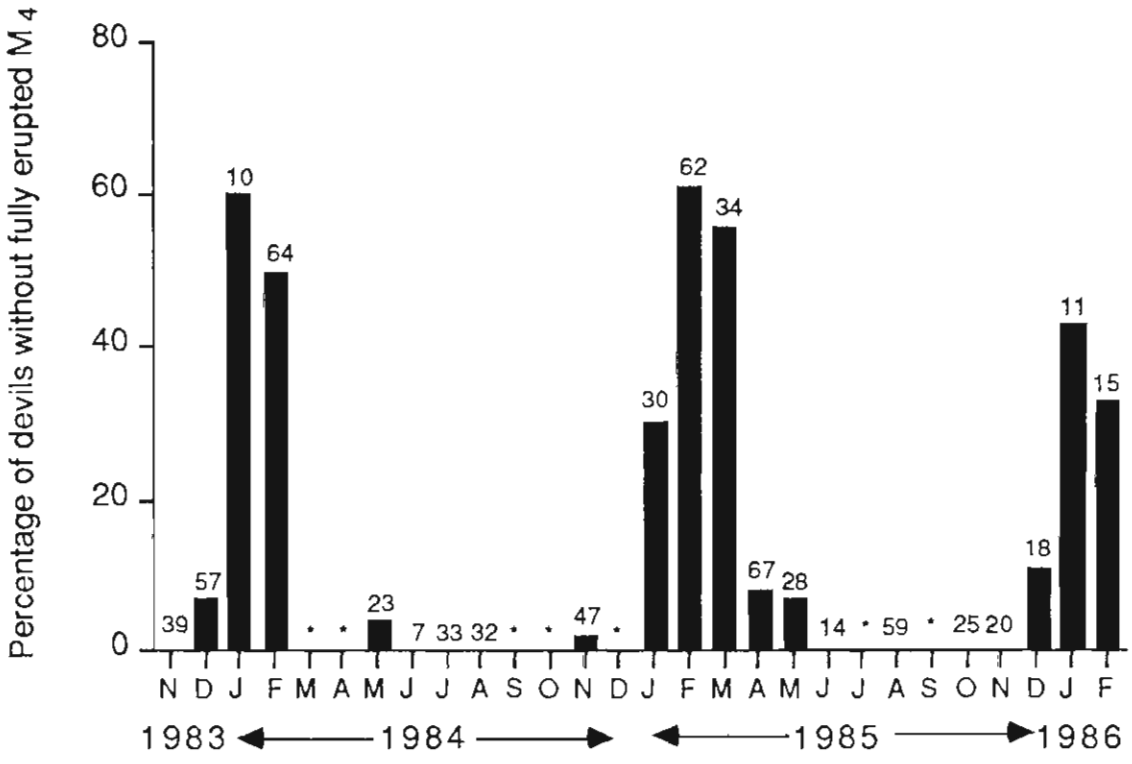


FIGURE 2.2 The percentage of devils captured which did not have a fully erupted M_4. Sample sizes of total number of devils trapped in each month are shown above bars.
* indicates no samples.

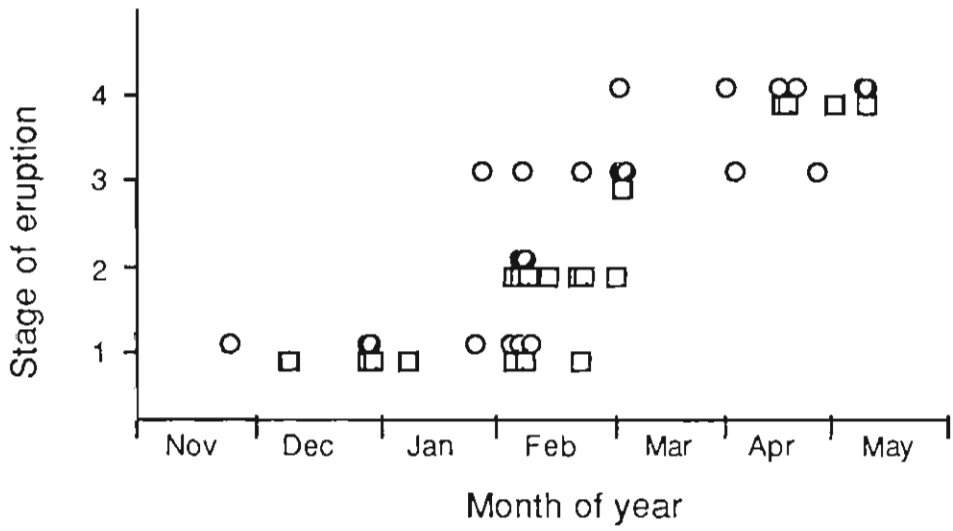


FIGURE 2.3 Stage of eruption of M_4 for males and females. Symbols (circle = female, box = male) have been shifted slightly for clarity. Stages of eruption are described in Table 2.1

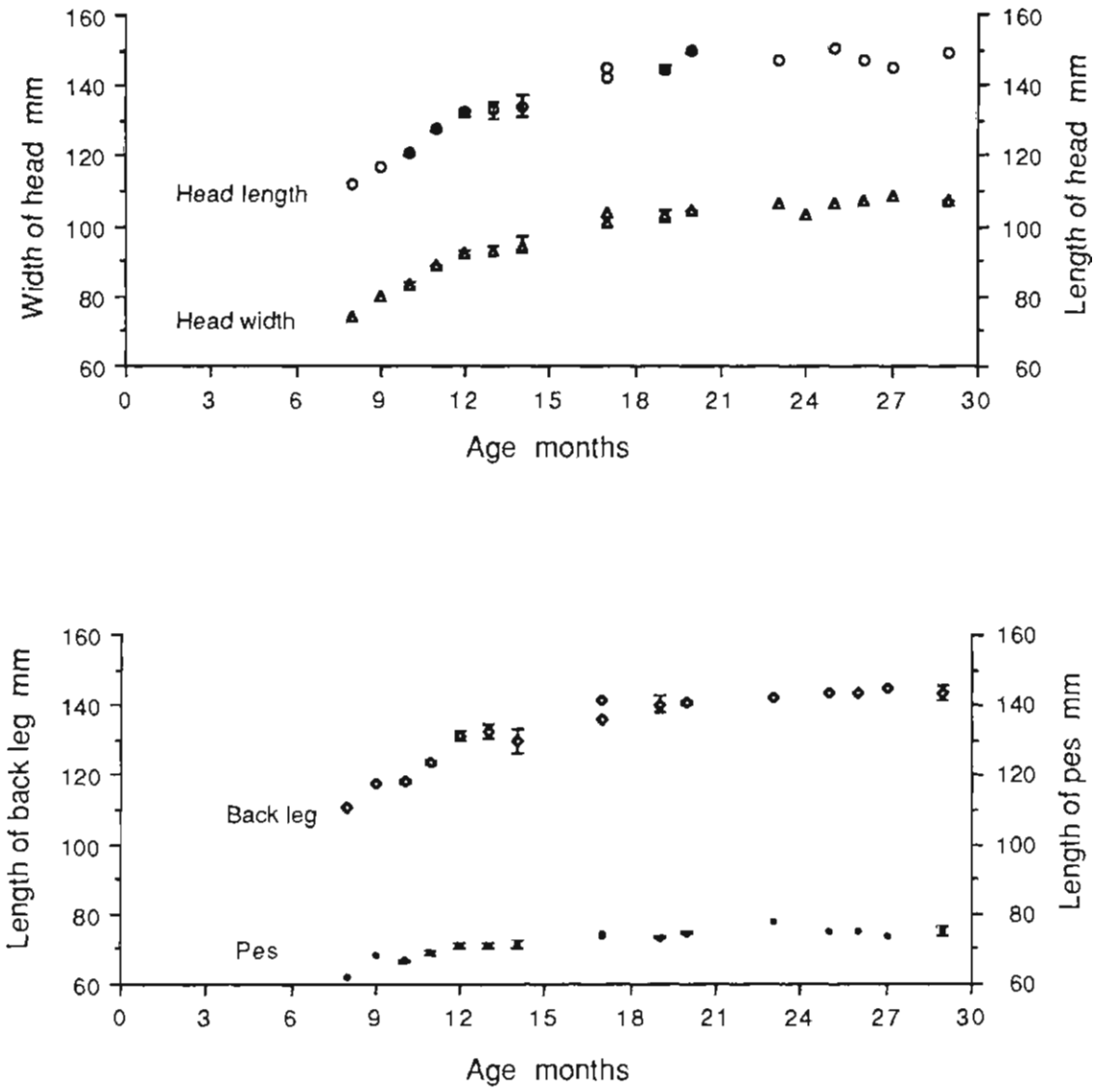


FIGURE 2.4 Growth curves for all known age females which lacked a M_4 at initial capture (mean ± S.E. when n > 2)

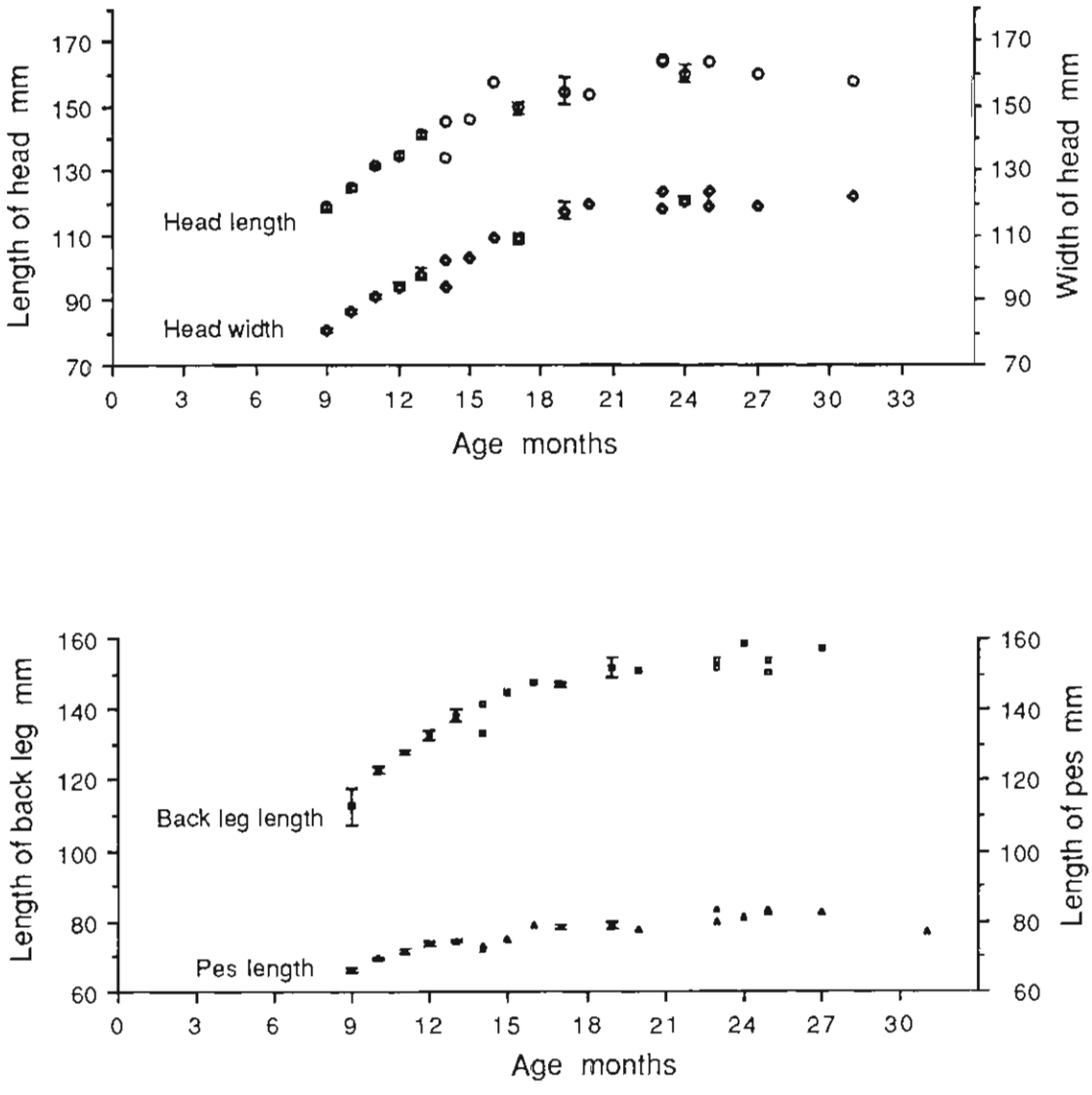


FIGURE 2.5 Growth curves for all known age males which lacked a M_4 at initial capture (mean ± S.E. when n > 2)

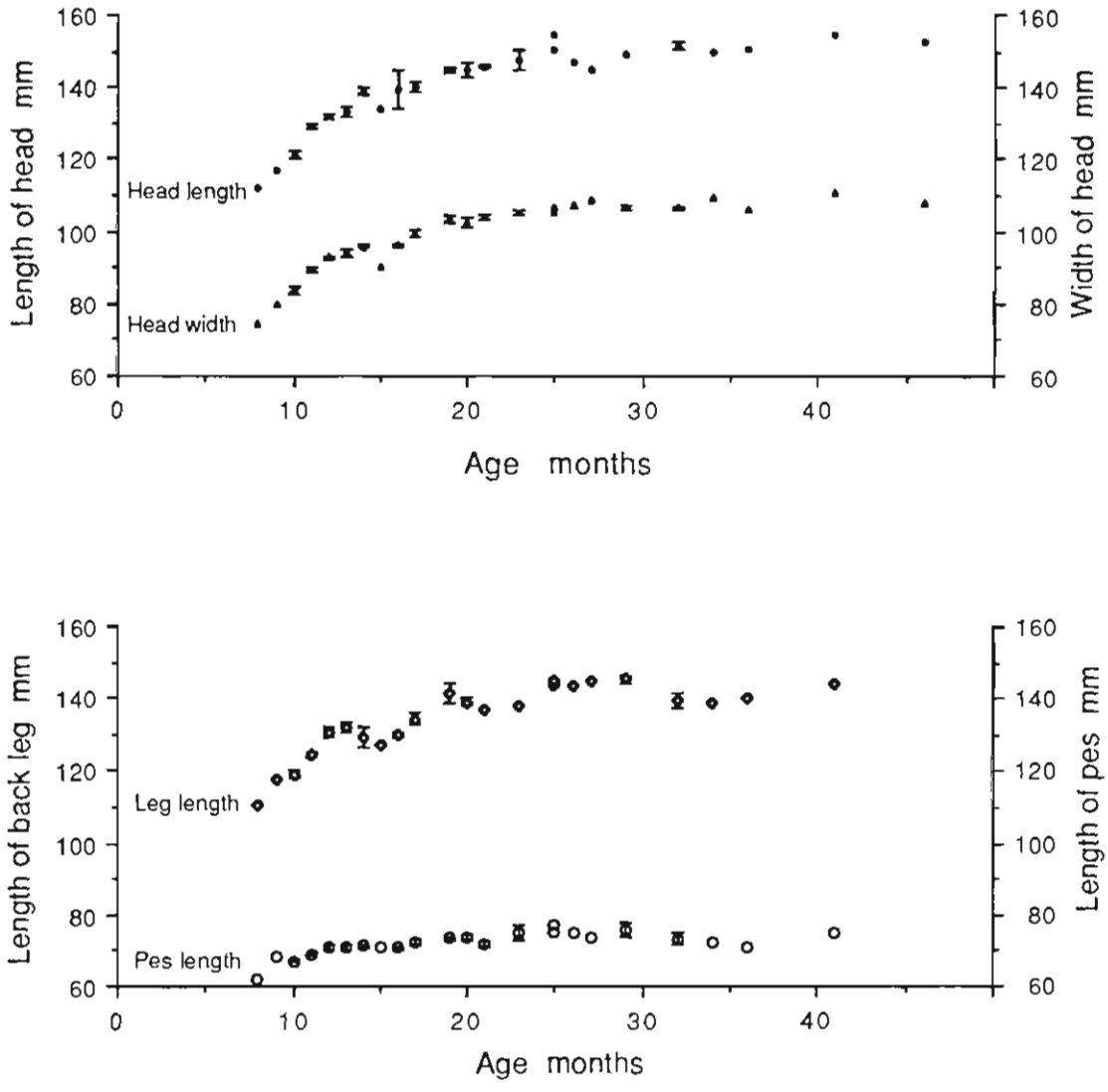


FIGURE 2.6 Growth curves for all known age females (mean ± S.E. when n > 2)

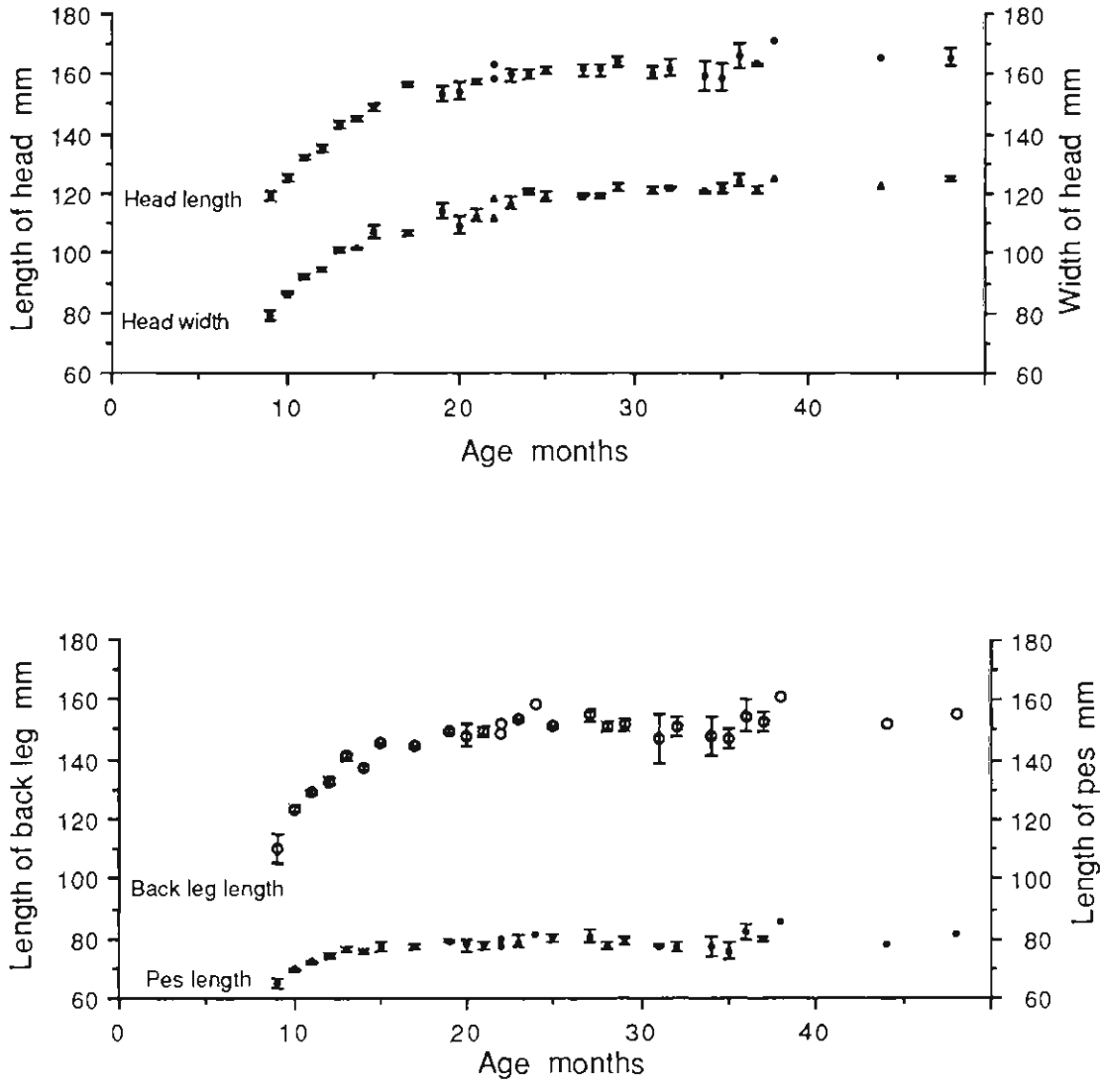


FIGURE 2.7 Growth curves for all known age males (mean ± S.E. when n > 2)

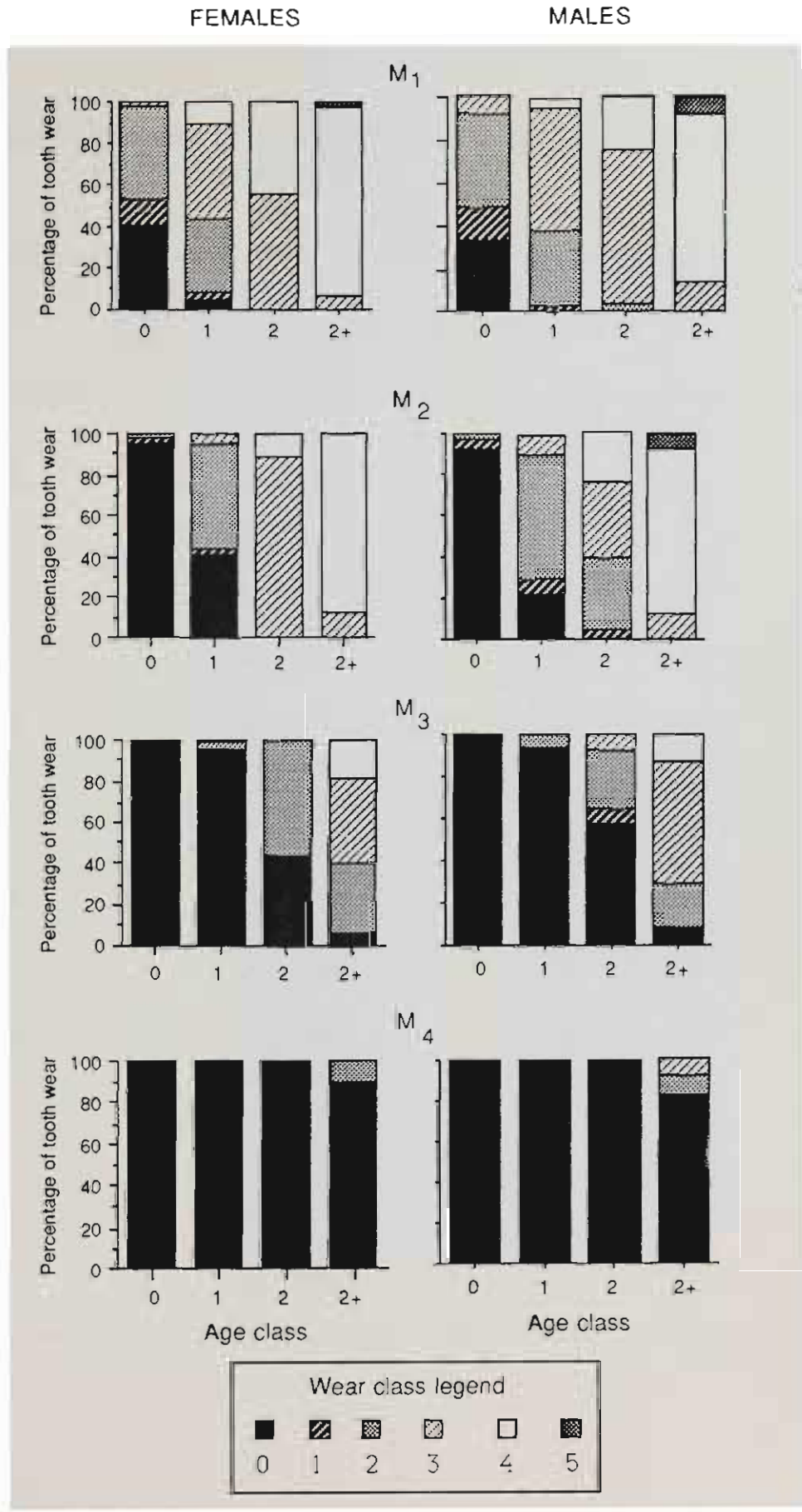


FIGURE 2.8 Frequency histograms of tooth wear on each molar for females and males. Characteristics of each wear class depicted in Figure 2.1

TABLE 2.4 Examples of the downward and posterior trend of tooth wear with time in devils

I.D.	Age years	Date	M1	M2	M3	M4
L118	1	May 1983	2	2	0	0
	1	Aug 1983	3	2	0	0
	2	Jul 1984	3	2	1	0
	2	Nov 1984	3	3	2	0
	2	Jan 1985	3	3	2	0
	3	Apr 1985	4	4	2	0
L123	1	May 1983	2	0	0	0
	1	Aug 1983	3	2	0	0
	2	Aug 1984	3	2	0	0
	2	Mar 1986	4	4	4	2
L144	1	May 1983	2	0	0	0
	2	Mar 1985	3	3	0	0
	3	May 1985	3	3	2	0
L178	1	Aug 1983	3	2	0	0
	1	Dec 1983	3	3	0	0
	2	Apr 1984	3	3	2	0
	3	May 1985	4	4	3	0
L12	1	May 1983	3	0	0	0
	1	Dec 1983	3	3	0	0
	2	Jan 1985	3	3	2	0

The frequency of the degree of facial scarring between age groups in the females does not show much variation as the females do not show extensive facial scarring at any age (Table 2.5). Male devils, however, do show a distinction where most two year olds (76 %) show class 2 scarring, whereas very few (2 %) one year old devils exhibit such scarring.

2.4 DISCUSSION

The determination of age in devils has been approached in this study by identifying absolute aged animals, using them to calculate a relative age for other animals and then following the development of these animals to help classify age classes. In addition to growth related parameters, time dependent features such as tooth wear were incorporated into the age-class classification.

Guiler (1970a) stated that weaned young lacking a full complement of teeth were never trapped in the wild. However, at Mt.William devils without a fully erupted M4 were trapped in the field from November until May. These animals were accepted as young of the year. All animals in the population had a fully erupted fourth molar by June. Hence, devils can be simply aged in months by calculating the number of months which have elapsed since the synchronized birth date in April (month 1). For example, animal R2 was captured on 10 December 1983, nine months after the birth date and is, therefore, nine months old.

The growth curves constructed from the pooled data reached the final adult dimensions (asymptotic value) by 24 months after the birth date for both sexes. Therefore, these morphometric parameters cannot be used to determine the age of devils which are more than two years old.

Chewing of food invariably results in the abrasion of the teeth. Tooth wear has been used to age a diverse range of mammals including warthog *Phacochoroes aethiopicus* (Spinage & Jolly 1970a), wildebeest *Connochaetes taurinus* (Attwell 1980), brush-tailed possum *Trichosurus vulpecula* (Winter 1980) and the spotted hyaena *Crocuta crocuta* (Kruuk 1972). However, caution must be exercised when extrapolating age from tooth wear as tooth wear is subject to two main sources of error. The first is that any variation in the composition of the diet may influence the amount of wear (Ryel *et al.* 1961, Grau *et al.* 1970, Morris 1972) and the other is the human error involved with a subjective assessment of tooth wear (Robinette *et al.* 1957, Ryel *et al.* 1961, Morris 1972). However, Morris (1972) and Caughley (1977) pointed out that if tooth wear is assessed in conjunction with other age related parameters, and calibrated against animals of known age, the technique can be useful.

TABLE 2.5 Frequency of occurrence (n) of facial scar index scores on devils

Sex	Age class	Scar index 0	1	2
Female	Weaner	54	0	0
	Juvenile	69	1	1
	Adult	7	2	5
Male	Weaner	77	0	0
	Juvenile	112	14	3
	Adult	5	3	26

In the case of devils, tooth wear can assist in the determination of age. However, because of the overlap of wear classes between ages it can only be used in conjunction with growth measurements (Table 2.6). Females, for example, with a tooth wear class of 3 or 4 on the M3 or 2 on the M4 are definitely more than two years old. Males with wear on the M4 or a wear class of 4 on the M3 are also definitely more than two years old. However, there may also be devils of over two years old that show no tooth wear on any lower molar. Given this, I regard tooth wear as a useful ancillary parameter which can be used to assess the age of devils.

By comparison to tooth wear, the scarring index was found to be of more limited use in determination of age, particularly when dealing with females which are not prone to facial scarring (Table 2.5). The scarring index can be of some use as it does provide another method for separating male one year olds from two year olds.

The parameters of length of head, width of head, scar index and tooth wear were used together to delineate three age classes: 0, 1 and 2+ (Table 2.6). These age classes translate to the descriptive age classes of weaners (0 - 12 months), juveniles (13 - 23 months) and adults (23 + months). These are functional descriptions which are in accordance with age related reproductive parameters including age of attainment of sexual maturity (Chapter 4).

Devils which are less than one year old are easily distinguished as their growth is at a peak, reducing variation across months and they lack an M4. Subsequent to this, as asymptotic values are approached, growth tends to slow down with the result that there is overlap in the growth measurements between age classes 1 and 2+. This overlap is greatest at the time approaching the assigned year boundary, March to April. To reduce the error caused by this overlap, animals caught during this period were not assigned age classes. Furthermore, although this reduced the sample size, the effect was not great as the easily distinguishable 0 age class was the most common in the trapped sample at this time of the year.

In summary, I have found that the use of growth parameters, in conjunction with tooth wear and scarring, can provide a reliable method for assigning year-classes to devils. Though this method gives only three year-classes this is adequate in a short-lived animal such as the devil (King 1979) where more than two-thirds of the individuals in the population fall into one of these two age-classes. Devils can live for about six years in the wild (Guiler 1978). The duration of the present study, together with the ageing technique made it possible to age marked animals to a minimum age of four years. Consequently, it is possible in this study to examine and discuss age-related phenomena for most of the expected life span of the devil.

TABLE 2.6 Parameters used in determination of age classes of devils*

Sex	Age class		Age months	n	Head width mm	Head length mm	Scar index	Tooth wear index			
								M1	M2	M3	M4
Males	weaners	0	0-12	79	$x \leq 96$	$x \leq 138$	0	0 - 3	0 - 1	0	not erupted
	juveniles	1	13-23	172	$96 < x \leq 118$	$x > 138$	0-1	1 - 4	0 - 3	0 - 1	0
	adults	2+	23+	37	$x > 118$	$x > 138$	1-2	1 - 5	1 - 5	0 - 4	0 - 3
Females	weaners	0	0-12	70	$x < 93$	$x \leq 133$	0	0 - 3	0 - 1	0	not erupted
	juveniles	1	13-23	99	$93 \leq x \leq 105$	$x > 133$	0	0 - 4	0 - 3	0 - 1	0
	adults	2+	23+	18	$105 \leq x$	$x > 133$	1-2	3 - 5	3 - 4	0 - 5	0 - 1

* Morphological parameters can only be used in conjunction with other measures (see text).

CHAPTER 3

THE SIZE OF THE TASMANIAN DEVIL POPULATION AT MT. WILLIAM

"Capture-recapture is an established method of
sampling animal populations"
"It would seem to me unwise now to reject
this technique , with the wealth of knowledge
of its behaviour, in favour of other techniques
whose limitations have not been explored. " *Cormack* 1979

"Capture-recapture sampling has been widely
used and abused for many years in the study
of natural animal populations." *Pollock* 1981

3.1 INTRODUCTION

This Chapter deals with the estimation of the abundance of Tasmanian devils in the study area. In any study of life history and social organisation it is essential to examine the population size (Seber 1973). More specifically, in this study there were two aims for which the determination of the size of the devil population at Mt. William National Park was a pre-requisite. Firstly, an index of population size was required in order to examine trends in this index and relate these to seasons, food supply, foraging mode and stress in the population. Secondly, information on the changes in absolute density of devils was required to relate the number of devils to changes in the potential food supply, food consumption rates and feeding behaviour.

Tasmanian devils are synchronized breeders, copulating in March, denning young in August and weaning young in January (Guiler 1970a 1970b, Green 1967, Chapter 4). These weaned young appear in the trapped sample until May but their numbers decrease from that time on. The population, therefore, fluctuates in both size and age composition.

Live-trapping has been widely used in investigations of the ecology of mammals. Most of the studies have been concerned with small mammals (reviewed by Krebs & Myers 1974, Stoddart 1979, Lee & Cockburn 1985) with the methodology being applied to larger mammals (e.g. Messick & Hornocker 1981, Melquist & Hornocker 1983, Baber & Coblentz 1986, Yodzis & Kolenosky 1986). Tasmanian

devils are medium-sized mammals and require an extended trapping area for effective random sampling. This results in inherent logistical difficulties when using the recommended trapping regimes developed for small mammals. For example, it is difficult to cover the home range of a devil with a trapping grid and at the same time clear the traps in a reasonable time. On the other hand, retrospective examination of the results of this study shows that the number of animals in the study area is large ($n \approx 300$), so samples of the population should be correspondingly large to enhance precision and reliability of estimates. These factors made the design of the study difficult and in many cases the sampling method had to be compromised due to practical constraints.

Many methods of estimating population size from capture-recapture data are available. These range from the deterministic Peterson index and more sophisticated stochastic models including the Jolly-Seber estimate and the Manly-Parr model, to the parametric and non-parametric models based on frequency-of-capture which reduce the problems of unequal catchability (for reviews see Seber 1973, Cormack 1979). The methods of total enumeration (minimum number known to be alive) and capture per unit effort (Davis 1963) are used extensively in small mammal studies (e.g. Nichols & Pollock 1983, Boonstra 1985, Nichols 1986) in an attempt to relax the assumption of equal catchability. All methods rely on the validity of certain assumptions and have inherent biases (Seber 1973, Smith *et al.* 1975). It is appropriate, therefore, to compare the results of a number of different methods of estimation of abundance. This approach also facilitates accurate comparisons between studies.

In this study the following methods were used: 1. Capture per unit effort; 2. total enumeration; 3. Jolly-Seber; 4. Manly-Parr; and 5. frequency-of-capture model (Caughley 1977). The underlying assumptions applicable to this study are :

1. The identification marks are permanent
2. The capture process does not affect the capture probability.
3. All animals are equally catchable and, if there are sub-groups in the population with different catchability, they should be analysed separately.
4. The loss to the trapped sample is equal for different sex and age groups.
5. The model can only be applied if the population is closed.
6. Sampling is instantaneous relative to the total time.

The validity of these assumptions will be addressed in this Chapter. It will be followed by the population analyses.

3.2 METHODS

3.2.1 LIVE-TRAPPING

3.2.1.1 Establishment of the trapping line

The trapping line was chosen to cover an appropriate area based on previous assessments of a devil's home-range, access to the traps and the time taken to clear all traps each day. The only information on the home range of the Tasmanian devil is from Guiler (1970 a, b) who suggested that devils could move up to 16 kilometres per night but that in areas of high abundance trapping revealed that the home-range was 3 km^2. Fifty traps were available for this study. In order to satisfy all the above considerations traps were set out as in Figure 3.1. This configuration incorporated the various habitats found in the study area (see Chapter 1).

Tasmanian devils were trapped in steel drop-door traps (Giles 1969). Each trap was baited with approximately 150 grams of Bennett's wallaby (*Macropus rufogriseus*), pademelon (*Thylogale billardie*) or wombat (*Vombatus ursinus*) meat which was usually obtained from animals found dead on the road. If the bait had not been removed after two days, or if it had dried out, it was replaced. Traps were covered with heavy branches to ensure that they were stable on the ground and to provide protection for trapped animals from the weather. Litter was placed over the floor of the traps to provide bedding material for trapped animals. Traps were cleared from sunrise and all animals were processed and released by 10 a.m. Each trap was numbered and a record was made of a capture, no capture or if the trap was set off without capture. Other species trapped were recorded and treated in the analysis as a set-off trap.

Ten major trapping sessions were carried out with the primary aim to provide data for population analyses. These sessions were generally of ten days duration (Table 3.1).

3.2.1.2 Development of efficient traps

After five trapping sessions the traps were increased from 0.5 m to 0.7 m in length. In order to determine the efficiency of the two trap designs, both sizes were used for a time. The original trap design (short traps) were set for a total of 276 trap nights. One week later the modified traps (long traps) were set for a total of 112 trap nights. The traps were set in the same sites. Long and short traps were not set

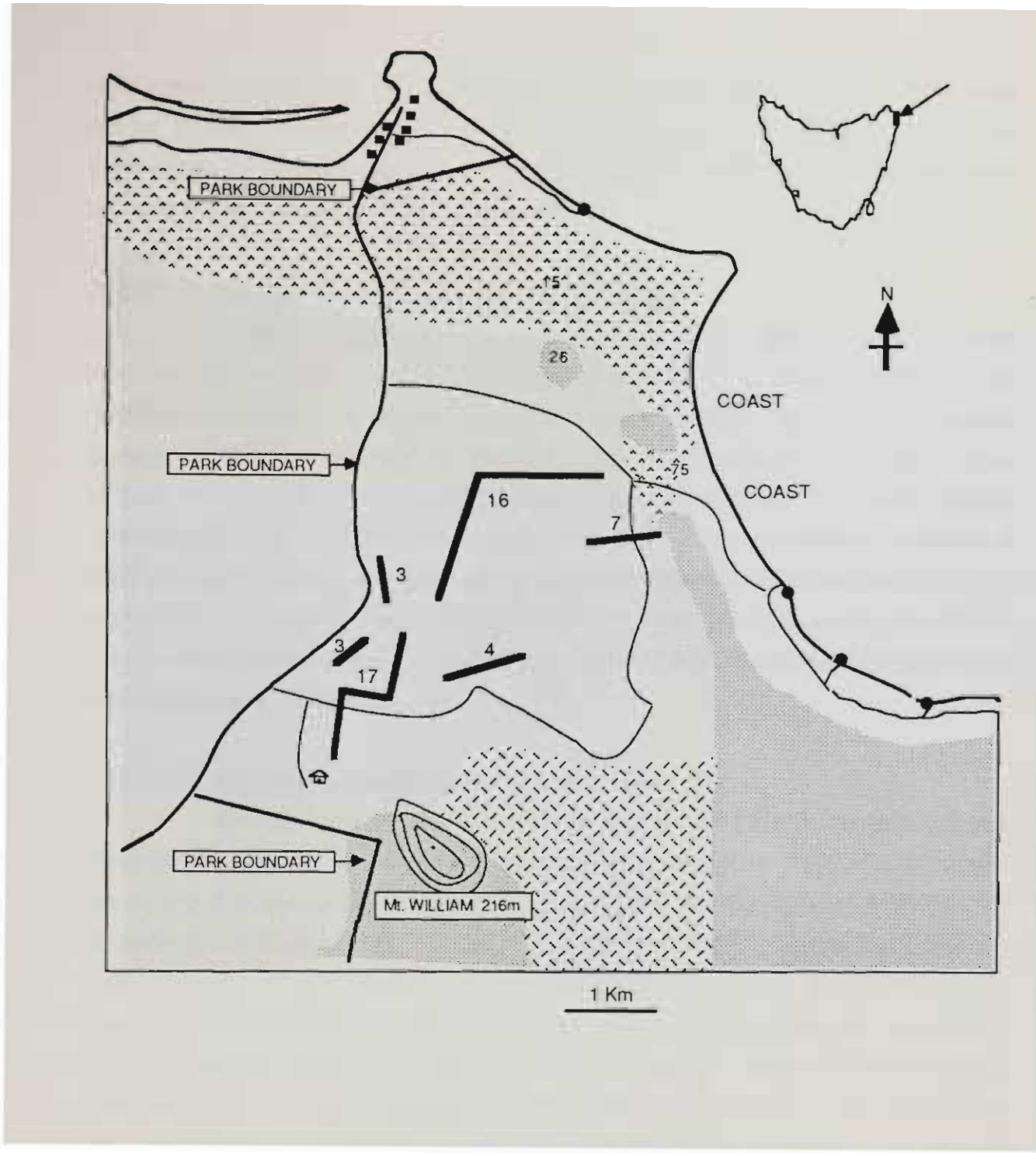


FIGURE 3.1 Location of trap lines at Mt. William National Park as used in this study. ——— Denotes configuration of trap lines and the number of traps in each line is indicated. Legend in Fig. 1.2 applies for other notations.

concurrently because the short traps were lengthened to make long traps. Both were set for a period of one week and the trapping efficiency recorded. Proportional capture rates were compared with a G-test, adjusted for small sample sizes, following an arcsine transformation (Sokal & Rohlf 1981).

3.2.1.3 The use of two traps at each trap site

In the first trapping session 24 trap sites were trapped with two traps at each for seven nights. The pair of traps was positioned as close together as was possible in the area. If a trap did not make a capture in three nights it was moved but always within a few metres of the other trap. This design offered the animals a choice of traps to enter. Traps that had captured a conspecific before are designated "tainted" and those that had not "odourless". Data were analysed to determine if two traps at each site increased the capture rate. In addition, the positive or negative effect on capture rate of odours left by trapped animals was evaluated by recording the species and sex of captured animals. The effect of a "tainted" trap on subsequent captures was tested against an "odourless" trap.

3.1.2.4 Handling, marking and ageing of devils

Animals were coaxed into a hessian sack by blowing on their rear quarters. They then became docile and could be handled easily and gently. Each captured animal was tattooed in one ear with tattooing pliers, chisel-pointed numerals and tattooing ink (Bainbridge Brothers, North Fitzroy, Victoria). The animal's natural markings also were recorded as an adjunct for visual identification. Trapped animals were aged according to the method described in Chapter 2. In the present Chapter detailed age-related analyses were only carried out on devils trapped during the major trapping sessions (Table 3.1) and these animals comprised juveniles (class1) and adults (class 2+), but not weaners (class 0). A record was made of each individual captured, the trap in which it was captured, the age of the animal and its sex.

3.1.2.5 Calculation of sample size required for population estimates

The first trapping session was for 1142 trap-nights and lasted for five weeks in May/June 1983. This trapping session was specifically designed to provide data on the capture rate of new animals. The cumulative catch of new animals was plotted against cumulative effort, producing a Davis graph (Davis & Winstead 1980). The curve of a Davis graph approaches an asymptote when all catchable animals are caught. The asymptote provides an estimate of the trappable population and the sampling intensity (trap-nights) required to trap a pre-determined proportion of the population.

3.2.2 TESTS TO ASSESS THE VALIDITY OF THE CAPTURE-RECAPTURE ASSUMPTIONS

3.2.2.1 Variation in individual trappability

Eberhardt (1969) showed that if the probability of capture is the same for all individuals and sampling efficiency is low (the mean number of times animals are caught per sampling occasion), then the capture frequency per trap session will approximate a zero-truncated Poisson distribution. Caughley (1977) provides formulae for calculation of the expected truncated Poisson distribution from the observed frequency. In this study, deviations of observed from the expected frequencies were tested using a Chi-square test with n-2 degrees of freedom. Classes were pooled when the expected values were less than five (Sokal & Rohlf 1981). However, if sampling efficiency is high, then a zero-truncated binomial distribution is more appropriate than the Poisson distribution (Leslie 1958, Caughley 1977). Therefore, sampling efficiency was tested for each sampling occasion by calculating the mean number of times an animal was captured. Following this, the appropriate test was applied.

3.2.2.2 Catchability across the total sample period

The first test applied was the "equal catchability" test of Leslie (1958), where only data for those animals known to be alive between two trapping sessions are used. Leslie's method is based on the premise that if recaptures are constant, a binomial distribution is expected (Caughley 1977). As the data were insufficient to permit analyses across the total study period, a period was chosen that provided sufficient data for the analyses. Individuals that were captured in sample session one and subsequently in sample sessions eight, nine and ten were accepted as having been alive in the interim sampling periods. The test of equal catchability was applied to this set of data and examined by a Chi-square test (Caughley 1977).

In addition, the recapture histories of individuals caught in the first sample were compared by a Kolmogorov-Smirnov (K-S test; D. Ratkowsky pers. comm.; Sokal & Rohlf 1981). Again, the paucity of data required pooling of age classes and sexes. The null hypothesis was that the samples came from the same populations with the same distributions.

3.2.2.3 Variation in capture frequency due to sex and age

Subsets of the population (sex and age) were tested to see if the capture frequencies of the respective samples came from the same population and hence could be pooled where necessary in the analyses. The K-S test was used to test the validity

of the null hypothesis that the samples have identical distributions and therefore come from the same population. This test was used because it allows for unmatched samples (D. Ratkowsky pers. comm.). The data, however, are discontinuous and the K-S test is designed for nonparametric continuous data. Therefore, the result is conservative (Sokal & Rohlf 1981).

3.2.2.4 The effect of previous capture history on trappability

The May 1983 sample was chosen to analyse whether the capture history of an animal affected its chance of recapture. The number of trap nights in this session was large (n = 1142) and hence provided more chance for individuals to display a perceptible trap response. Capture histories of individuals were analysed by sex and age and whether they were recaptured or not. Data, where sufficient, were analysed by the three-way log-linear model (Sokal and Rohlf 1981). To test the fate after first recapture a Row X Column G-test was employed (Sokal and Rohlf 1981). Each test has the null hypothesis that the samples are independent of one another.

3.2.2.5 Loss of different age groups and sex to the trapped sample

In order to determine whether differential loss (i.e. death, immigration and class 2+ness) occurred in different age and sex groups, data from the May 1983 sample and the August and November 1984 samples were compared. These samples provide a range of ages and reproductive conditions for both sexes. Animals were assigned to age groups (Chapter 2) and their capture and recapture history noted. Data were analysed by the three-way log-linear model (Bishop & Hartley 1979, Sokal & Rohlf 1981).

3.2.2.6 The effect of the sex of a captured individual on the following capture in the same trap

The sex and trap location of all captured animals were recorded. These data were subjected to a retrospective examination where the sex of animal caught on day $t+1$ was compared with that caught on day t. . Only next-day captures were used in this analysis. Due to the screening procedure sample sizes were small and so data were pooled according to season in the reproductive cycle (copulation, early lactation, middle lactation, late lactation-weaning). I considered these periods to be the most likely to show variability because the trap entry may be influenced by reproductive condition and social behaviour. Four combinations are possible, male-male, male-female, female-male and female-female entry. Data were tested using a R X C test of independence (Sokal & Rohlf 1981) with the null hypothesis that the criteria (sex-related entry to traps and time of year) were independent. In addition sex-related entry

to traps was tested within the pooled samples. The hypothesis being tested was that the number of captures of either sex on day $t+1$ was independent of the sex of the occupant of the same trap on day t.

3.2.3 METHODS USED TO ESTIMATE THE POPULATION SIZE

3.2.3.1 Trappability of the marked animals

Krebs & Boonstra (1984) assessed methods of calculating trappability of small mammals and concluded that Minimum Trappability and Jolly Trappability were the most appropriate. Minimum trappability has been defined by Hilborn *et al.* (1976) as an average over individuals in a population, where the number of times an individual is captured is divided by the number of times it is exposed to capture. The exposure time is the interval between the first and last capture of the individual. These two captures are subtracted from the total number of captures because by definition they must be caught at this time. Thus, all animals captured only once are excluded, as are animals caught on only two successive occasions. Therefore, if an animal was known to be alive for the ten trapping sessions and was captured in seven, then its trappability is (7-2)/(10-2) X 100= 62.5%. The trappability for the population is calculated as follows:

Minimum trappability (%) (after Hilborn *et al.* 1976) =

$$100 \frac{\sum_{i=1}^{n} \left(\frac{\text{no. of actual captures for an individual - 2}}{\text{no. of possible captures for that individual - 2}} \right)}{N}$$

where N = number of individuals potentially caught more than two times.
Jolly trappability uses the value for estimated marked population size (Mj) and is calculated as follows:

Jolly trappability (%) (after Jolly 1965, Jolly & Dickson 1983) =

$$\frac{\sum_{i=1}^{S} \left(\frac{\text{total no. of marked individuals caught at time } i}{\text{estimated marked population size at time } i} \right) (100)}{S}$$

where S = number of sampling sessions. Both trappability estimates were calculated separately for males and females. The results, being proportions, were transformed (arcsine $\sqrt{x}$) and the means tested with a t -test (Zar 1974). To calculate Jolly

trappability, the " estimated marked population" (Mj) was required. It was therefore necessary to calculate the Jolly-Seber estimate of population size (Begon 1979).

3.2.3.2 Choice of population estimate

Five methods was used to estimate the population size (Pi) and its fluctuation over time:

1) Capture per unit effort, Pi index
2) Minimum number known to be alive
3) Frequency-of-capture method, parametric model
4) Jolly-Seber, stochastic model
5) Manly-Parr, stochastic model

1) Capture per unit effort.

Capture per unit effort (CPU) was calculated following Caughley (1977). Basically, CPU can be considered as the number of individuals captured divided by the number of trap-nights for a trap session. There are, however, alterations to this formula to cope with high capture frequencies, traps set off without making a capture, and recaptures of individuals.

The catching of one animal should never interfere with that of another (trap saturation). Each capture has an effect on the capture rate of more animals, by virtue of its occupation of a trap. Catch per trap-night can never be greater than 1 and the regression of density on catch per trap-night is, therefore, curved. When catch per trap-night is greater than 0.2 the index is subjected to a frequency-density transformation (Caughley 1977). This transformation allows the direct comparison of indices. The catch per trap-night was calculated for each trap session to assess whether transformation was necessary. Correction was made for traps that were set off without making a capture, according to the method of Nelson and Clark (1973):

$$TU^* = (TU - TSO/2)$$

where TU* = the corrected traps available for capture, TU = traps set and TSO = the number of traps set off without a capture or containing animals of another species. Inherent in this method is the assumption that each trap is sprung for half a trap-night and therefore divided by two. In this study, except for the cases of a brown falcon (*Falco berigora*) and two echidnas (*Tachyglossus aculeatus*), traps were set off only at night. From direct observations of devils, and the presence of their hair under the drop door, it is reasonable to accept that most traps were set off by the devils at night.

Tasmanian devils are nocturnal and active from sunset to sunrise (Chapter 6). The middle of the trap night is therefore assumed to be the middle of the devil's activity cycle. The sprung trap is therefore inoperative for half an activity period. The same logic applies to the recapture of individuals that have already been added to the "animals captured " category. These individuals are effectively occupying traps that may be available to free-ranging animals. The resulting formulae for TU* is;

$$TU^* = TU - (TSO/2 + Recap/2)$$

where Recap = the number of recaptures in a trap session.

2) Minimum number known to be alive.

The minimum number known to be alive (MNA) is a method of population estimation which directly enumerates the population (Krebs 1966, Krebs *et al.* 1969, Hilborn *et al.* 1976). The minimum number of animals alive at time *t* is obtained by summing: (1) the actual number caught at time *t* and (2) the number caught prior to *t*, not at t but subsequent to *t* (Davis 1963, Krebs 1966, Blower *et al.*1981).

3) Frequency-of-capture methods.

The parametric frequency-of-capture model assumes that capture frequencies (the number of times an animal is caught 1,2,3.....n times) can be modelled to a known zero-truncated distribution. The zero class represents the animals that were never caught. Caughley (1977) suggests the use of three zero-truncated distributions: negative binomial, geometric and Poisson. The first two assume unequal catchability in two different ways, and the Poisson is most appropriate when catchability is constant (Eberhardt 1969, Caughley 1977). Caughley (1977) stresses that the three models should be used as a " triple-ball cartridge " and not independently. The model of best fit, tested by Chi-square goodness-of-fit, is that which best conforms to the frequency distribution of captures. The population size is then calculated by adding the zero class (untrapped) to the individuals captured. This method is only appropriate to closed populations where there has been zero mortality/emigration (Eberhardt 1978, Caughley 1977). In this study, the frequency of capture of individuals for each trap session was tallied and, where possible, analysed separately for age and sex. The trap sessions were of short enough duration (Table 3.1) to satisfy the assumption of a closed population. Analyses were carried out using formulae presented in Caughley (1977) and as modified by Caughley (pers. comm).

The final two methods used were the Jolly-Seber and Manly-Parr

stochastic models. Estimates of Pi were calculated according to the formulae in Begon (1979). Each trap session was considered as one sample and the sample size was the number of individuals captured, irrespective of the number of captures.

3.3 RESULTS

3.3.1 LIVE-TRAPPING

A total of 3 788 traps was set in 10 trap sessions. In all 328 males and 353 females were captured 554 and 515 times, respectively (Table 3.1). The catch rates varied from 8.8% to 24.2% for short traps and from 33.5% to 56.7% for long traps. The catch rates for males and females were similar (Table 3.1).

3.3.2 DEVELOPING AN EFFICIENT TRAP DESIGN

The short traps did not catch as many devils as did the long traps (Table 3.2). The long traps had a catch rate of 35.7% whilst the short traps had a significantly lower catch rate of 10.1% ($G_{adj(1)} = 20.79$, $p << 0.001$). Furthermore, a high proportion (43 %) of the short traps was sprung without making a capture. By contrast no long traps were set off by animals reaching into the trap for the bait.

3.3.3 CALCULATION OF SAMPLE SIZE REQUIRED FOR POPULATION ESTIMATES

Figure 3.2 shows the Davis graph for rate of capture of new animals per unit effort. The curve started to reach an asymptote after 1000 trap nights at approximately 150 animals. Any (trapping) effort after this point does not increase the sample size of the population to a significant extent. The tables of Robson and Regier (Begon 1979) were used to predict the required sample size (see section 3.4.1).

3.3.4 THE USE OF TWO TRAPS AT EACH TRAP SITE

Two trap sites (i.e. with 2 traps at each) had one capture record, while the rest showed multiple captures. The effect of a capture at one trap and not the other, on the subsequent captures is shown in Table (3.3). Of the 11 captures at the "odourless" trap, 10 occurred when both traps were occupied. So the possibility exists that either trap was occupied and either animal did not have a choice. Therefore, these captures were withdrawn from the analyses. One trap site had captures at both traps on the first night and then subsequently 5 animals at one trap and 3 at the other. These data were also excluded from the analyses because there was no " odourless " trap available. There is a significant difference ($G_{adj(1)} = 51.45$, $P << 0.001$) between the number of captures made by the "tainted" and "odourless" traps. The " tainted " traps caught 98% of the animals.

TABLE 3.1 The trap sessions used in the population calculations with total and individual captures. The catch rates (captures/100 trap nights) are shown in brackets.

Trap Session	Year	Day/month	Total No. traps set	Total No. captures	No. Individuals captured	No. of Males		No. of Females	
						individuals captured	total captures	individuals captured	total captures
1	1983	8/5-9/6	1142	276 (24.2)	159	78	145(12.9)	81	131(11.5)
2		2/8-15/8	400	51(12.8)	40	16	24(6)	24	27(6.8)
3		3/12-10/12	495	92(18.6)	53	22	47(9.5)	31	45(9.1)
4	1984	13/2-29/2	371	88(23.7)	62	29	40(10.8)	33	48(12.9)
5		17/5-23/5	331	33(9.9)	29	13	17(5.1)	16	16(4.8)
6		21/8-29/8	252	78(31)	57	27	38(15.1)	30	40(15.9)
7		17/11-30/11	181	86(47.5)	46	18	38(21)	28	48(26.5)
8	1985	4/2-10/2 23/2-25/2	248	130(52.4)	80	41	59(23.9)	41	71(28.6)
9		23/4-28/4 2/5-9/5	261	148(56.7)	95	50	92(35.2)	45	56(21.5)
10		3/8-30/8	260	87(33.5)	58	34	54(20.8)	24	33(12.7)
		TOTAL	**3788**	**1065(28.1)**	**679**	**328**	**554(14.6)**	**353**	**515(13.6)**

TABLE 3.2 Comparison of the catch rate of "long" and "short" traps.

Trap	Trap Nights	Captures	Proportional catch rate*	Set off**
Long	112	40	35.7	0
Short	276	28	10.1	119

* G adj = 20.7863 << X2 (0.05)(1) = 3.841
** The number of traps set off without making a capture.

TABLE 3.3 The number of captures made in "tainted" and "odourless" traps at each trap site.

Trap*	Subsequent Captures**	Capture with no choice of trap***
Tainted	53	43
Odourless	11	1

* "Tainted" traps are those that made the first capture, " odourless" traps are those that caught animals when a "tainted" trap was available.
** The number of captures in either trap after one had become "tainted"
*** The number of subsequent captures minus the captures made when both traps had occupants.

TABLE 3.4 The catch rate (mean number of captures per individual per trap session) of each sampling session.

Trap session	Number of animals	Number of captures	Mean
1	159	276	1.74
2	40	51	1.28
3	53	92	1.74
4	62	88	1.42
5	29	29	1.00
6	57	78	1.37
7	46	86	1.87
8	80	130	1.63
9	95	148	1.56
10	58	87	1.50
Total	**679**	**1065**	**1.51**

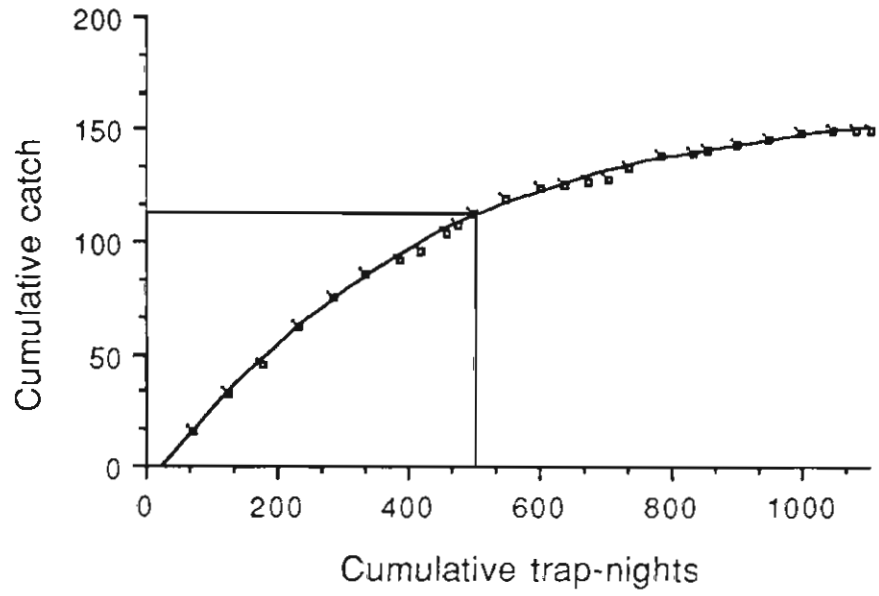


FIGURE 3.2 A Davis graph showing the rate at which new devils were caught during the May 1983 trap session. The straight line shows how many devils would have been caught in 500 trap nights.

3.3.5 THE PERMANENCY OF THE MARKING METHOD

The tattooing technique was simple and long lasting. Five animals were caught 33 months after been marked and the tattoo was still perfectly distinct. The white markings, when present, did not change with age of the devils. Thus, there were no problems identifying previously captured animals.

3.3.6 TESTS TO ASSESS THE VALIDITY OF THE CAPTURE-RECAPTURE ASSUMPTIONS

3.3.6.1 Variation in individual catchability

In this study the catch rate within a trap session varied from 1 to 1.87 captures per animal (mean = 1.51, SD = 0.24, Table 3.4). Therefore, the use of the zero - truncated Poisson distribution is valid. The comparison of capture frequencies and expected Poisson frequencies is shown in Table 3.5 . Of the trap sessions with sufficiently large sample sizes to permit the analyses (1, 3, 7, 8, 9), all showed a significant deviation from the expected Poisson distribution. This necessitated the rejection of the null hypothesis that all animals are equally likely to be captured. Sub-groups within trap sessions showed greater variation, with 5 out of the 8 tested showing no significant deviation from the expected distribution (Table 3.5). The observed and expected frequencies are shown in Appendix 3. It is clear that unequal catchability is a factor common to devils.

3.3.6.2 Catchability across the total sample period

Leslie's test is best used on a sample size of > 20 animals caught at time t and $t+1$ with sufficient captures between these two periods to give an indication of catchability (Begon 1979). In this analysis, for the time period chosen, only 25 individuals fulfilled the criteria, and hence the data could not be split into different sexes or age groups. Table 3.6 shows the result of Leslie's test of equal catchability. There was a significant difference ($X^2 = 51.87$, $p << 0.001$, d.f. = 24) between the observed variance and the expected. Therefore, the hypothesis that recaptures are binomialy distributed is not supported, and hence catchability is not constant for all individuals over the tested period.

The test of length of recapture history could be split into male and female groups (Table 3.7). The result was not significant ($D_{max} = 0.0167 << D_{0.05} = 0.217$). Therefore it was assumed that the samples came from the same distribution and population. There was no evidence to suggest that either the recapture histories or catchabilities differed between males and females .

TABLE 3.5 Test for homogeneous trappabilty, based on goodness of fit of capture frequencies to a zero-truncated Poisson distribution. Tests were run on total samples and by sex and age.

Trapping Session	*X2*	d.f.	Significance
A. Total for trap session			
1	6.214	2	*
2	N.A.		
3	3.934	1	*
4	N.A.		
5	N.A.		
6	N.A.		
7	4.335	1	*
8	10.005	2	**
9	5.107	1	*
10	N.A.		
B. Sub-groups within trap session #			
1/Males	3.045	1	N.S.
1/Females	0.969	1	N.S.
1/Males/1	N.A.		
1/Males/2+	4.208	1	*
1/Female/1	0.049	1	N.S.
1/Female/2+	1.326	1	N.S.
1/Males	5.612	1	*
8/Females	3.939	1	*
7/Males	0.085	1	N.S.

\# The trap session is identified, then sex and age class if applicable
N.A. No analysis because X2 test based on less than 3 classes after pooling of data so all expected classes > 5
N.S. Not significant at 0.05 probability level
* $P < 0.05$
** $P < 0.01$

TABLE 3.6 Leslie's test of equal catchability across the sampling periods.

Sample	Recaptures (n)	Times recaptured (i)	Number of animals (f)
2	8	0	4
3	13	1	9
4	5	2	1
5	2	3	5
6	8	4	3
7	11	5	2
		6	1
	$\Sigma n = 47$		$\Sigma f = 25$

$\Sigma n.n = 442$ $\Sigma fi = 54$ $\Sigma f(i.i) = 192$

Chi-square = 51.87, d.f. = 24
$p << 0.001$

TABLE 3.7 The length of the capture history, showing the raw data and the pooled data. This is the interval (in trap sessions) between an animal's first and last capture, If an animal was caught only once it is assigned to the 0 class.

RAW DATA			POOLED DATA		
Recapture history	Sex		Recapture history	Sex	
	Male	Female		Male	Female
0	55	51	0	55	51
1	1	4	1 to 2	9	9
2	8	5	3 to 6	8	8
3	2	2	7 to 9	10	9
4	1	0			
5	3	1			
6	2	5			
7	3	3			
8	6	3			
9	1	3			

3.3.6.3 Variation in capture frequency due to sex and age

The application of the K-S test to the capture frequencies within trap sessions, revealed no significant differences between males or females for all the samples tested ($D_{max} < D_{0.05}$ in all cases, Appendix 4). The samples which were compared therefore came from the same population. The first trap session was the only one with sufficient data to test for age-related differences and again there was no significant difference in the frequency distributions (Appendix 4). This suggests that the pooling of data for these variables is justified.

3.3.6.4 The short-term effects of initial capture on catchability

The fate of individuals after first capture, within a trap session, is shown in Table 3.8. A three-way log-linear model shows that all three variables are completely independent of one another (Table 3.9). There was no evidence of dependence of age or sex on the fate after first capture. Therefore, the data were pooled for the two age groups to analyse the response of animals to recaptures.

Table 3.10 shows the fate after first capture compared with that after first recapture. The result of the test ($G = 1.8116 < X^2_{(0.05)(3)}=7.815$) was consistent with the hypothesis that the criteria of sex, fate after first capture and fate after second capture are independent. There is no evidence that animals caught for the first time are less likely to be recaptured than those captured for a second time within a trap session. Thus, there was no evidence for trap avoidance and/or mortality after initial marking. In addition, there was no evidence of differences in the ability to recapture males and females within trap sessions.

3.3.6.5 Loss of animals between trap sessions

The data were analysed by sex and age to see if there was a differential loss of devils from the trapped sample. The data used in the analysis are shown in Table 3.11. The statistical analysis of the three-way log-linear test (Table 3.12) shows that none of the interactions were significant. Therefore sex, age and fate after first capture were independent. There is, therefore, no evidence of differential loss from the trapped sample. In addition, there is no evidence of different rates of recapture of the two sexes or age-groups. Therefore, these sub-groups do not display varying catchability between the first trap session and the sixth and seventh. The ability to capture either sex or age group between trap sessions was the same.

TABLE 3.8 The effect of age and sex on subsequent capture within a trapping session.

Age	Sex	Fate after first capture	
		Not Recaptured	Recaptured
1	Male	33	16
	Female	28	17
2+	Male	13	14
	Female	21	15

TABLE 3.9 Statistics of the interactions of age (A), sex (B) and fate after first recapture (C)

Statistics	ABC	AB	AC	BC	AB=AC=0
G	0.9	2.216	2.792	0.915	4.093
d.f.	1	2	2	2	3
P	0.65	0.3	0.25	0.64	0.25
X2*	3.8411	5.991	5.911	5.911	7.815

* Values from Tables in Zar (1974)

Table 3.10 Inter-sex comparison of the fate after first and second captures within a trap session.

Sex	Fate after first capture		Fate after second capture	
	Not recaptured	Recaptured	Not recaptured	Recaptured
Male	46	30	14	12
Female	49	32	8	12

TABLE 3.11 Fate after first capture of different age and sex animals between trap sessions.

Age	Sex	Fate after first capture	
		Not recaptured	recaptured
1	Male	41	7
	Female	43	4
2+	Male	21	5
	Female	45	4

TABLE 3.12 Statistics of the interactions of age (A), sex (B) and fate after first recapture (C)

Statistics	Interactions				
	ABC	AB	AC	BC	AB=AC=0
G	0.148	4.583	0.266	2.739	4.59
d.f.	1	2	2	2	3
P	0.702	0.099	0.88	0.25	0.2
X2 *	3.841	5.991	5.911	5.911	7.815

* X2 Values from Tables presented in Zar (1974)

3.3.6.6 Effect of previous trap occupant on trappability

The data used in this analysis were restricted because only those captures made in the same trap on the night following a capture were used. The sex-related entry to traps is shown in Table 3.13. The combinations of sex refer to the sex of the individual caught on day *t* and day *t+1*. The sex related trap entry is independent of time of year ($G_{adj} = 12.795 < X2_{(0.05)(9)} = 16.919$). In addition, Table 3.14 shows that the sex of captures on day *t* is independent of the sex of captures on day *t+ 1* for the same trap. Hence, there is no detectable effect of the sex of a capture of devil on the subsequent capture, both within and between samples.

3.3.6.7 Trappability of the population

The trappability for the total study calculated by the minimum trappability method was 54% and by the Jolly method was 60%. Minimum trappability over the total sampling period (Table 3.15, 3.16) was 52.9% (SD = 14.1) for males and 54.8% (SD = 19.1) for females. There was no significant difference between the sexes ($t_s = 0.177 < t_{0.05(2)57} = 2.002$). Jolly trappability estimates provide similar means for males (63.3%, SD = 4.6) and females (54.5%, SD = 5.2) which are also not significantly different from each other ($t_s = 1.43 < t_{(0.05)(7)} = 2.365$). Results of Jolly trappability for the trapping seasons are shown in Table (3.16). Jolly trappability was generally ≥ 50% with the lowest value in May 1984 (session 5) at 26.6% and the highest in August 1985 (session 9) at 78.5%.

3.3.7 POPULATION ESTIMATES

The capture per unit effort (CPU) index was corrected for " trap saturation" because the catch per trap-night exceeded 0.2 for 6 of the 10 trap sessions. The CPU index of population size is shown in Table 3.17 and the minimum number of animals known to be alive (MNA) in Table 3.18. The CPU index shows an annual trend from high values in the first half of the year to lower values later in the year. There is also a trend to an increase in CPU throughout the study. The MNA shows a similar trend within years. Both indices decrease substantially in the fifth trapping session when they are expected to rise. This is the period when a large proportion of traps were set off (36 %) compared to the same time the previous year (15 %).

The results of the comparisons of frequency-of-capture models are shown in Table 3.19. Except for the female age-class 1 (juveniles), the geometric distribution was the most appropriate model. The data for the females of age class 1 from the first sample approximated a Poisson distribution more closely. Three samples that had an expected frequency class of less than 5 (Caughley 1977) are included (trapping

TABLE 3.13 The frequency of occurence of trap entry by one sex with respect to the sex of the previous occupant (for eg. male/male = male capture on day t followed by male capture on day t+1).

Time*	Male/ Male	Male/ Female	Female/ Male	Female/ Female
1	36	29	28	28
2	13	4	7	4
3	21	7	9	4
4	15	12	14	16

* Time as follows:
1 = Months 2,3,4 period of breeding (pooled data)
2 = Month 5, period of early lactation, high population
3 = Month 8, period of middle lactation, denning of young
4 = Months 11,12, period of late lactation, weaning of young

TABLE 3.14 The number of captures of either sex in relation to the sex of the previous trap occupant *

Period 1

Capture on day t	Capture on day t+1 Male	Capture on day t+1 Female
Male	36	29
Female	28	28

G = 0.005
P = 0.941

Period 2

Capture on day t	Capture on day t+1 Male	Capture on day t+1 Female
Male	13	4
Female	7	4

G =0.0927
P = 0.759

Period 3

Capture on day t	Capture on day t+1 Male	Capture on day t+1 Female
Male	21	7
Female	9	4

G =0.0001
P = 0.989

Period 4

Capture on day t	Capture on day t+1 Male	Capture on day t+1 Female
Male	15	12
Female	14	16

G = 0.1641
P = 0.688

* Periods of time as in Table 3.13

TABLE 3.15 Minimum trappability calculated for males and females across all trap sessions.

Sex	n	Mean (%)	S.D.
male	32	52.9	14.1
female	27	54.8	19.1

TABLE 3.16 The seasonal trappability of male and females measured by the Jolly method

	Season	Mj	Captures	% Trappability	Mean ± S.D. *
Male	2	28	16	57.1	
	3	39	22	56.4	
	4	49	29	59.2	
	5	52	13	25.0	
	6	40	27	67.5	
	7	26	18	69.2	
	8	67	41	61.2	
	9	52	50	96.2	
					63.3 ± 4.6
Female	2	47	24	51.1	
	3	36	31	86.1	
	4	63	33	52.4	
	5	125	16	12.8	
	6	64	30	46.9	
	7	56	28	50.0	
	8	74	41	55.4	
	9	56	45	80.4	
					54.9 ± 4.9
Total	2	72	40	55.6	
	3	74	53	71.6	
	4	111	62	55.9	
	5	147	29	19.7	
	6	106	57	53.8	
	7	75	46	61.3	
	8	140	80	57.1	
	9	99	95	95.9	
					60.4 ± 2.3

* The means were calculated after arcsine transformations.

TABLE 3.17 Capture per unit effort (CPU) estimated by the density-frequency transformation method of Caughley (1977).

Session	Traps set (Tu)	Traps Set Off (TSO)	Recaptures (recap)	TU*	Individuals captured	f**	1-f	x***
1	1142	176	117	996	159	0.16	0.84	0.17
2	400	148	11	320	40	0.13	0.87	0.14
3	495	233	39	358	53	0.15	0.85	0.16
4	371	112	26	302	62	0.21	0.79	0.24
5	331	119	0	272	29	0.11	0.89	0.12
6	252	5	21	226	57	0.25	0.75	0.29
7	181	7	40	158	46	0.29	0.71	0.34
8	248	16	50	215	80	0.37	0.63	0.46
9	261	7	53	231	95	0.41	0.59	0.53
10	260	6	29	242	58	0.24	0.76	0.27

* Corrected traps available for capture
** Frequency of capture per trap
*** Estimated density of catches per trap

TABLE 3.18 Minimum number known to be alive (MNA) estimates for the sampling sessions.

Trap session	Captured	Not captured	MNA
1	159		159
2	51	30	81
3	92	19	111
4	88	38	126
5	29	45	74
6	57	44	101
7	46	38	84
8	80	39	119
9	95	47	142
10	58	21	79

TABLE 3.19 Zero-truncated Poisson, negative binomial and geometric distributions fitted to capture frequencies of age and sex classes in each trap session, where the sample size was large enough.

Model	Statistics	SAMPLING SESSIONS * 1 Total	1 Males 2	1 Males Total	1 Females 1	1 Females 2	1 Females Total	
Poisson	X2	6.214	4.208	3.045	0.049	1.326	0.969	
	d.f.	2	1	1	1	1	1	
	P	0.025 > P > 0.01	0.05 > P > 0.25	0.1 > P > 0.05	0.9 > P > 0.75	0.25 > P > 0.1	0.5 > P > 0.25	
	Estimated N	235	31	109	74	52	122	
-ve Binomial	X2	0.475	***	***	***	***	***	
	d.f.	1						
	P	0.5 > P > 0.25						
	Estimated N	602						
Geometric	X2	0.154	0.625	0.443	0.397	0.112	0.05	
	d.f.	2	1	2	1	1	1	
	P	0.975 > P > 0.9	0.5 > P > 0.25	0.9 > P > 0.75	0.75 > P > 0.5	0.75 > P > 0.5	0.9 > P > 0.75	
	Estimated N	392	47	182	128	85	211	

Model	Statistics	SAMPLING SESSIONS 3	4	6	7	8	9	10
Poisson	X2	3.938	0.211	5.295	4.335	10.005	5.107	0.265
	d.f.	1	1	1	1	1	1	1
	P	0.025 > P > 0.05	0.75 > P > 0.5	0.025 > P > 0.01	0.05 > P > 0.025	0.005 > P	0.025 > P > 0.01	0.75 > P > 0.5
	Estimated N	58	62	120	61	129	161	201
-ve Binomial	X2	***	***	***	***	***	***	***
	d.f.							
	P							
	Estimated N							
Geometric	X2	0.992	0.135	2.649	1.179	4.683	1.485	0.95
	d.f.	1	1	1	1	1	1	1
	P	0.5 > P > 0.25	0.75 > P > 0.5	0.25 > P > 0.1	0.5 > P > 0.25	0.05 > P > 0.25	0.25 > P > 0.1	0.5 < P < 0.25
	Estimated N	129	208	217	101	220	277	114.1

* Where sample sizes are large enough, capture frequencies are set out as sampling session/sex/age class

*** Sample to small for analysis.

sessions 4, 6, 10). The population estimates calculated from the 4th sample (208) are close to those for the 8th sample (220), supporting the use of the low frequency class. There was no sample large enough for August of each year, so population estimates were calculated using the small sample sizes of the 6th and 10th trap sessions. Hence, these values are used with caution.

A comparison of the five population estimates is shown in Table 3.20 . The Manly - Parr estimate is always lower than the Jolly - Seber except for the 7th sample. The 8th sample is the only one where the error bars of the two estimates do not overlap. The largest error bars for both techniques are in the 4th and 5th samples. During this time the sampling efficiency was low because of set off traps. All estimates were plotted against the time of year to assess the annual trend in population size (Fig. 3.3). The three population estimates calculated from the capture-recapture models show a strong trend from high values in the first half of the year to lower values in the second half. The MNA estimate remains fairly constant within the year and between years. The CPU index fluctuates with the higher values, corresponding with the use of the long traps.

3.4 DISCUSSION

3.4.1 THE TRAPPING METHOD

Effective sampling proecdures are difficult to design without a sound knowledge of the species and population involved (Begon 1979). In the present study, which involved recapture of marked animals, an understanding of the trapping method and its effect on the animals is essential to the interpretation of the results. The first trapping session was specifically designed to provide information on which to base the rest of the study.

The trap lines, based on assumptions of the animal's home range size, showed a high rate of capture for the first 500 trap nights (Fig. 3.2). After this period the catch rate of new and recaptured animals decreased. It was apparent that any trapping effort after this period would yield minimal results for the effort expended. In addition, the drop in capture rates suggested that animals were becoming " trap-shy ".

Robson and Regier (1964) provided tables of the sample sizes required to calculate population estimates to a particular level of accuracy. They based the tables on the Peterson estimate, but as pointed out by Begon (1979), the Jolly-Seber and Manly-Parr methods are both derived from the Peterson estimate, and hence the tables can be used as a guide.

TABLE 3.20 Population estimates and indices (± standard error where appropriate) for each trap session, as calculated by the capture-recapture models, minimum known to be alive and capture per unit effort methods.

Trap Session Month & Year	1 May-83	2 Aug-83	3 Dec-83	4 Feb-84	5 May-84	6 Aug-84	7 Nov-84	8 Feb-85	9 May-85	10 Aug-85
Capture-recapture :										
Jolly-Seber	•	159.8 ± 32.4	119.2 ± 16.5	624.2 ± 200.6	607.8 ± 246.9	207.8 ± 36.9	98.4 ± 10.2	400 ± 97.8	262.1 ± 62.5	•
Manly Parr	•	132.3 ± 25.2	99.1 ± 11.5	448 ± 161.2	495 ± 262	143 ± 23.7	107.3 ± 14.9	217 ± 41.9	237.5 ± 62.2	•
Frequency of Capture	392	••	129	208	••	217	101	220	277	201
Density estimates :										
Capture per unit effort	0.17	0.14	0.16	0.24	0.12	0.29	0.34	0.46	0.53	0.27
MNA	159	81	111	126	74	111	84	119	142	79

• No estimate because this was the first or last sample
•• No estimate because the sample size was too small.
MNA, Minimum number known to be alive.

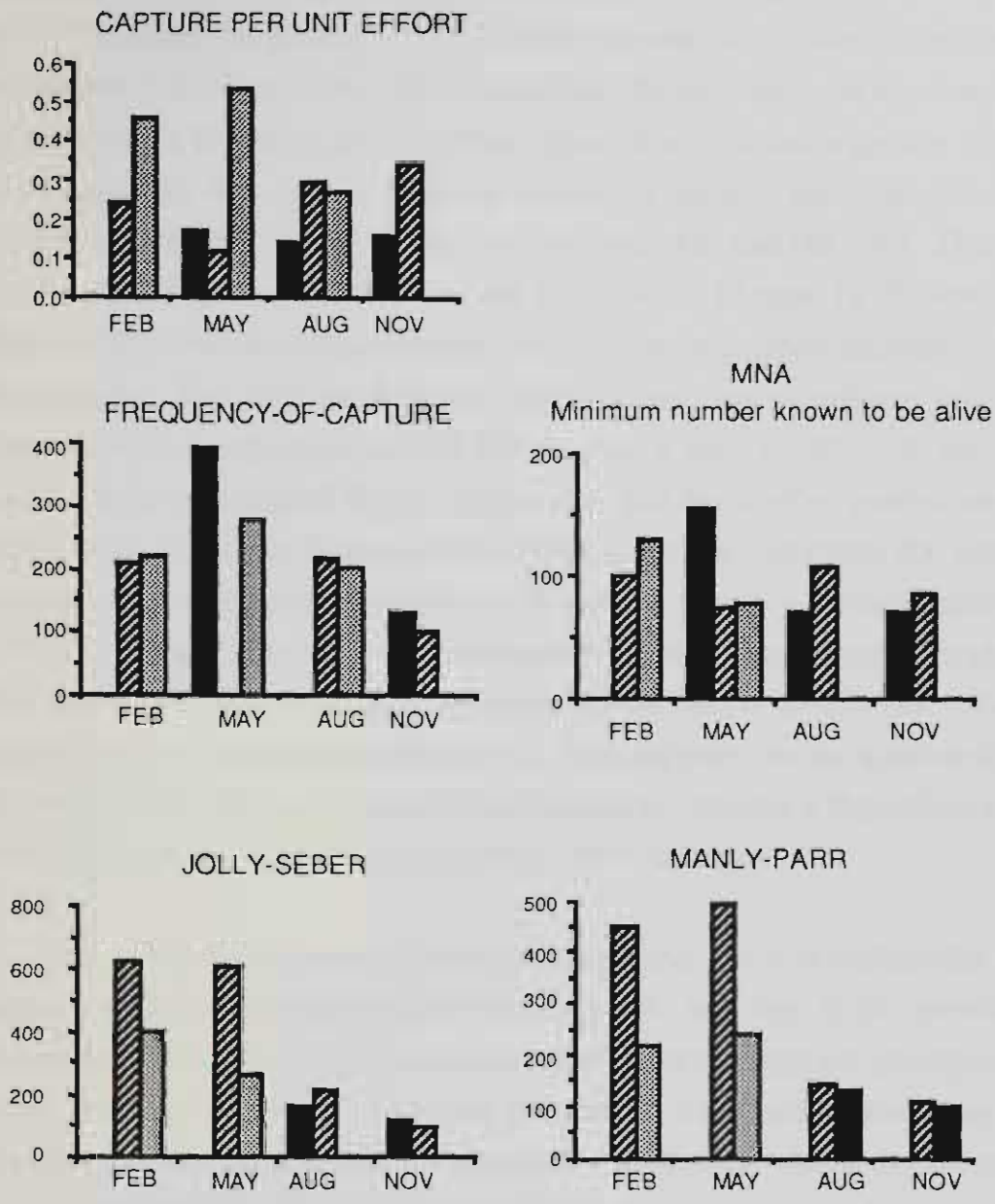


FIGURE 3.3 The population estimates (y axes) plotted against time (x axes). The estimates for each year are given where they could be calculated.

1983 ■ 1984 ▨ 1985 ▩

In the first sample the MNA estimate of 159 was still increasing at the end of the trap session. A frequency-of-capture estimate for this sample was between 372 and 392 animals, far greater than the MNA estimate. In addition, there are probably untrappable individuals in the population which did not contribute to either estimate. It seems prudent, therefore, to accept that the total population is greater than 250 and could approach 400. In this first trap session it became clear that the number of animals caught (n_j) would always be less than that marked (M_j). Therefore the Robson and Regier table allowing for $n_j = 1.5\ M_j$ (Begon 1979) was consulted. Begon (1979) recommends an accuracy of 10 % for population estimates in studies of demography. The Robson & Regier table shows that to achieve this degree of accuracy with a population of 250-400 animals, a total of 90 - 150 and 135 - 220 animals must be captured for the Jolly-Seber and Manly-Parr models respectively. Figure (3.2) shows that 50 traps set for 10 nights caught more than 100 animals. This trapping effort was judged sufficient to provide the accuracy recommended by Begon (1979) for a population estimate in demography studies. Retrospective examination of the trap sessions shows that M_j was always greater than n_j by 2.04 (SD = 1.2) with all but one session lying between 1.0 and 1.8. This supports the assumption that nj = 1.5 Mj, and that the corresponding table can be used to calculate a theoretical sample size necessary to estimate population size with ≈ 90 % accuracy.

The reason for using two traps at each trap site is to increase the number of captures while decreasing the effort of clearing the trap line. It also provides a clear choice for an animal so that the role of residual odours in traps on subsequent captures can be assessed (Stoddart 1983). The presence of trap-borne odours may introduce significant bias into analyses of population dynamics, which are based on live-trapping techniques (Stoddart & Smith 1986). In the present study, when traps were placed next to each other, only the first trap that caught a devil tended to be successful again. This was designated as the tainted trap and was almost always the only trap providing captures. There was never a case in which the odourless trap caught an animal when the tainted trap remained empty. Where both traps captured animals it was impossible to say which animal was captured first and therefore whether a choice was made the traps, or whether the animal caught second was attracted by the first animal caught in the other trap. It is apparent, therefore, that two traps at each trap site did not maximize the efficiency of the trap line. Results of the first trapping session revealed that animals readily entered tainted traps and generally avoided odourless traps. Furthermore, the second trap at a trap site was rarely used and so yielded little information on population density. Therefore, in subsequent trapping sessions only one trap was placed at each trap site.

During the first trapping session devils were observed entering traps. Often they entered traps, grabbed the baited trigger and then backed out. The trap was therefore set off without making a capture. Set-off traps make calculations such as capture per unit effort difficult, and result in additional effort to increase the sample size for reliable population estimates. In an attempt to increase trapping efficiency, traps were lengthened and the differences between catch rates in long and short traps were assessed. The use of long traps trebled the capture rate while the number of traps set off unsuccessfully decreased to 0 %, compared to 43 % with the short traps. Long traps were therefore far more effective. They were used from the August 1984 trapping session and onward.

Although there was no rigorous testing to assess the effect of weather on capture rates it was apparent throughout the study that it had little or no perceptible influence. An exception was an instance when extensive flooding covered roads and cut off bridges, and only two devils were caught overnight. Although climatological factors have been shown to exert a strong influence on trap response in other species (e.g. Gentry *et al.* 1968, Perry *et al.* 1977) I consider that the effect of weather on devil trappability is minimal, particularly when compared to the strong influences exerted by trap design and trap awareness.

3.4.2 THE CATCHABILITY OF THE ANIMALS WITHIN AND BETWEEN TRAP SESSIONS.

One of the greatest sources of error in population estimates is the assumption that all animals are equally catchable (Eberhardt 1969, Caughley 1977, Begon 1979). It is now widely recognized that this assumption commonly is not met (Otis *et al.* 1978, Burnham & Overton 1979, Pollock 1982), and this may result in large errors in population estimates (Manly 1971, Bishop & Sheppard 1973, Carothers 1979, Otis *et al.* 1978).

Roff (1973a, b) has cautioned that probability distributions are not able to distinguish between a population with equal probability of capture amongst all individuals, and a population with two or more classes comprising individuals having several different catchability classes (a simple versus a compound Poisson distribution). This has been emphasized by Caughley (1977) who stated that a non-significant result from the test may be ambiguous and should not be accepted *per se* . But he goes on to say that only those data for which unequal catchability *cannot* be demonstrated should be used in models that rely on the assumption of unequal catchability.

In the present study, heterogeneous catchability was common within all the trapping sessions where there were sufficient data to test for it. The observed and expected frequency distributions of the number of individuals in each modal class are shown in Appendix 3. In all cases there were too many animals in the modal class 1, usually too few in classes 2 to 3 and too many in class 4 and above. This suggests the presence of " trap-shy" animals in class 1 and "trap-happy" in class 4 and above (Andrzjewski *et al.* 1971). However, with those samples where the number of captures was large enough to split the population counts by age and sex classes, the test indicated that heterogeneous catchability could not be detected. As an example, from the total male and female samples for the 1st trap session analysed separately, no unequal catchability could be detected. But when the two samples were pooled together unequal catchability was significant. In addition, the frequency distribution of the two samples was not significantly different ($D=0.039 << D_{0.05} = 0.2143$, K-S test) suggesting that the samples came from the same population and can therefore be pooled (Sokal & Rohlf 1981). This suggests that the result for sub-groups has been affected both by the sample size and the insensitivity of the Chi-square test (Ratkowsky pers comm., Roff 1973b) and that heterogeneous trappability is present. The value of splitting the samples is therefore questionable.

The catchability of individuals over the total sample pertains to the use of the Jolly-Seber and Manly-Parr models, because these models utilize the data from all trap sessions to calculate the population estimate for the individual trap sessions. Leslie's test for equal catchability is limited, in the same way as the above test, by the problem of compound Poisson distributions and the efficiency of the Chi-square test (Roff 1973b). However, in this study, where there is a highly significant result ($p << 0.001$), it can be confidently accepted as indicating unequal catchability between the trap sessions (Caughley 1977, Begon 1979) . The violation of the assumption of equal catchability of individuals can result in a negative bias (if animals are "trap-shy"), a positive bias (animals are "trap-happy") or an unpredictable bias in the population estimate if animals show heterenogeneity in capture probability (Begon 1979).

The length of recapture history of male and females is similar. Therefore, males and females trapped over successive trap sessions can be considered to come from the same population and the sample pooled for the population analysis. In addition, data from all trap sessions were tested to see if the capture frequencies of male, female and different age groups, within the trap session, were significantly different. They were not significant (Appendix 4). Therefore the pooling of data is again justified.

Handling animals did not affect their chance of recapture to any detectable degree. The subsequent capture history after first capture did not differ among the different age or sex groups, suggesting that the reaction by animals to handling was uniform. In addition, the capture history of animals after second capture did not differ from that after the first capture. This supports the assumption that the capture process does not affect the future probability of capture within a trap session. Trap sessions were two to three months apart. The capture process did not affect capture probabilities within a trap session, therefore, it is unlikely that it would have between trap sessions when more time had elapsed for trap awareness to diminish. The unequal catchability detected by the Leslie method is therefore unlikely to be a result of the capture process.

Across the sample sessions, there was no detectable difference in the fate after first capture. This supports the assumption that there was no age or sex-dependent loss between trapping sessions. This does not suggest that there is no age-related difference in mortality. It is common in mammals for mortality to show a "U" curve in relation to age (Caughley 1966), and Guiler (1970 a, b) has suggested that this relationship occurs in Tasmanian devils. The finding here, however, relates to the loss to the trapped sample over the study period. The loss may be the result of mortality, dispersal and or trap avoidance. Loss is independent of the sub-groups tested, and therefore, these groups can be pooled for use in the capture-recapture models (Seber 1973, Blower *et al.* 1981).

The effect of conspecific odours in traps on subsequent captures has been closely studied in small mammal populations (Boonstra & Krebs 1976, Stoddart 1982, Stoddart & Smith 1986). Further, Stoddart & Smith (1986) warn that residual odours may affect retrappability and therefore estimates of population size estimated by capture-recapture techniques. In this study there was no detectable effect of the sex of the occupant of a trap on the next animal caught in the trap (Table 3.14). It is reasonable, therefore, to accept that trap entry was not in response to the sex of the previous occupant. The sampling was not biased towards either sex by conspecific odours. However, as discussed earlier, conspecific odours in traps did have a profound effect on the capture rate of a trap.

3.4.2 TRAPPABILITY

The accuracy of population parameters estimated by capture-recapture methods is strongly influenced by the trappability of the population (Hilborn *et al.* 1976, Boonstra 1985, Nichols 1986). Both the Jolly and Minimum trappability

methods give similar estimates for the total sampling duration. The trappability only dropped below 50% once (Table 3.16). Because the equal catchability assumption does not hold for this study the trappability estimates are probably overestimates (Nichols & Pollock 1983, Krebs & Boonstra 1984). The Jolly trappability varied for trapping sessions from a minimum of 19.7 % in the 5th sample to a maximum of 95.9 % in the 9th sample. The calculation of Mj in the Jolly-Seber model relies on the number of animals caught prior to and subsequent to the sample period (Jolly's z value). The high trappability in the 9th sample could be as a result of the low z value. If the z value is supplemented by animals that were trapped incidentally after the final trap session, Mj = 194.3, the trappability falls to 48.9 %.

The seasonal variation in trappability is shown in Figure 3.4. The low value in May 1984 is probably the result of the high number of traps set off without capture and the subsequent increase in trappability because of the use of long traps. The trappability of males is generally higher than that of females, although there is no significant difference between the values. There is a trend for lower trappability in the first half of the year and higher in the second half. Because the equal catchability assumption cannot be met and the trap design was changed, both trends should be interpreted with caution.

The mean number of captures per animal per trap session can be considered an indicator of the degree of trap interest (Kikkawa 1964). The variation with time in the degree of trap interest with time closely followed that of trappability (Figure 3.4). The two measures are essentially independent of each other with trappability relating to single captures of individuals and the degree of trap interest to the total number of captures. The close relationship therefore supports the trappability estimate. When there is no competition for traps, trappability will depend on the degree of interest in traps (Kikkawa 1964). This relationship supports the idea that there is no competition for traps and that the trappability estimate is reflecting the devils interest in the traps. Conclusions of causal factors in the variation of trappability between sexes and seasons can only be made with corroborative data on the dispersion and dispersal of the population. This is discussed in Chapter 4..

3.4.3 THE POPULATION ESTIMATES

The five population estimates show major differences with respect to total n and change in n (Table 3.20). The assessment of which method is most appropriate to these data is difficult, but as stated by Begon (1979), the models are all applicable to their own situations and these situations are distinct from each other.

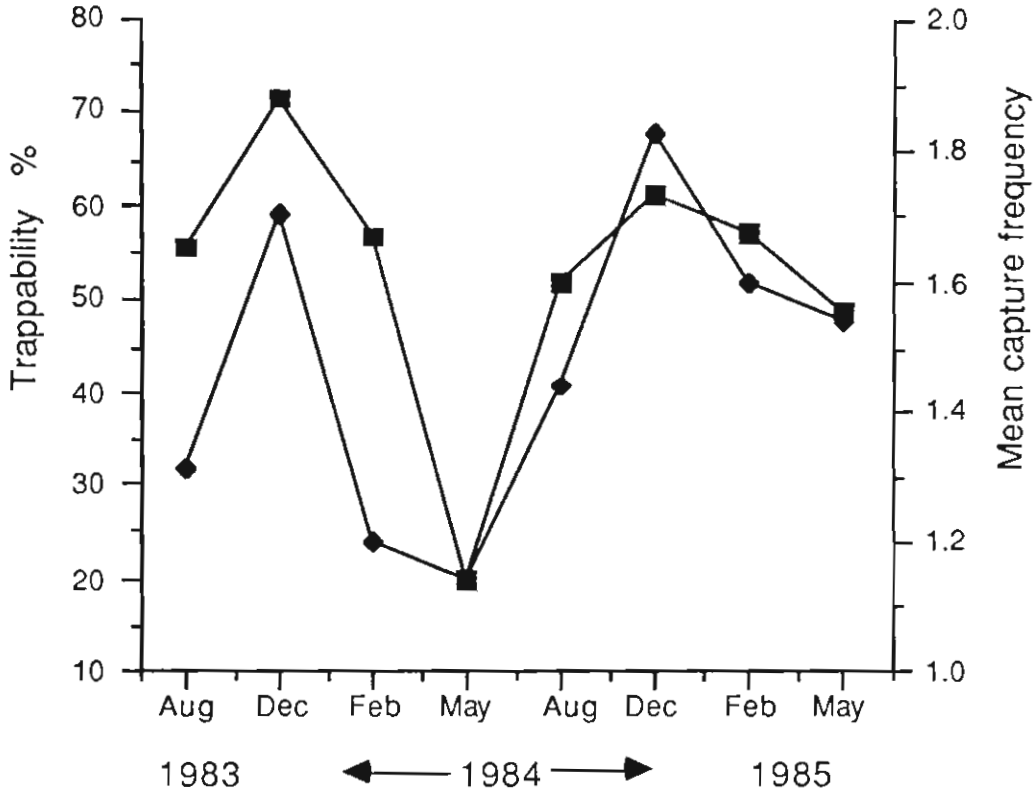


FIGURE 3.4 The variation in trappability (square) and capture frequency (diamond) with time of year

The enumeration method, or minimum number known to be alive (MNA), is used extensively in small mammal studies (e.g. Petrusewicz & Andrzejewski 1962, Krebs *et al.* 1976, Godsell 1982, Boonstra 1984, Adler *et al.* 1984, Stoddart & Smith 1986). It has been shown that under conditions of high trappability (> 50% by the minimum trappability calculation) the total enumeration technique is a robust technique (Boonstra 1985, Hilborn *et al.* 1976, Nichols & Pollock 1983). In the present study, the average minimum trappability for the total sample was above 50 % and the Jolly trappability also exceeded 50 % for each trapping session. But because of the unequal catchability these trappability estimates are probably overestimates making the accuracy of the MNA enumeration method doubtful. In addition, the MNA technique has a negative bias far greater than the Jolly model when catchability is unequal (Jolly & Dickson 1983, Nichols & Pollock 1983, Boonstra 1985, Nichols 1986). Hence, the use of MNA is of limited use in this study. Roff (1973a) points out that the accuracy of the MNA cannot be estimated and believes that the problems involved in its use are even greater than that for capture-recapture estimates. He concludes that complete enumeration is an unacceptable estimation technique. In the present study the MNA method does provide a minimum estimate of population number and an index of population change. Enumeration relies on the presence of the animals in the area for at least three trap sessions. Therefore, any dispersing animals in the area for less than six months will not be included in the calculation. The MNA technique measures the number of animals that remain in the population for more than six months, which therefore are probably residents. In this study the trappability, unequal catchability and inherent bias because of the sampling design all result in a negative bias to the MNA estimate.

The Capture-per-unit effort index of population is corrected for set-off traps and the curvilinear relationship of capture effort to population density (Nelson & Clark 1973, Caughley 1977) and, therefore, should show a similar trend to the other population estimates. There was a large increase in the CPU index after the introduction of the long traps (6th sampling session). The large decline in the 5th session is more difficult to explain. When compared with the other population models, CPU and MNA were the only ones showing a major decline in the population at this time (Table 3.20). Therefore, those models that calculate the untrapped portion of the population showed the opposite trend to those that only dealt with the trapped animals. In addition, the Jolly trappability estimate also declined at this time. A large number of animals were therefore untrappable. The one factor common to this trap session and not to others, at a similar time of the year, was the high proportion of traps set-off. Perhaps the number of captures was not only reduced by the set-off traps, but also by

a reaction of animals to the closed traps. This would effectively reduce the MNA and CPU indices that are calculated from the total number captured, but not the other models that rely on the proportion of marked to unmarked animals in the sample. With the problem of short and long traps it is probably prudent to only consider the CPU index after the introduction of the long traps and to treat this period as indicative of the population trend over the annual cycle.

The parametric frequency-of-capture models used here have attracted some criticism (e.g. Wilbur & Landwehr 1975, Cormack 1979). These authors emphasize that the distributions to which the data are fitted are statistical descriptions rather than models and, therefore, the extension to the zero frequency is not based on a "discussion". The attraction of this method, however, is that it allows for unequal catchability (Tanton 1965, 1969, Caughley 1977). The Chi-square test for goodness-of-fit is considered to be insufficient to distinguish between distributions with limited data (Eberhardt 1969, Roff 1973b, Cormack 1979). In this study, the choice between the models of best fit was, in all but one case, obvious, because they were separated by the Chi-square test by at least one level of significance (Table 3.19). In the case of the 4th sample, the data are limited and the population estimate should be interpreted with care.

The Jolly-Seber and Manly-Parr population estimates showed the same trend across the study period with the latter usually lower than the former (Figure 3.5). The Manly -Parr model is inaccurate if the W_j (i.e. the number of animals caught before, during and after the j occasion) is less than 10. The mean Wj for this study was 10.9 varying from 17 to 2 with three samples having values less than 10. This places the accuracy of some of the estimates in doubt. The Manly-Parr model is superior to the Jolly-Seber model under situations of strongly age-dependant loss to the sample (Begon 1979). In the present study there was no age-dependant loss, suggesting that the Jolly-Seber model would provide a better estimate.

The accuracy of the techniques is also difficult to assess. It has been shown that the error values for Manly-Parr and Jolly-Seber models are highly correlated with the population estimate. In this study the correlation of population size with standard error was $r = 0.97$ for the Manly-Parr estimate and for the Jolly-Seber estimate $r = 0.98$. These correlations cause underestimates to appear more accurate and overestimates to appear less accurate. Further, the standard error formulae are themselves questionable (Manly 1971, Roff 1973b) making the standard error values of limited use. The use of the Robson and Regier tables does provide a theoretical

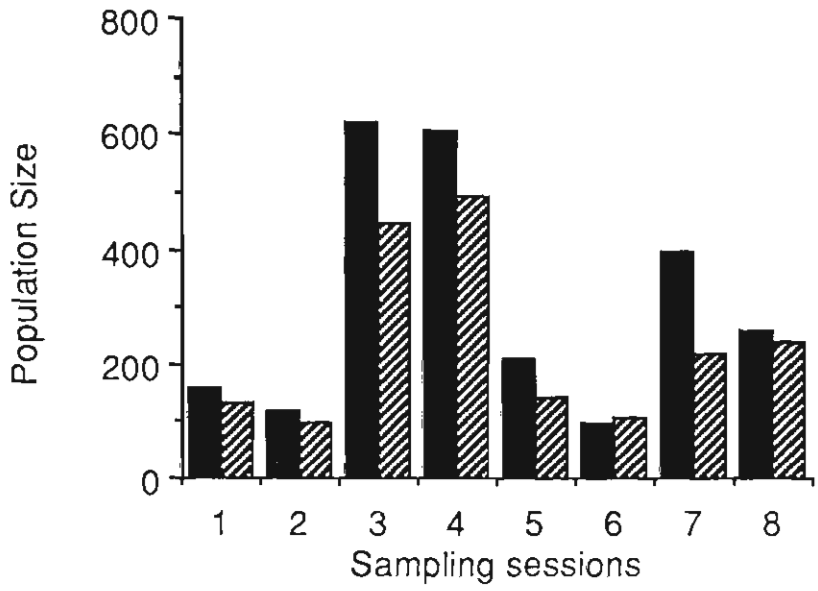


FIGURE 3.5 Comparison of the population size estimates derived by the Jolly-Seber (■) and Manly Parr (▨) models

degree of accuracy. The choice of the table where Mj = 1.5 nj was appropriate. Theoretically, therefore, the trapped sample was sufficient in size to provide the predicted accuracy of 10'%. Begon (1979) emphasizes that the accuracy of the estimates can be assessed by the above mathematical methods, but that, in addition, common sense must be applied in order to check their biological adequacy.

The MNA for the first sample was 159 individuals. The rate of capture of new animals decreased after 500 trap nights suggesting that the maximum size of the trappable population must have been approached (Table 3.1, Fig. 3.2). The only population estimate for this period (392) was computed by the frequency-of-capture method (Table 3.20). There is evidence, therefore, that a portion of the population was not trappable. The probability of capture is dependent on an animal being in the vicinity of a trap, and subsequent entry of the trap. Eberhardt (1978) extended Cormack's (1968) classification of the failure of animals to be captured and suggested three causes:

1. The result of a learning process where animals become trap-shy or trap-happy.

2. A property truly inherent in the individual which is expressed in the vicinity of the trap
3. A property resulting from the movement of animals and the positioning of traps. The existence of any fixed movement patterns provides an *a priori* argument against random mixing of marked and unmarked animals.

The test of equal catchability, using frequency distributions and the Poisson distribution as the expected values, showed the presence of both trap-happy and trap-shy animals. The fate of captured and recaptured animals, however, was the same, suggesting that the effect of capture was the same as that of recapture and that trap avoidance was not prevalent (Bishop & Hartley 1979). The conclusions of these two separate tests is in apparent contradiction. The explanation lies in the data used (Appendix 3, Tables 3.8 & 3.10). The first test used all the capture and recapture data whilst the latter analysis was carried out on a select group of animals. The latter were animals that were captured once and their subsequent capture histories, versus those recaptured and their capture histories. This test lumps all animals over the trap session and does not take into account the capture possibilities available, as does the Poisson method. The Poisson method leads to the conclusion that individuals, when given the chance to be trapped on x number of days, will show both trap-happy and trap-shy responses. The other test leads to the conclusion that across one trap session the animals will eventually be captured and show no trap avoidance. The difference is

important, because as pointed out by Erlinge (1983), the population models relying on the frequency-of-capture within a trap sample will be affected if there is bias in the trap response within the trap session. While those models such as the Manly-Parr and Jolly-Seber rely on one capture of an individual in a trap session they will only be affected if the trap response is so strong that it remains to the next trap session and prevents or increases the chance of capture. There is a response by animals to initial capture which could bias the frequency-of-capture models, but which should not affect those models relying on a single capture.

Radio-tracking studies have provided an insight into the other two factors (the movement and behaviour of radio-tracked animals are fully discussed in Chapter 6). Firstly, animals were tracked along trap lines but failed to be captured even though they probably passed within a few metres of the traps. In addition, traps set at the entrance to dens did not always capture the tagged animal when it left the den to forage in the evening. Therefore, it appears that the individual's response to traps was truly inherent and showed variation. Secondly, the home range analysis (Chapter 6) shows that individuals occupied fixed areas and therefore the trap line did not randomly sample the area. Thus, the trapping methodology had an *a priori* influence on the size and composition of the sample. The probability of capture was strongly influenced by the location of trap sites in relation to home ranges. The non-random distribution of traps promotes unequal catchability (Eberhardt 1969).

It is apparent that these factors operated in the present study. Both the Jolly-Seber and Manly-Parr models rely on the assumption of equal probability of capture (Seber 1973), which is clearly not met in this study. There are situations where an individual's probability of capture is either diminished ('trap-shy') or enhanced ("trap-happy") by its previous captures and where the probability of capture varies between individuals irrespective of the capture history ("heterogeneity"). Heterogeneous catchability results in a negative bias to the population estimates (Edwards & Eberhardt 1967, Begon 1979, Jolly & Dickson 1983). Trap-happy and trap-shy animals cause a negative and positive bias respectively (Blower *et al.* 1981). In the present study, unequal catchability is probably as an integrated result of all three forms of catchability. The effect of this is to bias the estimation of the population to an unknown degree and in an unknown direction (Begon 1979). The accuracy of the estimates are therefore unreliable.

Samples in May of each year give a population estimate of 277 using the frequency-of-capture method, minimum estimates of 233 and 175 by the Manly-Parr

model, and 362 and 200 by the Jolly-Seber model (Table 3.20). I therefore accept that the minimum population size at this time of the year would be in the range of 200 to 400 animals. This conclusion is corroborated by estimating the number of young that would have been weaned in the area. A total of 48 females with 99 young were caught in 1983. Accepting that they all weaned and that the sex ratio is parity (Chapter 4), there were 48 females, 48 males and 99 young, totalling about 200 animals. Population estimates at the end of the year are 129 and 101 from the frequency-of-capture method, 102 and 88 by the Jolly-Seber model and 87 and 93 by the Manly-Parr method. The MNA estimate for this time of year is 70 and 85. I conclude, therefore, that the population was at a minimum of 80-100 animals at this time of year.

The primary aim of the population estimate is to show the annual trend in population size. A conservative approach was suggested by Eberhardt (1978) who stated that methods which normally yield absolute values should be treated conservatively as measures functionally related to density (indices) in order to minimize the effects of potential bias. Because of the unknown bias in the population estimates used in this study they will be treated as indices.

The estimates for the period when short traps were used and when long traps were used have been plotted separately (Figure 3.6). This is to satisfy the criterion that the trapping method was kept constant for the CPU and MNA techniques. The first period is from August 1983 to May 1984 when the short traps were used. The Jolly-Seber and Manly-Parr population estimates fluctuated from a high in late summer/early winter to a low in late winter/spring (Fig. 3.6). This trend is also seen in the MNA and CPU estimates, but both decrease substantially in May 1984. This capture rate prompted the change in trap design. The decrease was as a result of traps having been set off and as can be seen in Figure 3.6 the MNA and CPU estimates that rely on the total number of animals captured showed a major decline but the capture-recapture estimates that rely on the proportion of marked to unmarked animals, and not the total number captured, did not decrease. This decrease is probably the result of the trap response of the animals and not a decline in the population.

When the long traps were used from August 1984 to May 1985, population estimates showed an increase in the beginning of the year and a decrease in late winter through to autumn. The difference between the Jolly-Seber and Manly-Parr methods in February 1985 is difficult to explain. The Manly-Parr estimate is supported by the frequency-of-capture estimate as well as by the MNA and CPU estimates

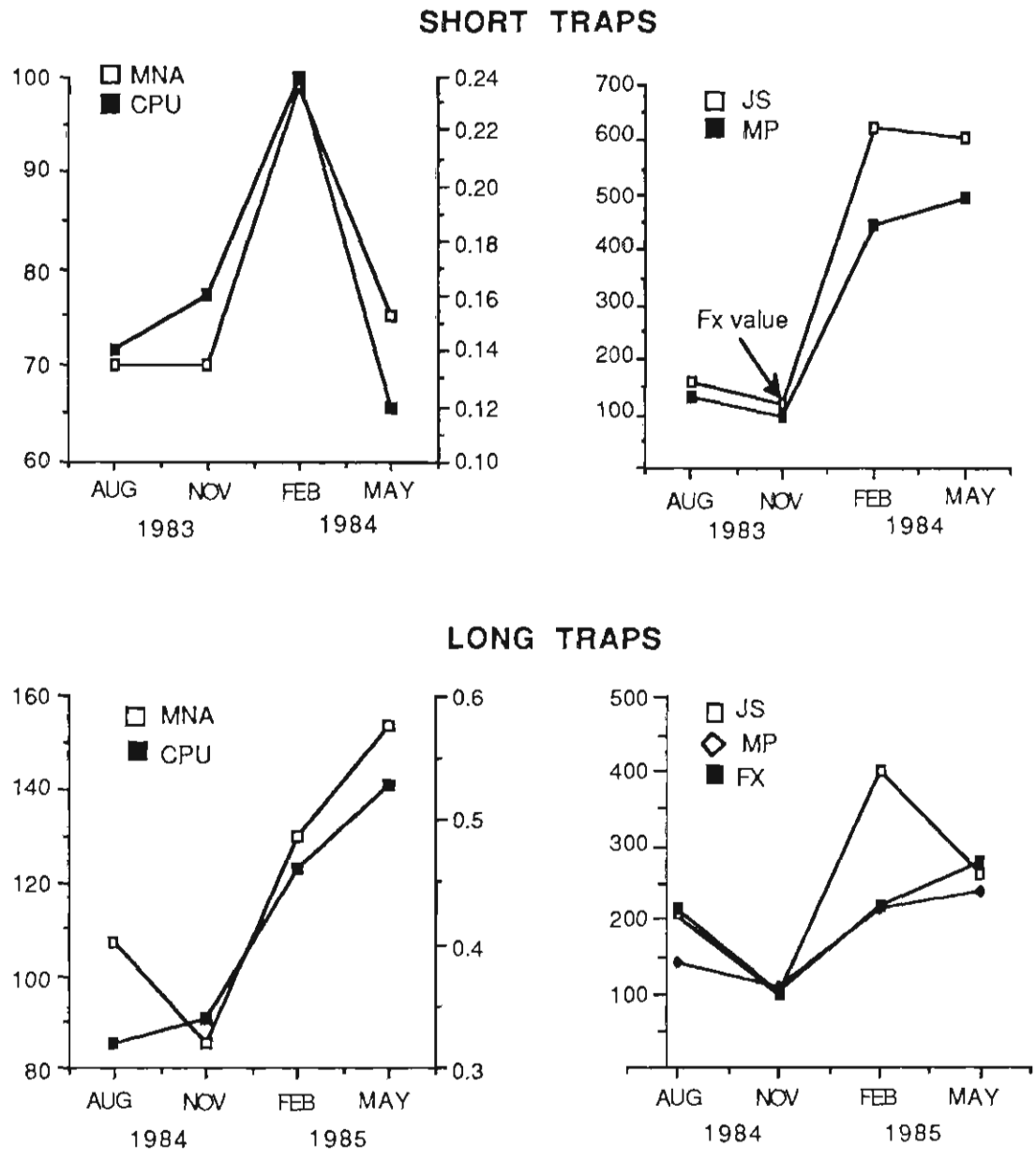


FIGURE 3.6

The population estimates and indices plotted separately according to method of calculation (see Section 3.2) and the type of traps used. The first two graphs show the estimates calculated using the short traps and the second two those using the long traps. Population estimates/indices (MNA: minimum number known to be alive; CPU: capture per unit effort; JS: Jolly-Seber; MP: Manley Parr; FX: frequency of capture) are shown on the y axis in each graph.

(Figure 3.6). The Jolly-Seber estimate for February 1985 is 440 ± 98 and for May 1985 is 262 ± 63. For reasons discussed earlier, I do not think that the accuracy of the estimate is sufficient to say that the population declined between February and May.

The population size shows an annual trend of high numbers in autumn and winter and then a decline through spring and summer. This trend is replicated for all years of the study (Figure 3.7).

The observed annual change in the population is considered reliable for the following reasons. The change follows the *a priori* knowledge of the biology of the animals. The change is found in the range of models, from the stochastic models applied to open populations, to the frequency-of-capture model which is applied to each sample separately as a closed system and allows for unequal catchability. The MNA and CPU estimates that do not rely on mathematical calculations of the uncaptured animals show the same trends. The observed change in population size in the first period (1983-1984) is similar to that in the second (1984 - 1985).

3.5 SUMMARY

1. In order to provide reliable estimates of the population size more than 135 animals had to be captured in each sampling session. Based on the capture rate of session 1, subsequent trap sessions were conducted for 10 days with 50 traps set each night. With capture rates approaching or exceeding 50 %, the minimum number of animals could usually be obtained in 500 trap nights.

2. Tasmanian devils entered traps previously occupied by a conspecific irrespective of the sex of the previous occupant more frequently than traps which had not previously been occupied. When given a choice of tainted or odourless traps, they chose the former.

3. "Long" traps had a higher capture rate than "short" traps and less were set off without making a capture. Therefore from the 6th trap session and on, the traps were lengthened.

4. Unequal catchability was common both within and between trap sessions. Unequal catchability was comprised of trap-shy, trap-happy and heterogeneous trap responses. The accuracy of the population estimates is therefore biased to an unknown degree.

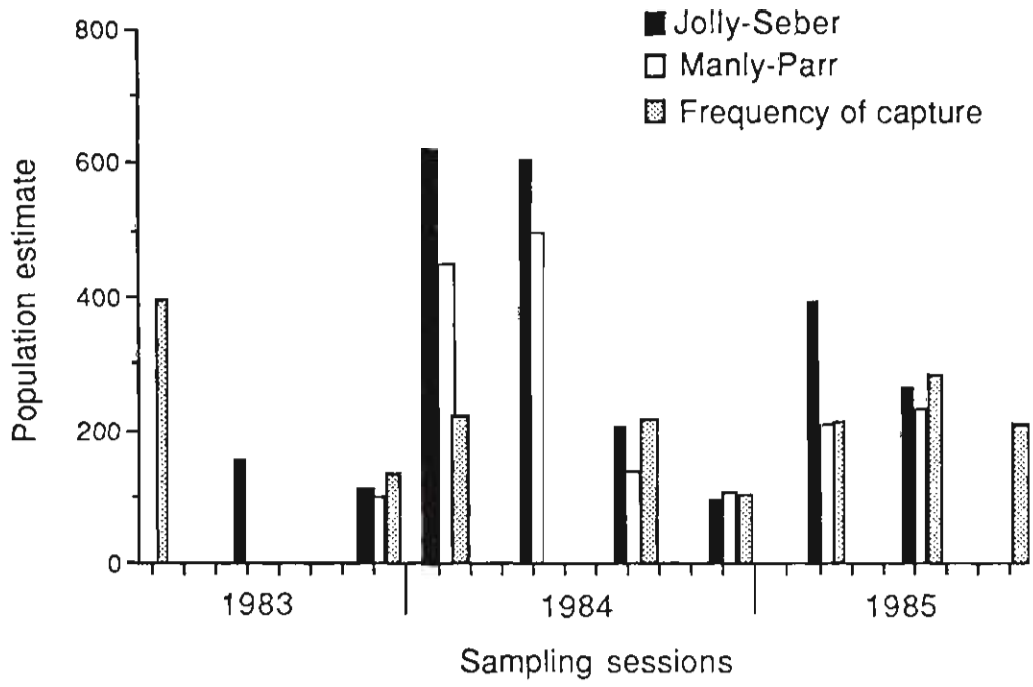


FIGURE 3.7 The trend in population size through the year according to the Jolly-Seber, Manly-Parr and Frequency of capture models.

5. The length of capture histories was the same for both sexes, as were their capture frequencies within trap sessions. Therefore, male and female samples were pooled where appropriate.

6. The capture history of singly and multiply captured animals did not differ suggesting that handling did not affect the chance of recapture, either within or between trap sessions.

7. There was no age dependent loss to the trapped sample. Thus old and young animals alike disappeared at similar rates from the trappable population.

8. Trappability was generally above 50 %, which is the minimum allowable level for the use of some enumeration techniques. There was no competition for traps as seen by the degree of trap interest.

9. The CPU index changed as a result of the introduction of long traps. The MNA trend with time was similar to that provided by the capture recapture models except for fifth trap session, where the trappability fell to 19.7 %, making MNA unreliable.

10. Taking all the estimates into account, the potential number of young weaned, and the unreliable accuracy of the estimates a commonsense approach suggests that in the first half of the year until spring, there were between 200-400 animals in the study area and 80-100 in summer before the young are weaned.

11. A conservative approach to the population estimates was taken. They are treated as indices with respect to population fluctuation over the annual cycle of the Tasmanian devil. There is a rapid increase in the population size at the end of summer which is maintained until spring, when the population declined again. This trend was shown by all estimation methods and for all years sampled.

CHAPTER 4

POPULATION DEMOGRAPHY

> Demography is a guide to understanding adaptive syndromes. We badly need more field data and life tables from field studies. *Eisenberg* 1981

> Much of the morphology, physiology and behaviour of marsupials is shared with other mammals, but there are some areas of considerable difference. In particular, the pattern of reproduction in the female, giving rise at birth to a very small undeveloped young which completes its development in a pouch or attached to a teat on the abdomen of the mother, has had far reaching consequences for parental behaviour, and ultimately for social behaviour and social organization. *Russell* 1984

4.1 INTRODUCTION

The aim of this chapter is to describe the population demography of the Tasmanian devil at Mt. William National Park in order to more effectively interpret its social organization. The demographic features of sex ratio, season of birth, fertility, age distribution, mortality, development of the young, and dispersal are considered in this Chapter.

The demographic features described follow the methods of Caughley (1977) and Russell (1982 a, b). The term *fertility* is used in preference to *fecundity* . Fertility refers to the potential reproductive capacity of an organism measured by the number of gametes, whereas fecundity is the actual reproductive performance of an organism (Wynne-Edwards 1962, Lincoln *et al.* 1983). In this study the fertility of the the population and its individuals is described, since this is the parameter which is applicable to social organisation (Russell 1982b).

The dispersal pattern of the population is described in detail as dispersal patterns play important roles in the demography of many species of mammals (Lidicker 1975, Krebs & Myers 1974). Further, the survival of a species is as dependent on dispersal as it is on reproduction and longevity (Caughley 1977). Howard (1960) defines *dispersal* as the movement of an individual from its point of origin to the place where it reproduces, or would have, if it had survived and found a mate. Greenwood

(1980) points out that this refers only to juveniles and further clarifies this type of movement as *natal dispersal.* Greenwood (1980) goes on to define *breeding dispersal* as the movement of individuals, which have reproduced, between successive breeding sites. These definitions have been followed in this study.

4.2 METHODS

4.2.1 SEX RATIO

The sex of adults and pouch young with a head length greater than 11 mm was determined by direct observation of external genitalia. Sex ratios were compared between and within age groups and seasons by means of G-tests, adjusted with the William's correction factor where appropriate (Sokal & Rohlf 1981). Differences between categories of animals used in the analyses were accepted only at the 5 % level when using a two-tailed test. Results are expressed as the proportion of males (Pm), used synonymously with sex ratio throughout.

4.2.2 SEASON OF BIRTH

The extent to which the birth of young was synchronized was determined by measuring the growth of pouch young and relating this to the calender date. The head length of pouch young (occipital crest to tip of nose) was measured with vernier calipers (±1 mm). These measurements were plotted against the day of year, and each year was treated separately. When more than one pouch young from a "brood" was measured, the mean of the measurements was used. Linear regressions were fitted to the data. Because the smallest head length of a new born Tasmanian devil measured is 2.8 mm (L. Hughes pers comm.; D. Pemberton pers obs.), the "y" value for an "x" value of 2.8 mm on the line of best fit was calculated using the method of predicting x from y (Sokal & Rohlf 1981). In this way, the median birth date and 95 % confidence limits were calculated.

4.2.3 DURATION OF STAGES OF PARENTAL CARE

The times from birth to first pouch exit (FPE), young left in nest (LIN), permanent pouch exit (PPE), young leaves nest alone (LNA) and time to weaning were calculated from retrospective examination of the trapping records (terminology following Russell 1982a). Calculations were made in days from the median birth date.

4.2.4 FERTILITY

The reproductive performance of the population was measured as the number of live births per female per age class per year. This was expressed as mx, the number of female live births per female. Retrospective examination of the data was undertaken to calculate a fertility table showing the mean number of births per age class. Comparisons were made between years. A Kruskal-Wallis nonparametric test (Sokal

& Rohlf 1981) was used to test for differences in mx between years.

For individuals caught in different years, the number of pouch young may either show a decline, remain static, or increase, thereby indicating how fertility changes with age. Data from individuals caught over more than one year were examined for the number of pouch young they carried in successive years. These values were analysed using Kendall's coefficient of concordance, and compared to the area of a normal curve (B. Brown pers comm., Sokal & Rohlf 1981). The age of individuals, and the number of pouch young they carried, were analysed and Kendall's statistic applied to test for fertility change with age.

4.2.5 MORTALITY

The mortality rates of the males and females were calculated separately and according to Methods 2 and 6 of Caughley (1977, p. 90-93). Method 2 relies on the marked one-year-old cohort of May 1983. This cohort was followed until the animals reached three years of age and mortality rates were calculated. Method 6 was applied to the final year's data (1985), where the age distribution was calculated for the sample and mortality rates were calculated. Both methods used data derived from trapped samples, and hence generally lack the young animals less than 12 months old that are not readily trapped. As a result, all these calculations refer to animals more than 2 months beyond weaning. The mortality of the young less than 12 months of age was assessed separately.

4.2.6 AGE DISTRIBUTION

As with mortality, age distribution was calculated for animals which were one year of age or greater. The distribution was assessed for yearly variation by sex and month of the year using a log-linear model of a three-way contingency table (Sokal & Rohlf 1981). Data were analysed separately for the same time of the year between the years of the study.

4.2.7 DISPERSAL

Three specific questions were posed about dispersing animals:

1. When does dispersal take place?
2. Is there a sex-biased dispersal of young from their natal areas?
3. What are the comparative costs of dispersal and of philopatry ?

In order to answer the first question, residents and transients were identified, and the relative proportions of these individuals in the trapped population were calculated. These data were analysed according to season and age. The aim of these analyses was to identify any changes in the proportion of resident and transient

animals, and thereby examine whether dispersion was occurring.

Retrospective examination of the data showed that there were essentially two groups of devils. Individuals that were caught on three or more occasions in three or more months were defined as *residents* . Other individuals were considered to be temporarily in the population, i.e. *transients* . Data from the three years were pooled and the seasonal variation in proportions of the two groups were compared. The two groups were also split into age groups 1 and 2+ (see Chapter 2) and compared between seasons for both sexes separately. A row by column (R x C) G-test (Sokal & Rohlf 1981) was used to test the hypothesis that the number of transient and resident animals did not change with season. The sex, age and reproductive condition of residents were also assessed.

To examine Question 2, whether young of one sex dispersed from the natal area to a greater extent than the other sex, it was assumed that animals caught prior to being weaned were in their natal area. Their subsequent capture history was analysed to determine if they remained in the area and hence to test for the presence of philopatry. The data were analysed to identify if sex-biased dispersal occurred.

The cost of dispersal, Question 3, was assessed in adult females by comparing the number of pouch young carried by both transients and residents. Transients were assumed to represent animals undergoing breeding dispersal. A Mann-Whitney U test was used to test whether the number of pouch young carried by the animals in the two groups differed significantly. The cost of dispersal to juveniles was measured by comparing the mortality rates of young captured and marked prior to weaning with those captured for the first time in winter (post-weaning). The sample caught prior to weaning was considered to have a higher potential of containing philopatric animals than the sample caught in winter, which was composed predominantly of dispersed, or dispersing young.

In addition to the above analyses, the capture histories of all resident animals were assessed and plotted for a visual representation of trends in the timing of movements. Where gaps of greater than four trap sessions occurred between captures, the animal was considered to be absent from the study area. An animal that was captured, then absent for four trapping sessions or more and then captured again, thereby satisfying the definition of a resident but having a gap in captures of a year or more, was defined as a *discontinuous resident* . Those that remained in the area for more than this period (i.e. one year) were defined as *continuous residents*, and by definition would have been caught in at least two of every four trapping sessions. The fertility of these two groups was compared by means of a Mann-Whitney U test.

4.3 RESULTS

4.3.1 SEX RATIO

In a sample of 26 litters (n = 59 pouch young) where the sex of the pouch young could be determined, there was no significant difference between the number of males and females (Pm = 0.51, G_{adj}= 0.02, ns). The three age classes showed no significant deviation from sexual parity (Table 4.1), nor was there any significant difference for combined age classes between years (G_{adj} = 3.09, ns). Where appropriate, yearly samples were pooled.

The age classes 1 and 2+, treated separately, were evaluated and assessed for significant deviations from parity with season (Table 4.2). Animals of age class 0 were only in the trappable population from late spring until late summer and so they were not included in the analysis of seasonal variations. Animals within age classes 1 and 2+ did not differ from parity (G_{adj} =1.19, ns; G_{adj} = 5.75, ns; respectively). The sex ratio of all age classes, and across all seasons, showed no deviation from parity and therefore, there was no differential mortality of sexes with age or season.

4.3.2 MEDIAN BIRTH DATE

The relationship between length of head and date for each year of the study is shown in Figure 4.1. The r^2 values support the use of the linear equation for initial growth and the F-values support the hypothesis that the variance around the line was small (1983: $F_{0.05(1),1,27}$ = 396.1, P ≤ 0.0001, r^2 = 0.94; 1984: $F_{0.05(1),1,7}$ = 163.8, P ≤ 0.0001, r^2 = 0.96. 1985: $F_{0.05(1),1,23}$ = 334.1, P ≤ 0.0001, r^2 = 0.94). The birth date and 95 % confidence limits, calculated from the head length at birth (2.8 mm), were 106 ± 15 days (1983 data), 99 ± 5 days (1984 data) and 99 ± 24 days (1985 data) from the beginning of each of the three years (Fig. 4.2). Therefore, the modal birth date was close to April 10 each year.

4.3.3 DURATION OF STAGES OF PARENTAL CARE

The nature of the trapping protocol made it difficult to distinguish between the first emergence of pouch young (FPE) and permanent exit from the pouch (PPE). Similarly, the timing of pouch exit, and the period when young are first left in the nest alone (LIN), were also difficult to ascertain. The latest recorded dates of young in the pouch, and the earliest recorded dates of mothers trapped with enlarged teats but without pouch young, are shown in Table 4.3. The presence of lactating mammary glands with the absence of pouch young was taken to indicate that the young had been left in a den. The mammary gland of an animal was judged as active if the teat was enlarged and could be stimulated to produce milk. The earliest record of young being left in a den was August 6, and the latest record of a mother carrying young was August 22. The animal carrying young on August 22 had one pouch young and two

TABLE 4.1 The sex ratios of the three age classes of devils trapped during the study period. (Pm = proportion of males).

Year	Age Class	Male	Female	Pm	Significance *
1983/84	0	26	33	44.1	NS
	1	55	58	48.6	NS
	2+	48	31	60.8	NS
	Total	129	122	51.4	NS
1984/85	0	24	33	42.1	NS
	1	45	28	61.6	NS
	2+	42	28	60.0	NS
	Total	111	89	55.5	NS
1985/86	0	7	1		
	1	32	49	39.5	NS
	2+	30	31	49.2	NS
	Total	69	81	46	NS

* NS: Not significant.

TABLE 4.2 The seasonal variation of sex ratios of devils in age classes 1 and 2+.

Age class	Season	Female	Male	Total	Pm	Kimball's method(Pm)
1	Autumn	83	89	172	51.2	
	Winter	54	54	108	50.0	
	Spring	17	25	42	59.5	
	Summer	22	26	48	54.2	
	Total	176	194	370		
2+	Autumn	57	58	115	50.4	49.0
	Winter	32	36	68	52.9	51.1
	Spring	25	15	40	37.5	48.7
	Summer	43	25	68	36.7	43.9
	Total	157	134	291		

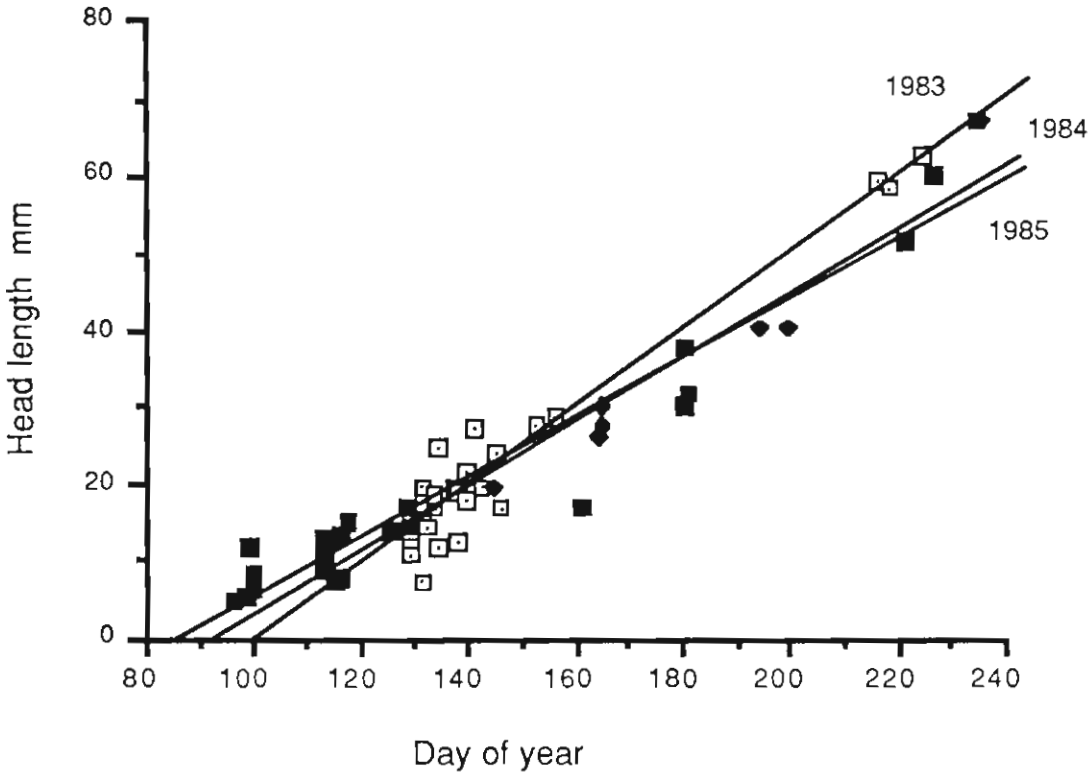


FIGURE 4.1

Relationship between head length and day of the year for pouch young captured in 1983 (□), 1984 (■) and 1985 (◆).

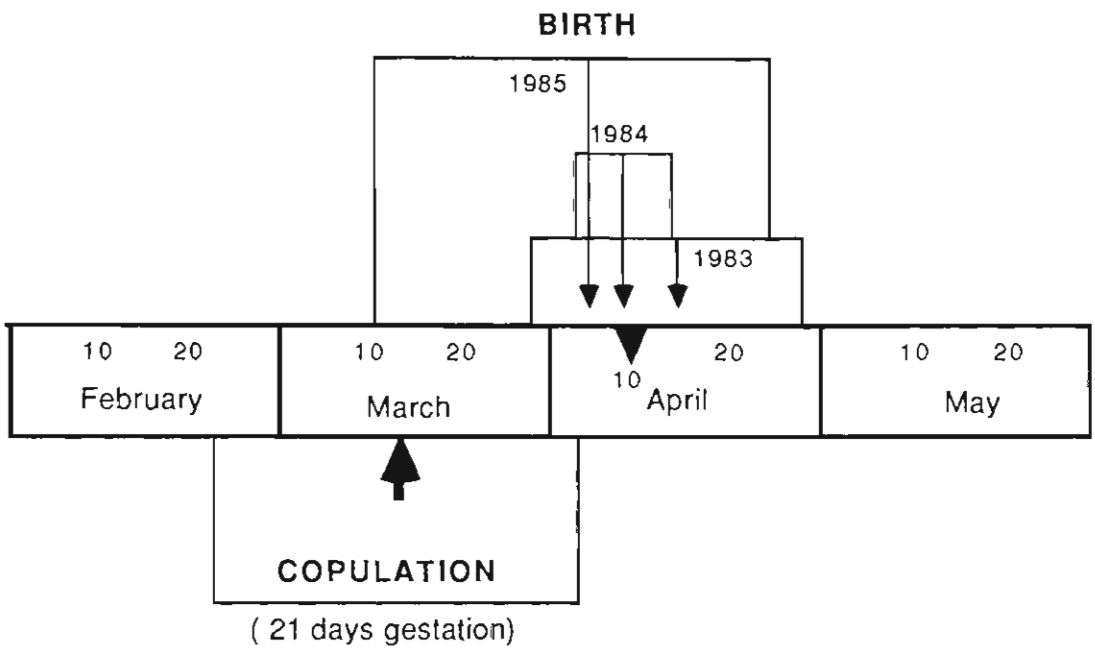


FIGURE 4.2

The calculated date of birth and copulation with the mean ▲ and 95% confidence limits ⊓ for the three years sampled and the pooled sample ▲

TABLE 4.3 The earliest recorded dates of of lactating females with no pouch young (A) and the latest recorded dates of suck. young in pouch (B)#

Lactating (A)	Suckling (B)
6 August	11 July
12 August	17 July
12 August	4 August
13 August	6 August
21 August	9 August
22 August	14 August
24 August	22 August*
25 August	
30 August	

Each record represents one individual
* I young suckling plus 2 nipples lactating.

TABLE 4.4 The earliest recorded date of capture of dependant young.

Date	Capture Location
8 November	At den
16 November	At den
21 November	At den
21 November	At den
23 November	Trap line
3 December	Trap line
7 December	Trap line
8 December	Trap line
10 December	Trap line
10 December	Trap line
12 December	Trap line
13 December	Trap line

TABLE 4.5 The latest recorded date of capture of lactating animals and those with retracting nipples##.

Lactation	Retracting
10 December	4 February
10 December	4 February
12 December	9 February
13 December	22 February
1 January	22 February
2 January	23 February
2 January	23 February
3 January	
3 January	
4 January	
7 January	
11 January	
13 January*	
14 January	
18 January**	

Each record represents one individual
* 3 nipples lactating and 1 retracting
** 1 nipple lactating and 1 retracting

other lactating teats without young attached. It is possible that she had already left one or two young in a den. The date of PPE was taken as August 15, or 130 days after the median birth date. This is also the maximum time to FPE.

A similar examination of the data showed that the earliest that young were trapped around maternity dens was November 8 (Table 4.4). By November 23 young animals were appearing in the trap line. Young were, therefore, leaving the nest from 214 days after the birth date. They were at least 240 days old before being routinely caught on the trap line. The median date for LNA was 227 days.

All females that had recently carried young and were caught prior to January 13, had fully lactating teats (Table 4.5). One animal was caught on the 18 January with one lactating teat and one retracting teat. Young of the year were prevalent in the trapping record in January (Chapter 2, Fig. 2.2). Therefore, weaning is estimated to occur on about January 10, i.e. 278 days after birth.

4.3.4 MORTALITY

The general pattern of mortality is shown in Table 4.6. The first method uses the capture history of the cohort of known age resident devils which were followed throughout the study (Method 2 in Caughley 1977). The alternative method employs the data of the age distribution at, or close to, a birth pulse (Method 6 in Caughley 1977). There was a difference between the mortality rates of sexes for the two year old cohort, with the males showing a higher mortality rate. The sample size is well below the 150 recommended for calculating qx curves (Caughley 1966, 1977). Therefore, the validity of the difference in the qx values for the sexes is doubtful. The ≥ 2 years of age group includes all those animals caught as at least 2 year olds in 1983. There are animals with the potential to be greater than 3 years old. The number of animals surviving to ≥ 2 years was similar for both sexes.

The young caught within one month of weaning tended to show a different age specific mortality pattern than did the juveniles caught for the first time in winter. The former group of animals had a lower mortality rate between one and two years of age than did the latter group (Table 4.7).

4.3.5 AGE DISTRIBUTION

The frequency distribution of the number of male and female devils in the three age classes for each of the three years are shown in Table 4.8. Comparisons of the age distribution within months and between years did not show any significant variation for the February, May and December samples but the variation in the August samples were significant. The pooled August sample however showed no significant difference

TABLE 4.6 General pattern of mean annual mortalities of male and female devils *

	Age years	Frequency fx	Survival lx	Mortality dx	Mortality rate qx	Survival rate px
A. Method 2						
Females	1	64	1.00	0.83	0.83	0.17
	2	11	0.17	0.03	0.18	0.82
	3	9	0.14			
Males	1	55	1.00	0.82	0.82	0.18
	2	10	0.18	0.09	0.50	0.50
	3	5	0.09			
B. Method 6						
Females	1	33	1.00	0.70	0.70	0.30
	2	10	0.30	0.03	0.10	0.90
	3	9	0.27			
	≥2	12				
Males	1	54	1.00	0.80	0.80	0.20
	2	11	0.20	0.11	0.55	0.45
	3	5	0.09			
	≥2	14				

* Notation follows Caughley (1977)

TABLE 4.7 The mortality rate of the weaned young.

Sex	Year of first capture	Age years	Frequency fx	Mortality rate qx
Female	1983/84	0	24	0.5
		1	12	0.25
		2	9	
	1984/85	0	22	0.64
		1	8	
Males	1983/84	0	34	0.65
		1	12	0.42
		2	7	
	1984/85	0	34	0.65
		1	12	

TABLE 4.8 Age distribution of Tasmanian devils for the same months and different years. The statistics of the interaction of all the parameters for each month are shown

Month	A Year	B Sex	C Number in age classes			ABC interaction #		
			Weaned young 0	Juvenile 1	Adult 2+	G value	DF	Significance
May	1983	Male	0	47	33			
		Female	0	48	26			
	1984	Male	0	13	4			
		Female	0	10	2			
	1985	Male	0	10	6			
		Female	0	11	10			
						0.901	2	N.S.
	Total	Both	0	129	81			
August	1983	Male	0	16	6			
		Female	0	9	7			
	1984	Male	0	12	4			
		Female	0	9	10			
	1985	Male	0	11	9			
		Female	0	25	7			
						6.816	2	P < 0.05
	Total	Both	0	82	43			
December	1983	Male	4	8	10			
		Female	1	14	15			
	1984	Male	0	9	3			
		Female	1	10	10			
						1.14	2	N.S.
	Total	Both	6	41	38			
February	1984	Male	25	1	3			
		Female	22	2	10			
	1985	Male	21	4	6			
		Female	18	1	7			
						2.439	2	N.S.
	Total	Both	86	8	26			

Test = log linear model three way contingency table;
N.S. denotes lack of statistical significance (P > 0.05)

between the frequency of males and females ($G_{adj(1)}$ = 0.0004, ns). The data for all years and sexes were pooled and the data tested to see if the age distribution changed significantly throughout the year. There was a highly significant change ($G_{(3)}$ = 32.84, P << 0.001) with time of the year. Weaned young dominated the February sample, whilst juveniles were prevalent in the May sample. Adults increased their representation in the latter half of the year (Fig. 4.3).

4.3.6 FERTILITY

The mean number of female pouch young produced per female (mx) was 1.031, 1.145 and 1.150 for the three successive years (Table 4.9). There was no significant difference in the mx value for each of the three years (H = 0.2307 < $X^2_{(0.05)(2)}$ = 5.991) and the pooled mean mx was 1.11. In 1983, 76.6 % of females carried pouch young, 69.7 % in 1984 and 76.7 % in 1985.

The capture of known age animals showed that females were sexually mature in their second year. A high percentage (81 %) of two year olds carried pouch young and had a mean mx value of 1.214 . Only one one year old devil carrying young was ever caught.

The mean total number of pouch young, regardless of sex, produced per female for the total sample was 2.23, with a bias towards four young and zero young. (Fig. 4.4). These data were analysed further by splitting the sample into two groups: 1) the ≥ 2 year old group comprising animals which were at least 2 years old or more (adults of unknown age); and 2) the animals which were definitely 2 years old (known age adults). The frequency of occurrence of the number of pouch young for the two age groups is shown in Figure 4.5. The predominance of four young in the 2 year olds, and the lack of three young relative to the older group, is striking. This suggests that the number of pouch young carried is related to the age of the mother and, therefore, further analyses were carried out to test for a decrease in fertility with age.

There is evidence that the fertility of female devils decreased with age. For 17 females which were caught repeatedly during the study, the numbers of pouch young being carried in each year were compared (Table 4.10). Kendall's nonparametric test gave a result corresponding to P ≤ 0.0618 (see Appendix 5). In addition, the recorded number of pouch young for all adult females captured was tabulated against age classes (Table 4.11). Kendall's test of concordance gave a result corresponding to P ≤ 0.0676 (see Appendix 5) which constitutes evidence of a similar strength to the previous set of data. The ≥ 2 year old group is the group that contains the oldest animals. This group also contains animals as young as two years old which had not been captured previously. The " oldest" group is biased towards the younger groups,

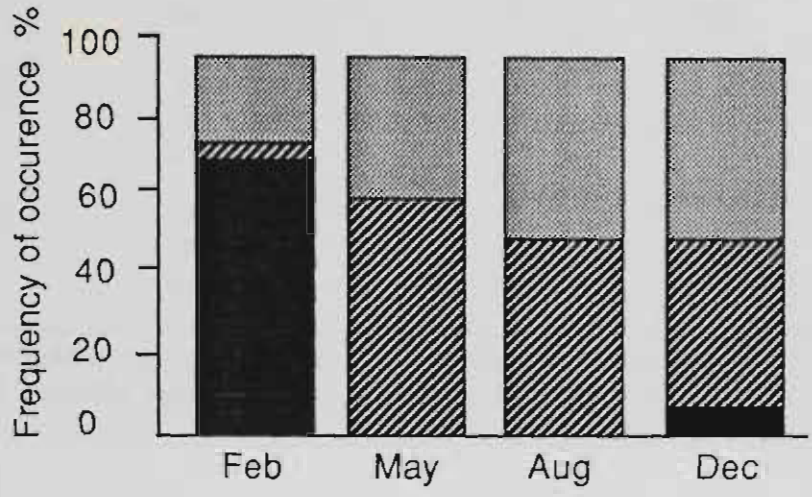


FIGURE 4.3 Frequency of occurrence of the three age classes captured in the main trap sessions

TABLE 4.9 The fertility of the trapped sample by age and year.

Year	Age class	Frequency fx	No. young Bx	No. female young per female * mx
83/84	0	25	0	
	1	67	0	
	2+	48	99	1.031
84/85	0	23	0	
	1	45	0	
	2+	31	71	1.145
85/86	0	10	0	
	1	33	4	0.061
	2+	30	69	1.150

* The mx value for age class 2+ represents an average for all cohorts greater than 2 years of age.

TABLE 4.10 The number of pouch young and age of mother for each cohort.

I.D.	Age class at 1st capture years	Number of pouch young			Change in number of PY
		1983/84 cohort	1984/85 cohort	1985/86 cohort	
L7	2+	3	2		<
L29	2+	3	4	4	>
L38	2+	1	4		>
L55	2+	2		2	=
L66	2+	3	3	3	=
L95	2+	4	4	3	<
L108	2+	3	0		<
L128	2+	4	3	2	<
L137	2+	4		1	<
L214	2+	2	2	0	=
L215	2+	1	3		>
L224	2+	2	1		<
R247	2+		4	4	=
R250	1		0	3	>
L21	1	0	1	1	=
L147	1	0	4	3	<
L210	1	0	4	3	<

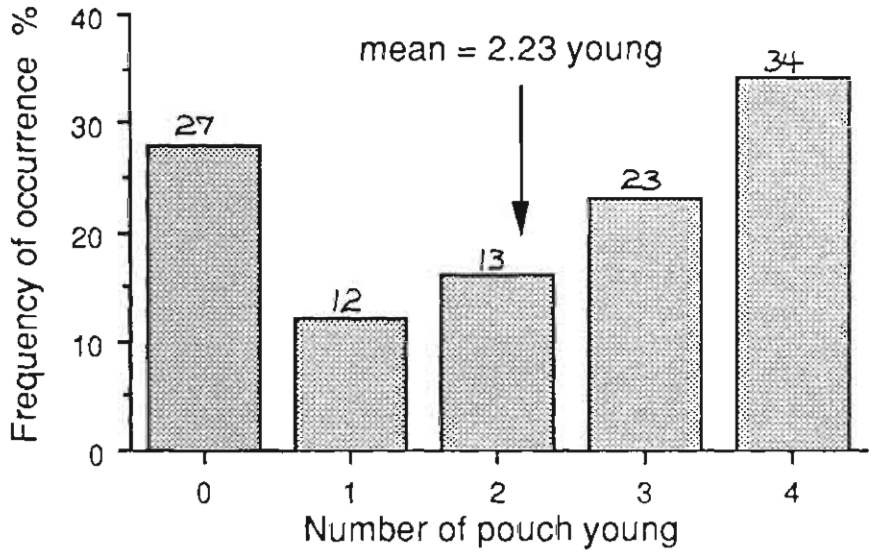


FIGURE 4.4 Frequency of occurrence of the number of pouch young of all mature females. Sample sizes above bars.

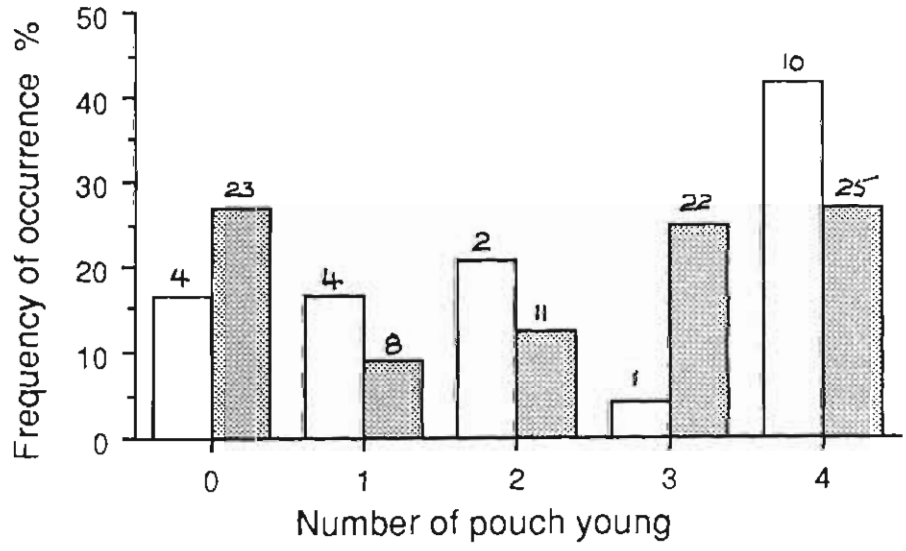


FIGURE 4.5 Frequency of occurrence of the number of pouch young of "young" (☐ 2 years old) and "old" (▨ > 2 years old) females. sample sizes above bars.

making real differences harder to detect. Therefore, the test is conservative, and the results support the occurrence of a decrease in fertility with age.

There are few data on the survival of pouch young up to weaning. Twenty-six adult females were captured in successive stages of lactation. Of these, seven (27 %) were lactating on fewer teats than when previously captured, and 19 were lactating on the same number as when previously captured (Table 4.12). Of nine animals recaptured during the period of permanent pouch emergence (PPE), two animals had lost pouch young. Therefore, there is a loss of young prior to weaning, but due to insufficient data, it is not possible to say whether the loss takes place before or after PPE .

4.3.7 DISPERSAL

The frequency of capture of transient and resident animals (male and female) in different seasons is shown in Table 4.13. Clearly, the structure of the population, in terms of residency status, showed significant changes related to the time of year. The number of transients declined in the latter half of the year, whilst the number of residents increased (Fig. 4.6).

The frequency distribution of the residents and transients was also tested for the relative occurrence of adults and juveniles of both sexes (Table 4.14). The proportion of males showed no significant variation with season . Hence, for both resident males and transient males there is no reason to reject the null hypothesis that the proportions of the age groups changes with season. The females, however, did show a significant seasonal change in proportions of adults and juveniles. These observations are summarized in Figure 4.7. The pertinent points are that the transient sector of the population was comprised predominantly of juveniles until summer when adult females contributed a significant proportion. The residents were comprised equally of adult females, males and juvenile males. Juvenile females were in the minority, particularly in the latter half of the year.

A retrospective analysis was made of all animals classified as residents and the age at which they were first captured (Table 4.15). There was no significant difference between males and females in the age at first capture. However, more females than males were captured as transient adults, but similar numbers remained to become residents (colonizers) (Table 4.16). There was *no* significant difference between the sexes in the number of animals arriving as adults and successfully colonizing the area ($G_{adj(1)} = 0.637$, $P = 0.57$). More adult females than males passed through the area without taking up residence.

TABLE 4.11 The number of pouch young recorded for all females observed during the study period, categorised against age-classes.

Age group*	Frequency of number of pouch young per female					Total
	0	1	2	3	4	
2	4	4	2	1	10	21
3	1	1	1	2	3	8
≥3	2	1	2	5	4	14
≥4	1	1	2	2	1	7
≥2	19	5	6	13	16	59
Totals	27	12	13	23	34	109

*: 2 and 3 are known age animals, ≥3 and ≥4 were caught as adults 1 or 2 years ago respectively. ≥2 are adults of a minimum age of 2 and up to the maximim longevity.

TABLE 4.12 The number of young, per mother, surviving through the stages of lactation to weaning#. Notation as in Section 4.2.3.

Year	I.D.##	Stages of lactation			Weaning
		pre-PPE	PPE	LNA	
1983	L7	3		2	
	L34	4		0	
	L29	3		3	
	L37	3		3	
	L66	3	3	3	
	L95	4		4	4
	L122	3		3	
	L128	4	4	4	
	L154	2	2		
	L214			2	2
	L224			2	2
	L80	3	3		
1984	L214		2	1	1
	L18		2	2	
	L66	3	3	3	3
	L128		3	3	
	L210		4	4	4
	R254			3	3
	L95			4	4
1985	R54	4		3	
	R247		4	4	
	L66	3		2	2
	L210	3	1		
	L128	2	2		
	R34	4	3		
	R35	4	4		

#: No. of young indicated by presence of young or no. of enlarged nipples. Where there are no records the parent was not caught in that period.

TABLE 4.13 The frequency of occurrence of transient and resident animals trapped in different seasons.

Sample	Season	Transient	Resident	G test	DF	Significance
Total	Autumn	174	128			
	Winter	63	101			
	Spring	14	64			
	Summer	28	82	64.184	3	P << 0.001
Male	Autumn	82	65			
	Winter	26	55			
	Spring	6	32			
	Summer	8	39	39.0523	3	P << 0.001
Female	Autumn	82	63			
	Winter	37	46			
	Spring	8	32			
	Summer	20	43	28.309	3	P << 0.001

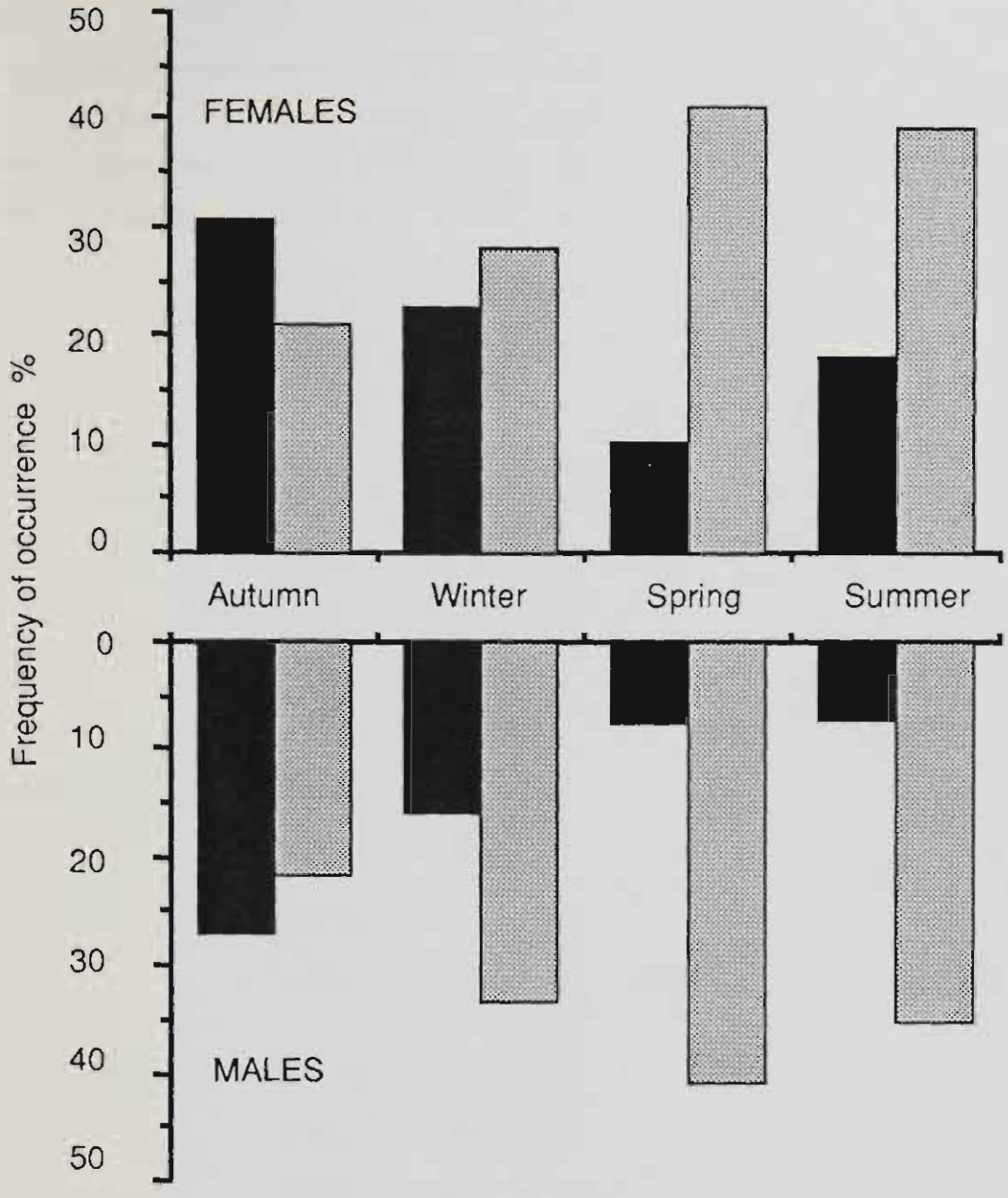


FIGURE 4.6 Relative proportions of transient ■ and resident ▨ males and females for each season. Data based on pooled samples from each year of the study. Therefore one individual may contribute to each season once and to more than one season.

TABLE 4.14 The seasonal frequency of occurence of transient and resident animals of different ages and sex.

Sex	Status	Season	Juvenile	Adult	G test	DF	Significance *
MALE	Transient	Autumn	63	19			
		Winter	23	3			
		Spring	6	0			
		Summer	5	3	5.7835	3	N.S.
	Resident	Autumn	27	38			
		Winter	24	31			
		Spring	16	16			
		Summer	21	18	1.816	3	N.S.
FEMALE	Transient	Autumn	59	23			
		Winter	31	2			
		Spring	5	3			
		Summer	4	15	31.066	3	P << 0.001
	Resident	Autumn	19	44			
		Winter	18	28			
		Spring	9	23			
		Summer	4	29	7.603	3	P = 0.0546;

* NS: Not significant.

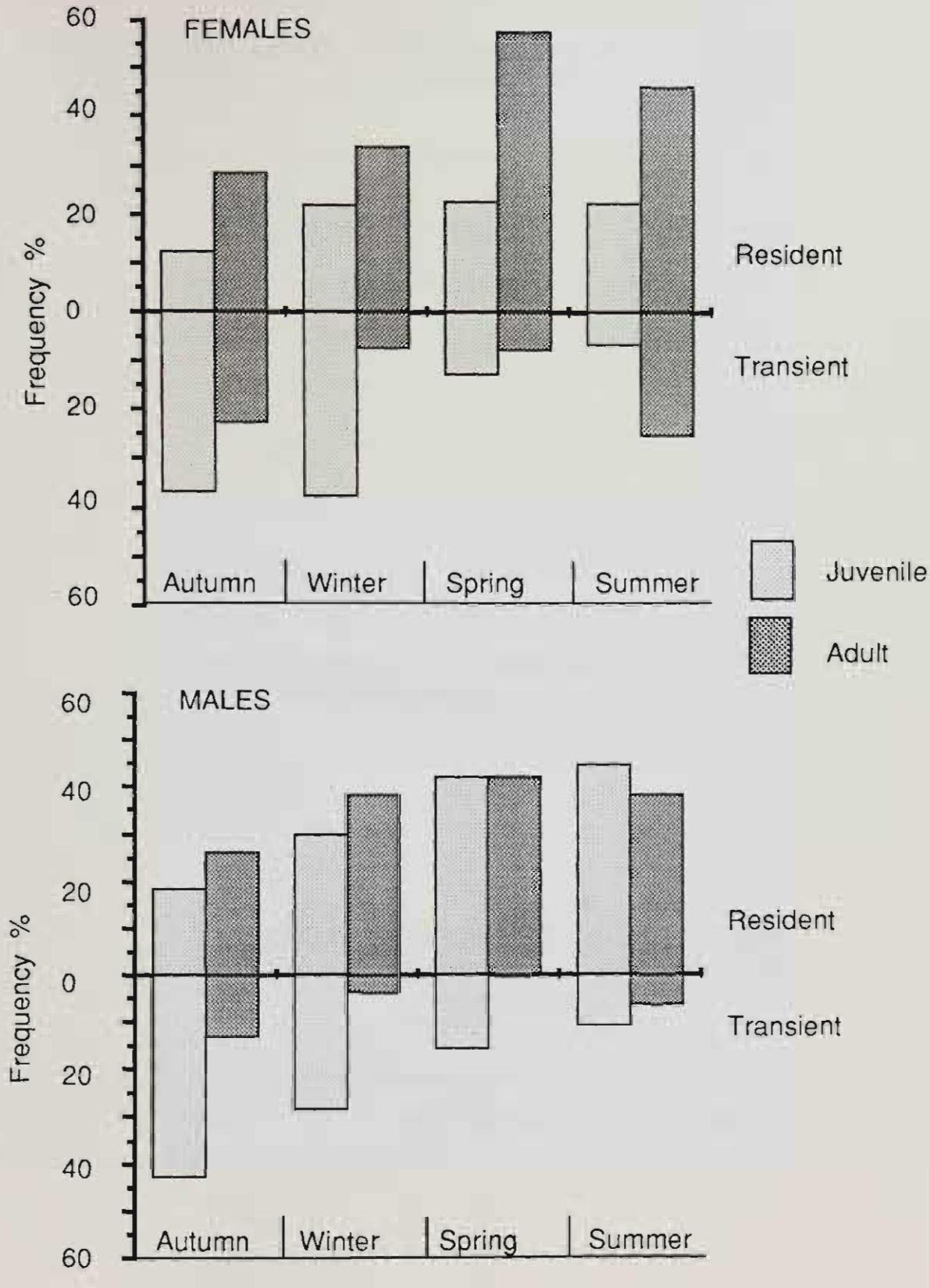


FIGURE 4.7

The relative proportions of residents and transients plotted according to sex and age for the four seasons.

TABLE 4.15 The frequency of occurrence of adult residents and the age at first capture.

Age at first capture	Female	Male
0	6	3
1	16	17
2+*	12	10
2+	7	5
Total	41	35

*: Adults caught in the first trap session that remained as residents.

TABLE 4.16 The number of animals that entered the population as adults and remained to become residents.

Sex	No. entering	No.residents
Female	23	7
Male	7	5

The capture histories of the resident animals, caught initially as either adults or juveniles, are shown in Figures 4.8 and 4.9 respectively. It is evident that more adult females show a discontinuous residency in the population compared with males (Fig. 4.8). This trend is also present with the juveniles (Fig. 4.9). In total, 29 devils were caught in every year of the three year study, and 65 devils in two years, equally split between the sexes.

Of the 29 devils which showed a gap of ≥1 year between successive captures, there were 22 females and only seven males. Within the female component there were both juvenile and adult animals. Some juvenile females (e.g. L17, L21, L108, L147 and L173) were recaptured in their first year of maturity. Others (e.g. L90, L107, L128, L138 and L184) appeared again as three or four year-olds, that is, in their second and third year of maturity. Animals first caught as adults showed similar forms of behaviour. Two animals, L55 and L137, were recaptured two years after the initial captures. The other adults, L38, L220 and R40, were caught again after one year.

Of the juvenile males, only one (L144), was recaptured after two years, whilst L178, L183, R15 and R24 were caught again after one year. One mature male (L59) returned after an absence of one year. There are insufficient data to compare the movements of juvenile and adults in and out of the population, but there is a difference between the number of continuous and discontinuous resident males and females. More females display a discontinuous occupancy of the study area than do males.

The length of occupancy by residents appears to be similar for both sexes. Of the 12 adult males known to be resident in the study area in 1983, eight were still being recaptured in 1985. Eight of the 17 females resident in 1983 were also still resident in 1985. The resident juveniles showed a similar pattern with nine of the 19 females present in 1983 still being caught in 1985, and five of the 18 males resident in 1983 still resident in 1985. The number of animals trapped and identified as residents was similar for both sexes (Table 4.17). In 1984, there were 25 adult males and 22 adult females resident in the population. These are minimum figures based on the trapping record. In 1985, there were 35 adult males and 33 adult females resident in the population. Over the complete study period a total of 77 male and 71 female residents were identified. The number of residents was similar between years and sexes.

The fates of animals caught in their natal area are shown in Table 4.18. The females tended to remain in their natal areas whereas the males did not. Two of the six females were recaptured as breeding adults, whilst none of the seven males were captured again.

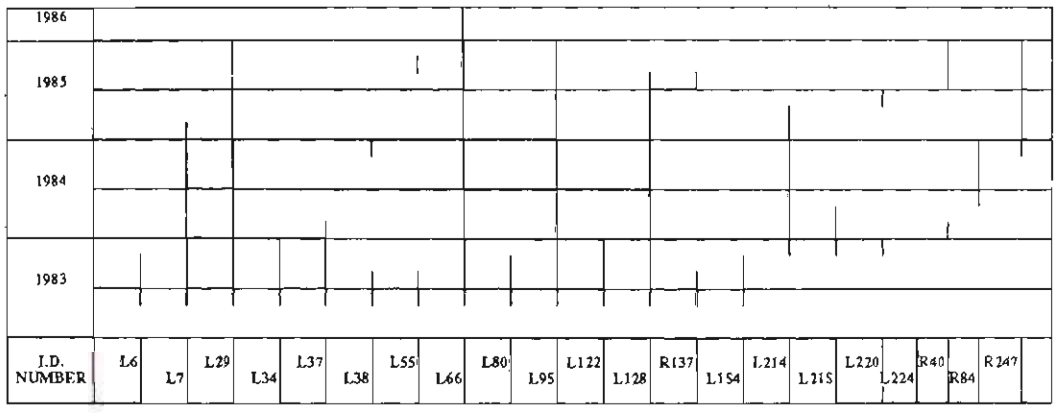
TABLE 4.17 The number of residents captured during the study period and the age at first capture. The number of juveniles that were present as adults is also shown.

Sex	Juvenile	Juv - adults	Adult	Total
Male	60	28	17	77
Female	51	28	20	71

TABLE 4.18 Recapture history of animals marked prior to the end of weaning (dependant on mother)

Year	Age captured	Female	Male
1983/1984	dependant	6	7
	1	5	0
	2	2	0
1984/1985	dependant	7	4
	1	4	1
Total captured		13	11
Total recaptured		4	1

FEMALES



MALES

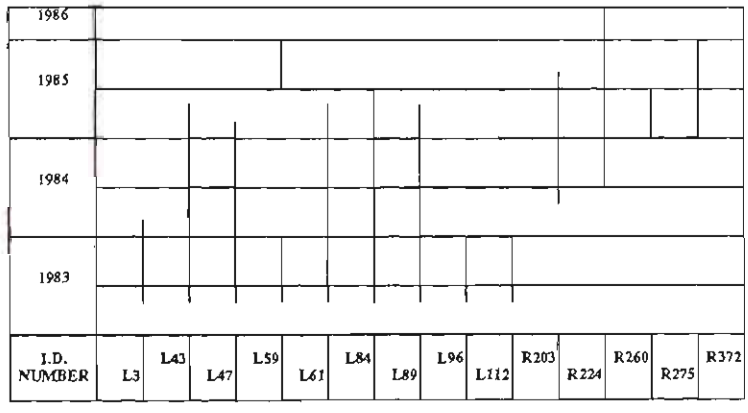


FIGURE 4.8

Examples of the capture histories of adult residents.
Vertical lines represent the presence of the animal in the area, with the inividuals identification number at the bottom.

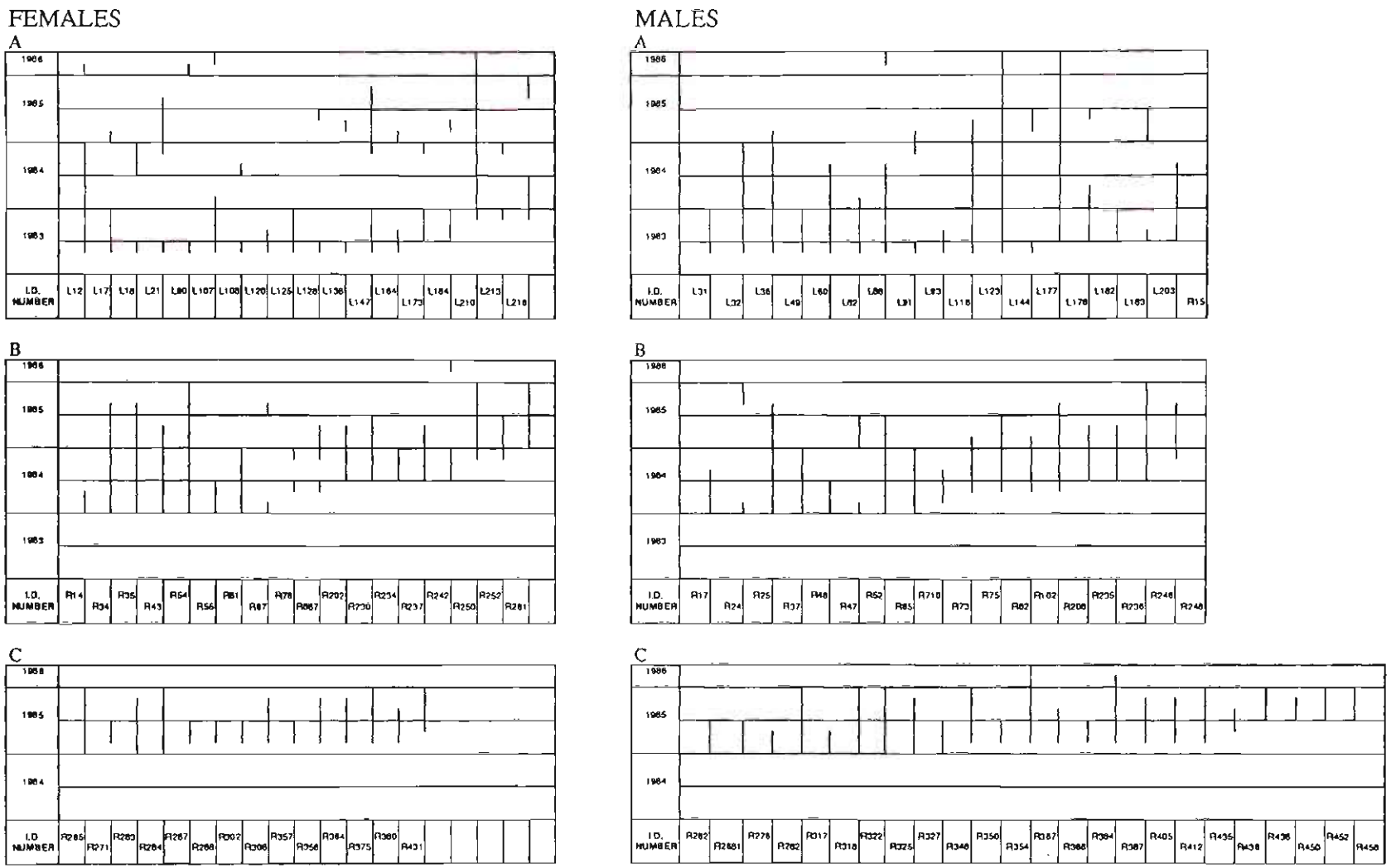


FIGURE 4.9

Examples of the capture histories of the young devils of the 1984/85 cohort (A), 1983/84 cohort (B), 1982/83 cohort (C). Notation as in Fig. 4.8.

There was a significant difference in the number of pouch young carried by resident and transient females (Z corr= 3.288 > $t_{0.05(2)\infty}$ = 1.960). The transient females carried fewer young, and many carried no young, compared to resident females (Table 4.19). There was also a significant difference in the number of pouch young carried by continuous residents versus discontinuous residents (Z corr= 2.382 > $t_{0.05(2)\infty}$=1.960), the continuous residents carrying more pouch young (Table 4.20).

4.4 DISCUSSION

4.4.1 SEX RATIO

The five factors which could affect the calculated sex ratio for a population sampled by trapping are: 1) the sex ratio of neonates; and the difference between males and females with respect to 2) growth rate, 3) survival, 4) trappability and 5) movement (Myers & Krebs 1971). Populations of mink (*Mustela nivalis*) appear to be male-biased as a result of differential trappability and movement (King 1975), and Clout & Efford (1984) reported similar observations on the Brush-tailed possum (*Trichosurus vulpecula*) in New Zealand. The sex ratio of Tasmanian devils observed at Mt. William National Park in the present study showed no significant deviations from parity among pouch young, between age classes, seasons or years. This indicates that none of the factors mentioned above were significantly influencing sex ratios in devils.

There is, however, the slightly skewed sex ratio in spring and summer of the animals of age class 2+. This deviation from parity, although not significant at the 5 % level, warrants further discussion due to the importance to population analyses of any biased trapping response. Accepting that the juvenile sex ratios and mortality are the same for both sexes, Kimball's method (Hanson 1963) can be used to calculate the expected sex ratio in the age class 2+ portion of the population. Kimball's method uses the relationship between sex and age ratios to calculate the sex ratio of a population from the age ratio of the same population. Assuming that the age ratio is correct, the expected sex ratio was calculated (Table 4.2). This differs from the observed ratio in spring and summer. Because the sex ratio of all classes does not change, survival was not selective on sex. Therefore, the possible bias that may be present at these times may be a result of differential trappability and movement of the sexes.

In this study, the sex ratio did not vary from parity to a significant degree. However, biased sex ratios have been reported in other Tasmanian devil populations. Guiler (1970b) commented that there was a female-biased sex ratio in a trapped sample of devils at Cape Portland, near Mt. William National Park. However, re-analysis of Guiler's data shows that this apparent bias in the sex ratio was not significant (G_{adj} =

TABLE 4.19 The number of pouch young carried by adult resident and transient devils.

Number of pouch young	No. of adults	
	Transient	Resident
0	8	1
1	3	2
2	1	5
3	1	7
4	2	8
mean	1.1	2.8

TABLE 4.20 The number of pouch young carried by discontinuous and continuous residents.

Number of pouch young	No. of resident adults	
	Discontinuous	Continuous
0	7	1
1	6	0
2	4	4
3	4	8
4	8	9

0.548, P >> .05). Guiler (1978) later suggested that there is also a sex ratio bias amongst juvenile devils at Granville Harbour, S. W. Tasmania. This conclusion is to be expected because he used body mass to estimate age, and pooled all data for the year. In the present study females gained weight at a slower rate than males (Fig. 4.10) and as a result a pooled sample for a year would produce a sex ratio biased towards females amongst the juveniles (Pm= 0.36, G_{adj}=15.283, P << .05).

Hughes (1982) observed a female bias in a sample of 75 pouch young devils (Pm = 36.0). This is difficult to explain without more information on the population structure and a larger sample size. Of possible relevance, however, is that Hughes (1982) has selectively culled animals, mainly females, from his study population in the Fingal Valley, eastern Tasmania, for 10 years. In addition, the farmers in the area also cull devils under crop protection permits (S. Mc Shane pers. comm.). Hughes (1982) only recaptured five out of 200 marked animals (2.5 %) one year after initial marking. This suggests that the demography of that population may be very different from that of the present study area, where up 30 % of the animals marked in one trapping session were recaptured in the following year. It is possible that the observed sex ratio in Hughes' study is as a result of the artificial influence of culling of the population.

4.4.2 SEASON OF BIRTH

The median birth dates are similar for all three years of the study (Fig. 4.2). Births are highly synchronized, occurring over a three week period. The gestation length for the devil is 21 days (L. Hughes pers. comm.) and copulation takes place from approximately February 20 to the end of March (Fig. 4.2). All young have been denned by the middle of August and weaning occurs in the middle of January, approximately nine months after birth. The results of this study differ substantially from those of Guiler (1970a), who states that the young are first left in the den at 105 days and that weaning takes place at 240 days of age. In the present study, young were first left in the den at about 130 days and were weaned at approximately 278 days. Guiler's results, however, were based on animals in captivity and the difference is probably due to the readily available food supply of captive animals, resulting in faster growth rates and earlier weaning. The stages in the development determined in the present study are summarized in Figure 4.11.

4.4.3 FERTILITY

There is evidence to suggest that fertility decreases with age. The change in fertility was manifested in the frequency of occurrence of the numbers of pouch young for the younger (2 year-old) and older animals (≥ 2 year-old), the number of pouch young carried changing with age of mother. More of the older animals carried three pouch young than did the younger animals. The older animals also had a higher

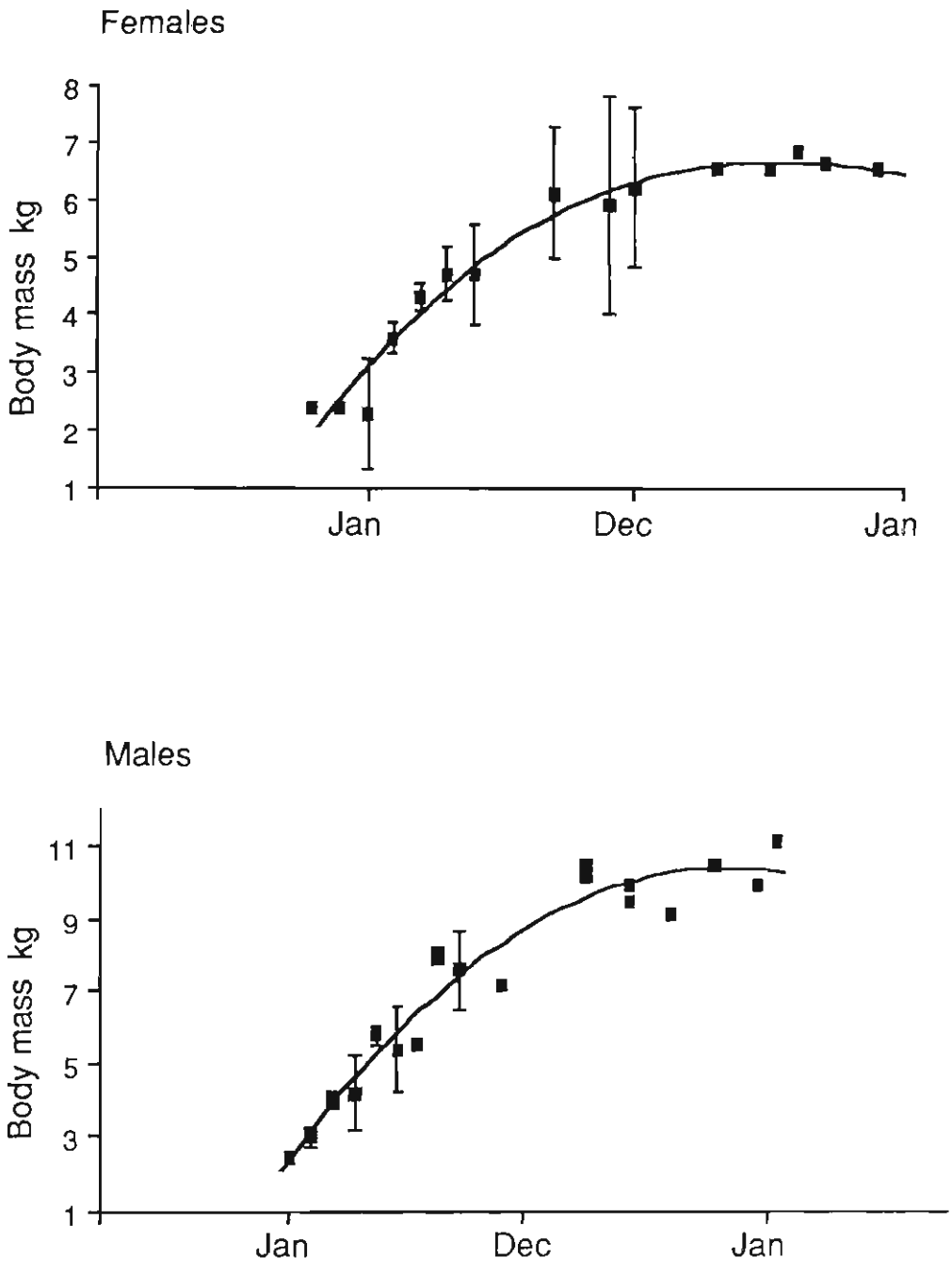


FIGURE 4.10 Growth curves of body mass for males and females (95 % confidence limits shown when n > 3)

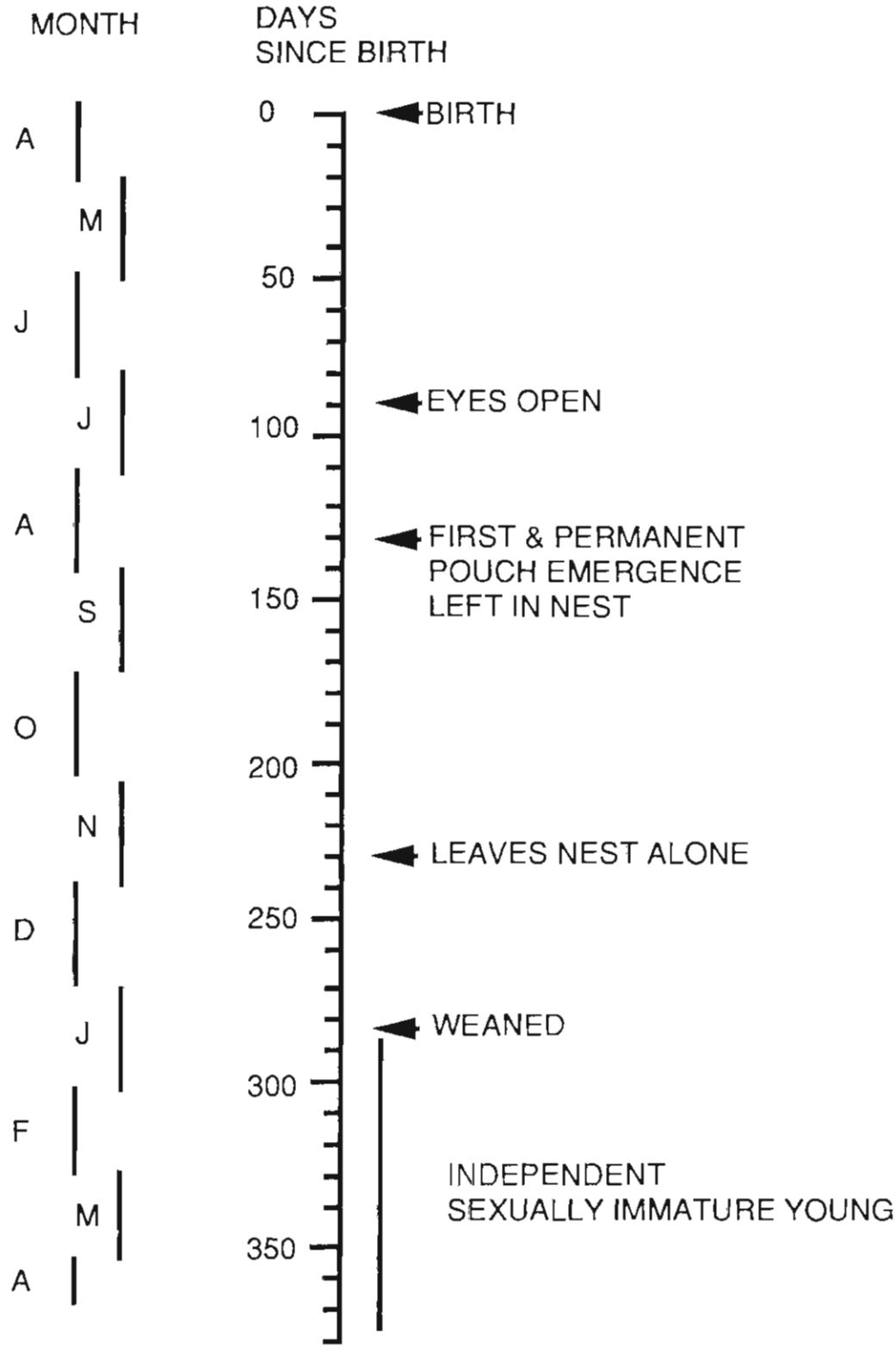


FIGURE 4.11
Stages in the functional development of the young and pattern of parental care.

frequency of no pouch young (Fig. 4.5, Table 4.11). There was an increase in reproductive failure (in terms of birth of young) and a reduction in the number of pouch young with age. A similar pattern of decrease in reproductive investment was found in the Eastern Quoll (*Dasyurus viverrinus*) (Godsell 1983). There is evidence of reproductive failure after birth, but there are insufficient data to detect any change with age. Twenty six females carrying young were recaptured within a single season. Of these 27 % lost young, suggesting that reproductive failure may be higher than has been previously considered (Russell 1982a). It has been shown in *D. viverrinus* that if young are lost after being denned, the remaining young can keep all the lactating teats active (Green & Eberhard 1983). Thus, it is likely that the loss of young after denning will not be reflected in a reduction in the number of lactating mammary glands. Therefore, estimates of reproductive failure after birth that are based on numbers of lactating mammary glands may be seriously under-estimated.

4.4.4 AGE DISTRIBUTION

The age distributions showed no significant differences between the sexes. There were no significant differences between years except for the August sample, where there was a trend from more juvenile males in the first two years to more females in the last year (Table 4.8). There is no obvious reason for this. There was no overall difference in the age distribution of the sexes within the August sample when the data for all three years were pooled. In addition, because of the low G value (6.816) it was considered justified to pool the sample for an overall analysis.

There was a large influx of weaned young into the population at the beginning of each year. These animals attained juvenile status in April and remained the predominant fraction of the population until early summer (Fig. 4.3). In early summer the population was equally composed of adults and juveniles but by late summer the influx of weaned young swung the balance towards juveniles again.

4.4.5 MORTALITY

It is extremely difficult to distinguish between mortality and emigration (Caughley 1977, King 1980). Caughley (1966) points out that life tables based on less than 150 animals can be inaccurate, and that death and emigration are complicating factors. In the present study there has been no attempt to distinguish between emigration and death. Mortality is used here to indicate the loss to the population under study, whether it be through emigration or death. In an attempt to improve the accuracy of the mortality estimate two methods of Caughley (1977) were used. The first relies on the capture history of animals, marked as juveniles, of known age. The second relies on a sample taken in the last year of the study when there were more known age animals. The latter can be inaccurate because it includes the total year's captures,

whereas only those captured at, or near, the breeding pulse should be used (Caughley 1977). The aim of using this method is to "back up" the first.

The mean annual mortality rates were similar for both sexes. There was 80 % mortality between the first and second year of life. The mortality rate then decreased to < 20 % for females and 50 % for males (Table 4.6). Tasmanian devils can live for more than five years in the wild (E. Guiler pers. comm.). In the present study, age-specific mortality could not be assessed beyond three years of age. The number of animals in the population in 1985 that could only be aged as adults (≥ 2 years old) was similar for males (n = 14) and females (n = 12). Of these, 10 were definitely greater than two years old in both sexes. The sex ratio of devils has been shown to be equal, hence both males and females have the same number of individuals contributing to the 0 age class. There was no difference in the age structure up to 3 years of age ($G_{(2)}$ = 0.6134, p=0.741), and the number of animals greater than 2 years of age is the same for both sexes. Therefore, the higher mortality rate for males between two and three years of age is probably not significant, but merely an artefact of the sample size from which the mortality rates were calculated.

Caughley (1966, 1977) showed that mammals are characterized by a "U-shaped" mortality curve with increasing age. There is high juvenile mortality followed by initially low mortality and then progressively higher mortality. Guiler (1978) suggested that devils showed a similar pattern. Because of the short duration of the present study, relative to the lifespan of a Tasmanian devil, complete life tables could not be calculated. However, in an attempt to see if this same curve may apply to the population in this study, the data for both sexes were pooled and subjected to theoretical mortality rates. In the pooled sample there were 87 one year olds, and a total of 62 animals greater than two years old. The average qx value from the life tables is 0.79 (Table 4.6) and this was applied to the one year old group. A series of progressively higher mortality rates was then applied to the older animals. The cut-off point was taken when the total number of animals in the theoretical sample equaled 62 or more (the number in the real population) and when the animals reached six years of age, the maximum longevity for devils in the wild (Guiler pers. comm., information from Mole Creek Wildlife Park). Table 4.21 shows the results of this modelling exercise. If the population showed a " U- shaped" qx curve, a mortality rate of 0.3 would be too high because the expected number of animals (62) would never be attained. A qx of ≈ 0.2 would produce the expected number of animals and necessitate an increase in qx in the later years of life to produce zero animals by six years of age.

TABLE 4.21
Model showing application of theoretical mortality rates (in italics) to life history data. Assumptions in the model are listed below.

Age years	No. devils remaining in each age group	Mortality rate applied qx
1	**87**	**0.79**
2	18.3	*0.10*
3	16.5	
4	14.9	
5	13.4	
6	12.1	
No. devils > 1 year old	75.2	
1	**87**	**0.79**
2	18.3	*0.20*
3	14.6	
4	11.7	
5	9.4	
6	7.5	
No. devils > 1 year old	61.5	
1	**87**	**0.79**
2	18.3	*0.30*
3	12.8	
4	9	
5	6.3	
6	4.4	
No. devils > 1 year old	50.8	

Assumptions and known values (in bold) include:
1. no. of devils 1 year old = 87
2. no of devils > 1 year old = 62
3. qx between 1-2 years old = 0.79
4. Maximum age = 6 years

4.4.6 DISPERSAL PATTERNS

Examination of trapping records has shown that devils have a variety of movement patterns, according to the sex and age of the animals involved. The patterns of movement do not strictly comply with the commonly used definitions, such as breeding dispersal and migration. Therefore, for clarity, I have described and defined the patterns observed. Where appropriate, the new terms are explained in the context of traditional terminology.

There were three types of movement pattern readily identifiable from the trapping record:

1.Animals born in the study area showed male-biased natal dispersal and female philopatry.

2. Animals that were trapped in one trap session and never again (transients).

3. Resident animals that were trapped in more than two trap sessions. Because of the design of the sampling methods these animals were present in the study area for at least four months. Residents were further classified as continuous or discontinuous (see section 4.2.7).

The detection of dispersing animals relies on the identification of dispersers (Dueser *et al.* 1984). In small mammal studies, dispersers can be identified using body mass as an indicator, or exclusion grids and removal techniques are sometimes employed (Myers & Krebs 1971, Dueser *et al.* 1984, Tamarin *et al.* 1984). Dispersers can be identified outside the study area by trapping or radio-telemetry. These methods were not used in this study. Body mass would be meaningless as an identification of dispersers in a species such as the Tasmanian devil that ceases mass gain early in its life. The vacuum grid and other grid techniques are impractical in a large animal with a relatively large home range. In this study pouch young were not marked because the rate of capture of females carrying young was too low to provide sufficient return of weaned young. Hence the detection of dispersal relied upon the trapping record of animals after weaning.

In this study, patterns of dispersal were detected from the capture record of each trap session, where animals were classified as residents or transients, based on retrospective examination of their capture histories. This protocol provided information on the number of resident and transients of either sex and age-group, and the continuity of the residency pattern with time. It has already been shown that the sex ratio is even between the years and within age classes. Furthermore, mortality is similar for males and females, and the age distribution of the population changes with season at the same rate for both sexes. It is logical, then, to expect that a variation in the proportions of male and female residents and transients is the result of dispersal.

Analyses of the resident status of captured animals raises three points of relevance:

1. The proportions of resident and transient males and females is the same, and both sexes change with season (Fig. 4.6). This trend is similar to that shown for the age distribution data. Mortality and/or dispersal was taking place in both sexes by spring.

2. The resident portion of the male population was composed equally of juveniles and adults, whereas the female residents were dominated by adults (Fig. 4.7). There was a significant difference between the number of juvenile male and female residents in summer, males being more numerous (Appendix 6).

3. The proportions of both male and female transients in the population decreased in summer. There was a significant influx of adult females as transients in summer (Fig. 4.7).

In this study it has already been shown that juvenile devils can be captured before the end of lactation, and therefore are probably in their natal area. Examination of the subsequent capture history of the animals captured prior to weaning showed that most females were recaptured in the study area and most males were not (Table 4.15). The females therefore showed natal philopatry while the males dispersed. As stated above, there were more male than female juvenile residents in the population, and the number of transient juveniles was the same for both sexes and decreased throughout the year. It is therefore plausible that the dispersing males contribute to the resident population that is decreased by mortality of the philopatric females, and that dispersal continues until summer, when the number of transients decreases.

The number of males (n = 5) and females (n = 7) that entered the population as adults (after 1983) and remained to become residents was similar. There were, however, 16 adult females and only two adult males that were captured only once and therefore classified as transients. Most of these females were captured in summer. The fate of the animals that did not remain to become residents is unknown, but there were clearly more females than males showing this form of dispersal.

In addition to the capture of adult transients, a large proportion of the resident females and some males were absent from the study area for more than a year (Figs 4.8 and 4.9). Migration, as defined by Caughley (1977), is the movement of young away from their natal area and back again to breed. Behaviour broadly similar to this was recorded for 17 females and six male Tasmanian devils . However, in this study, this form of dispersal cannot be called migration because there were no observations to verify that the males did in fact breed, and there were also no data to show that the breeding males or females were born in the area. Therefore, this form of movement is

referred to as discontinuous residency. Breeding dispersal is defined by Greenwood (1980) as the movement of individuals between successive breeding sites. The pattern of movement shown by some adult resident devils, where they are absent from the trapping record for more than a year, does not comply with the requirements of this definition. There are no data to show whether the animals involved were moving between breeding sites. Therefore, for the juveniles, this form of movement will be referred to as discontinuous residency. More females than males showed discontinuous residency patterns and the fertility of female discontinuous residents was lower than that for continuous residents (Table 4.19).

Discontinuous residency is probably linked to the observations of the number of resident and transient animals in the population. Figures 4.8 and 4.9 show that many of the females caught in the first trap session displayed a discontinuous pattern of residency. The apparent lack of this pattern with the juveniles caught in 1984 is a result of the duration of the study and the definition of a " gap " in captures. For a " gap " to be present, I only accepted those animals that were not caught in at least four consecutive trap sessions. The animals caught in 1984 therefore had less chance, in real time, to be recaptured one year later and classified as discontinuous residents.

Adult females that showed a discontinuous pattern of residency in an area, other than the study area, probably contributed to the animals classified as adult transients. The pattern of discontinuous residency shown by the juvenile females would lower the number of juvenile female residents, relative to the males, but should increase the number of animals classified as transients. This increase is not present because these females were not in the population for a year or more, so when they returned they were adults. Therefore, as adults, they contributed to the adult data set, not the juvenile. There was an influx of transient adult females in summer and a decrease, relative to males, of resident juveniles at the same time.

In order to understand the adaptive nature of dispersal patterns of a particular species, it is necessary to measure the reproductive success of philopatric, and dispersing animals. The costs and benefits of dispersing and philopatric behaviour should be measured in terms of reproductive fitness (Waser & Jones 1983, Clout & Efford 1984, Caughley 1977). This is difficult to measure because of the relatively short duration of the study and the difficulty of comparing philopatric individuals with dispersing individuals which are moving away from the study area. An indirect measure of the advantage of philopatry to females can be obtained by comparison of the resident with the transient individuals. Resident females had higher fertility rates than transients. This suggests that there is an advantage in terms of reproductive fitness to females remaining resident in one area.

The cost of dispersal to juveniles was measured by comparing mortality rates of individuals that dispersed into the population with those that were born on the study area. The samples are small but there was a higher rate of mortality of females which dispersed compared with those which stayed in their natal area. However, this was not the case for the young males.

Male-biased natal dispersal, and the resultant natal philopatry of females, is common in mammals and there has been much debate regarding the causes (Baker 1978, Greenwood 1980, Dobson 1982, Horn 1983). This type of animal movement has been recorded in many Dasyurids including *D. viverrinus* (Godsell 1983), *Antechinus stuartii* and *A. swainsonii* (Cockburn *et al.* 1985). Greenwood (1980) and Dobson (1982) have argued that sex bias in dispersal is the consequence of the type of mating system. Greenwood (1980) argues that a " mate defence" system would show male biased dispersal. Similarly, Dobson (1982) argues that competition for mates by males of both polygamous and promiscuous species would produce a male-biased dispersal. Their work was based largely on the frequency of sex-biased dispersal in mammals (male-biased) and birds (female-biased).

Inbreeding avoidance (usually used in this context to mean incest avoidance) has also been suggested and shown to provide an adequate explanation for natal dispersal (Shields 1983, Cockburn *et al.* 1985). Shields (1983) argued that, by limiting the effective population size, philopatry results in inbreeding at appropriate intensities to promote reproductive success (Wallace effect). The assumption of a single cause for a phenomenon often leads to the rejection of important causal factors and Dobson & Jones (1985) go on to suggest that inbreeding avoidance, competition for mates and environmental resources may all play a role in causing dispersal. In a study of proximal causes of natal dispersal in ground squirrels, Holekamp (1986) concluded that a complex suite of variables causes natal dispersal but that dispersal reduces family incest, optimizes inbreeding, and improves access to mates. Identification and discussion of the proximal causes of dispersal and the role they play in the social organization of the Tasmanian devil can only be fully developed after the dispersion and mating system have been described in the following Chapters.

Detection and interpretation of the pattern of dispersal of Tasmanian devils has been restricted by the difficulty of distinguishing between emigration and mortality and by small sample sizes. There is evidence to suggest that male-biased natal dispersal takes place. Residency is not continuous for all animals. More females showed a discontinuous pattern of residency than did males. Many female Tasmanian devils show a form of dispersal in which they continue to move in and out of the population throughout their lives. The males, however, take up a more permanent residency as

juveniles. These forms of behaviour are referred to as discontinuous and continuous residency respectively. There are animals that were only caught once and referred to as transients. There were significantly more females than males showing this form of dispersal. The male transients became continuous residents whilst most of the females were never trapped again.

4.5 SUMMARY

1. The sex ratio showed no significant deviation from parity among age groups, years or seasons.

2. Females were sexually mature in their second year with 81% carrying pouch young. The mean number of pouch young per female was 2.3. There was no change in the number of young produced during the study period. There is evidence to suggest that fertility decreased with age. At least 27 % of mortality occurred before weaning.

3. The breeding season was characterised by a highly synchronized birth-pulse taking place over a three-week period and was similar for all three years. The median birth date was April 10, with copulation taking place from February 20 to early March.

4. The young left the pouch in early August (PPE $\approx$ 130 days of age) and stayed in the den until they first emerged in November (LNA $\approx$ 227 days of age). Young were weaned by early January ($\approx$ 280 days of age).

5. There was a predominance of juveniles in the population until early summer when adults constituted the major part of the population.

6. Juveniles suffered about 80 % mortality, whereas annual adult mortality was approximately 20 %. Mortality probably increases in the older animals.

7. The young females tended to remain in the natal area whereas more of the males dispersed. The mortality rate of animals philopatric to their natal areas as compared to dispersers was higher for females than for males.

8. The number of transients relative to residents decreased through the year. Juvenile males and females contributed equally to this group. The number of adult female transients increased in summer.

9. There were similar numbers of resident adult males and females throughout the year. The number of resident juvenile females decreased relative to the males by summer.

10. Resident females had higher fertility rates than did transients.

11. Discontinuous residency was identified in both sexes, with more females than males showing this form of movement. Females classified as discontinuous residents had a lower fertility than continuous residents.

CHAPTER 5

BEHAVIOURAL AND FEEDING MECHANISMS CONTRIBUTING TO THE SOCIAL ORGANISATION OF THE TASMANIAN DEVIL

5.1 INTRODUCTION

Central to the functioning of a society is the communication system used by members of the society. This communication takes the form of vocalizations, scents and visual displays. Communication in the Dasyuridae has been reviewed by Croft (1982), who suggested that because the majority of species are solitary and nocturnal, scent and vocalizations were more important forms of communication than visual displays, though visual displays were used by all species to varying degrees. Croft (1982) emphasised that the communication portfolio of the Dasyuridae was well developed with respect to the niche that they occupied, and that their communicatory behaviour was as well developed as in the eutherians.

Various aspects of the behaviour of the Tasmanian devil have been described from captive studies. Early descriptions of the agonistic behaviour, vocalizations, maintenance behaviours and development with age were made by Le Souef & Burrel (1926) and Fleay (1935, 1952). Ewer (1968, 1969) described visual, vocal and scent signals used by devils and their mode of killing prey, which she likened to that used by the Felidae, where a simple neck bite is delivered to the nape of the neck. Buchman & Guiler (1977) interpreted the killing behaviour as inept and did not confirm Ewer's (1969 a,b) observation of the use of a neck bite. Buchman & Guiler (1977) give a detailed account of communication in the devil describing visual displays, vocalizations and the use of scent marking via displays such as cloacal drag, a behaviour which Ewer (1968) described as anal drag and Eisenberg *et al.* (1975) as ano-genital drag. Vocalizations were thoroughly investigated by Eisenberg *et al.* (1975), who described 14 sound forms which they suggested were based on four syllables, namely click or cluck-like sounds, coughs or snorts, growls and hisses. They also describe the copulatory behaviour of the devil. Copulation lasts 4 to 8 hours, the male using a neck grip to mount the female and neck threats to inhibit aggression. Eisenberg *et al.* (1975) interpret this as being homologous with a similar display used by the Canidae. The devil also uses a yawning display which, as with the neck threat, has a homologous display in the eutherian *Papio anubis* (Ewer 1968). These similarities between communication pathways used by the devil and some eutherians were investigated by Eisenberg & Golani (1977). They showed that there were many similarities between the postures used by devils and *Canis aureus*, but cautioned that differences were also discernible when close examination was made of the motor interaction sequences of the two genera. In addition, they identified a graded series of vocalizations in the devil

which related to the intensity of the form of the interaction and the distance between the dyad.

Buchman & Guiler (1977) found that devils which were cage mates in captivity established dominance hierarchies after a series of agonistic encounters. They suggested that in the wild, individuals that feed together regularly may form truce relationships within feeding groups that are partly closed to outsiders. The existence of dominance hierarchies and the interrelated group formation in devils in the field has not been proven. If it exists, there are important implications to the social organisation of devils, particularly with respect to population regulation via the inter-relationship of resource dispersion and group size (Bradbury & Vehrencamp 1976).

It is apparent therefore that an extensive literature and understanding of communication methods and social behaviour of devils in captivity exists. An understanding of these systems in the wild is critical to a description of the social organisation of the devil and an understanding of how this relates to the resources available.

Studying the forms of communication that contribute to the social organisation of a species such as the Tasmanian devil that is small, solitary, fast moving, nocturnal and wary of humans is fraught with difficulty. It is rare to see a devil exhibiting any behaviour in the field other than fleeing across a road. In an attempt to overcome these problems devils were enticed into social situations with conspecifics by the placement of food in the field situation.The subsequent behavioural and feeding mechanisms of the animals whilst in contact with each other could then be observed. In this way the obvious difficulties of extrapolating social behaviours from captive studies, which have been the principal method of studying behaviour in dasyurids, were avoided. The method of investigation used in the present study however, does place some constraint on interpretation of data as all communication was essentially measured around conspecific aggression in response to food. However, being solitary animals, the intraspecific behaviour of devils is mainly restricted to encounters of all cohorts of the population around food, relationships between mother and young, and pair formation during courtship and mating. Therefore the conclusions drawn in this Chapter, whilst being restricted to one form of intraspecific interaction, are relevant to much of the social organisation of the devil. This is particularly so because interactions around carcasses are the one situation when many members of the population communicate. This Chapter describes the first examination of the behaviour and feeding mechanisms relating to the social organistion of the devil in the wild.

5.2 METHODS

5.2.1 MARKINGS

The position and extent of white pelage on trapped devils was recorded. The extent of the white markings was measured by dividing each potential mark site (rump, chest, left and right shoulder) into four equal squares and one extra on either shoulder joining the shoulder markings to the chest markings. The maximum possible area of white marking was similar for each site. The degree of marking at each site was then quantified by allotting a score of 1 to each square more than half covered in white pelage and 0.5 to a square with half or less white pelage. Thus the degree of white markings per individual was corrected for body size allowing comparison across size ranges. The minimum score possible was 0 for a black animal and 18 for an animal with full markings.

The frequency of occurrence of devils with white markings was calculated and used to describe the variation in the position of colouration for the total sample and for males and females separately. The scores describing the extent of the white markings were compared on the frequency of occurrence data of animals of different sex and resident status (Kolomogorov Smirnov test for ordinal data). The data were grouped to increase all frequency of occurrence values to more than five.

5.2.2 SOCIAL INTERACTIONS AROUND FOOD

Observations were made on the social interactions between animals feeding or attempting to feed on carcasses of Bennett's wallaby and wombats. These carcasses were placed in a paddock approximately 15 m from the edge of the tea-tree scrub running along a creek in the south of the study area. A hide was positioned 15 m from the carcass. The carcasses were always ≈ 20 kg in weight and were tied with thin wire to a stake imbedded in the ground to prevent animals dragging them away. Lights were set up on the left and right hand side of the carcass to reduce the amount of light shining directly at the observer or the animals which usually approached the carcass from the bush edge. The lights used were motor vehicle reverse lights powered with a 12 volt battery. The lights were connected to a switch box so that lights could be switched on one at a time to reduce the glare. The lights were switched on only after one feeding animal started to interact with a second animal. No animals left the carcass site when lights were switched on, and soon after intense interactions began there were animals moving within the white light, around the hide, and through the hide under the observers chair. By positioning the lights, reducing the glare and waiting for intra-specific interactions to start, the use of lights had little perceptible affect on the behaviour of the animals. Observations were made with the naked eye and 7 x 50 binoculars. Carcasses were placed in the paddock during the day and observations

were usually made from the arrival of the first animal until the carcass was consumed. These trials were run on 15 separate nights.

The first five nights of observation were used to create an ethogram of the behavioural postures which were used by the sender and the recipient during dyadic displays associated with feeding. The recipient was defined as the animal feeding and the sender as the animal to which the recipient reacted. The behavioural postures were considered as events as they were instantaneous behaviours contributing to a state of aggression (Altmann 1974). The ethogram was coded to allow for rapid recording of events.

On the remaining 10 nights the interactions between the recipient and all senders were recorded as they occurred by focal animal sampling (Altmann 1974). The focal animal in this case was the animal feeding on the carcass, or if more than one animal was feeding, the one that reacted to the presence of a new animal was the focal animal. The start and finish times of events such as feeding by the recipient and lying down by the sender were noted. These events were usually terminated as the result of aggressive interactions by the dyad, consisting of the initiator and recipient. The postures used in these interactions were recorded and assigned to the recipient or the sender, whichever carried out the posture. There was no attempt to measure the effect of the senders behaviour on the resultant behaviour of the recipient. Hence, no attempt was made to describe the functional significance of behaviours. Instead, the frequency of postures used by both the sender and recipient was measured with respect to the distance of the sender from the recipient. This distance was based on the recipient being at the carcass and feeding when the first interaction took place. The position of the sender was recorded as either in the forest, 15 - 5 m from the carcass, less than 5 m from the carcass, in physical contact with the recipient or feeding if it displaced the recipient. If the sender displaced the recipient it in turn became the recipient for any animals attempting to feed.

The duration of interactions was measured with a stopwatch. Due to the speed at which interactions took place, and the attempt by the observer to record the postures of both the initiator and the recipient, it was not possible to measure the exact duration of each posture. Rather, the total time of the interaction and the number of postures that took place within this period was recorded. The duration of a posture was calculated by dividing the number of postures which occurred during the interaction by the time of the interaction. This method therefore assumes that all the postures within the interaction were of the same duration.

The time taken to complete a feeding bout was recorded and if the bout was interrupted, the time off the carcass was also recorded. This allowed calculation of total time spent feeding or away from the carcass. On four nights, the total number of animals feeding and the time taken to feed was related to the mass of the prey consumed over this period. These data, together with that on the dyadic interactions, were combined to describe the feeding method of the devils at carrion.

The number of animals feeding on the carcasses at any one time was recorded for all the nights of observation and opportunisticly during the study when devils were seen feeding on road kills.

The feeding pattern through the night was examined by presenting the number of animals that fed on the carcass in any one hour as a percentage of the total number that fed on the carcass. This was compared with the percentage activity per hour of radio-tracked animals (for methods of calculating the percentage of activity see Chapter 6).

5.2.3 FOOD CONSUMPTION RATES

Food consumption rates were determined from sodium influx rates which were measured via isotope turnover techniques. The ^{22}Na turnover technique (Green 1978, Green & Dunsmore 1978) has been validated for the Tasmanian devil by Green & Eberhard (1979), who found a mean error of -6.6 % when comparing Na turnover as derived from isotopes with known Na intake from controlled feeding. Animals were trapped, weighed, tatooed in the ear and given intraperitoneal injections of 10 micro curies of hypotonic $^{22}NaCl$ in 0.5ml water. The animals were left in the traps for 6 hours to allow equilibration of the isotope with the exchangeable sodium body pool (Green & Eberhard 1979). After equilibration, approximately 2 ml of blood was collected from the marginal ear vein in heparanised vials. The samples were then centrifuged and the serum drawn off with a pipette and transferred to a plastic vial. The samples were frozen until processing in the laboratory.

Serum samples were assayed for ^{22}Na by liquid scintillation spectrophotometry (Green & Dunsmore 1978). The Na concentrations were measured by atomic absorption spectrophotometer (Varian Techtron model 1000) after diluting 5 µl samples to 2 ml with de-ionised water.

The exchangeable sodium pool (ES) was determined by the dilution of injected isotopes. If there was a greater than 10 % change in body mass, the animal was re-equilibrated to obtain the final pool size and a mean of initial and final pool sizes used

to calculate ES (Green 1978). All serum samples and standards were assayed together at the conclusion of the study.

The turnover of sodium was calculated as follows where meq refers to milliequivalents:

Turnover (meq) = ES(ln I - Ln F),

and where I and F are initial and final serum activities of ^{22}Na, respectively (Green 1978, Green *et al.* 1984). The food intake was derived from the expression;

Food intake (kg/day)= 1.1[Na turnover(meq)] / t(days) X Na_d (meq/kg)

where Na_d is the total sodium content of the prey and 1.1 a correction factor as derived from validation experiments on Tasmanian devils by Green & Eberhard (1979). The sodium content of prey was assumed to be 55 meq/kg, the mean for marsupials (B. Green and K. Newgrain pers comm).

Food intake rates were calculated for animals at the study site and for a site at Kempton, southern Tasmania. The latter data were based on unpublished information provided by Dr. B. Green. All values are given as means ± standard deviation (SD). Differences between means were tested by two-tailed t-tests or analysis of variance (ANOVA). As some devils at the Mt.William study site were sampled more than once during each period, the data are not strictly independent. When testing for differences, serial results obtained from the same animal were averaged , a process which yields a mean whose variance is thus lower than other single animal observations. While this formally violates the homogeneous variance assumption of ANOVA, it is a conservative procedure because improved accuracy of a few "new" observations results, while claimed degrees of freedom are reduced. When testing for seasonal differences, it also makes group samples sizes more similar and thus provides protection against the effects of unequal variances. Food intake was only calculated for those turnovers where there was at least a 50 % change in ^{22}Na activity (Herd 1985, Gales 1989).

5.3 RESULTS

5.3.1 PELAGE MARKINGS

A total of 220 animals (102 males and 118 females) were described in terms of the position and extent of pelage markings. There were 14 patterns of markings evenly distributed between the sexes (Table 5.1). A total of 87 % of the animals had some form of white marking, the extent of which varied considerably, and the remaining 13 % were completely black (Fig. 5.1). Of all the possible combinations of the positions

TABLE 5.1 The position, number of combinations and extent of white markings for males and females *

Position of marking	n	Male		Female		Extent of marking mean ± SE
		No. of combinations	No. of animals	No. of combinations	No. of animals	
Full markings	75	24	40	27	35	12.5 ± 3.9
Chest	43	7	14	9	29	3.3 ± 1.4
Chest + rump	41	12	20	12	21	5.3 ± 1.8
Split chest	12	4	6	3	6	3.5 ± 0
Rump	6	3	4	2	2	2.5 ± 1.7
Left flank+right flank+chest	3	1	1	2	2	6.8 ± 2.4
Left flank+right flank	3	3	3	0	0	1.8 ± 1.3
Left chest	2	1	1	1	1	2
Right chest	2	1	1	1	1	2
Right flank+rump	2	1	1	1	1	3, 2
Left flank+right flank+rump	1	1	1	0	0	4
Left flank	1	1	1	0	0	1
Black	29	0	9	0	20	0
TOTAL	220	59	102	58	118	

* The extent of marking was calculated from the scores allocted to the differing degrees of white colouration. The number of combinations refers to the number of different white patterns within each position (see Section 5.2.1)

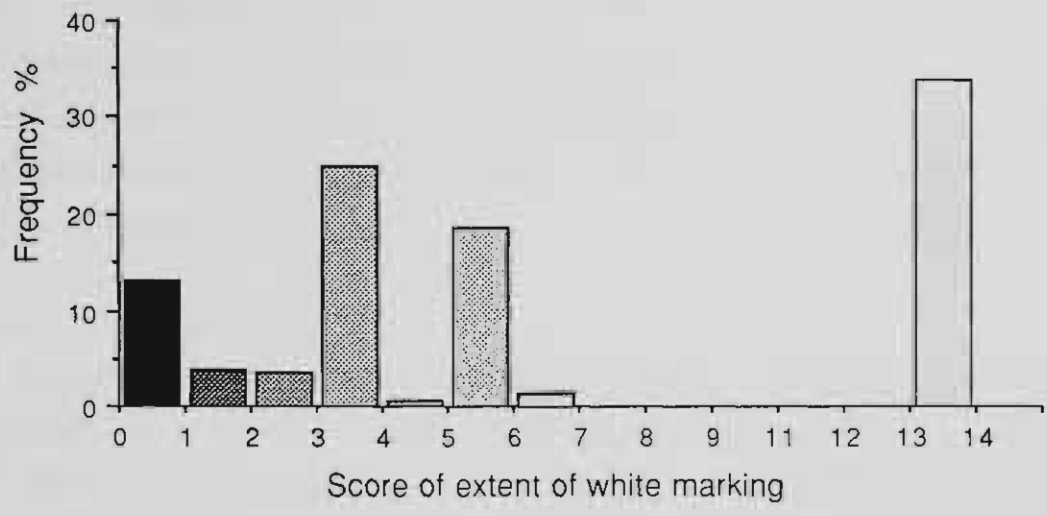


FIGURE 5.1 Frequency of occurrence of the scores describing the extent of white marking. Different shading indicates increasing extent of white marking with increasing score.

of the white markings, the chest and rump where the most common part of the body to be marked (61 %). There was no difference in the extent of the markings of resident males and females (Md = 0.116, n = 93) or transient males and females (Md = 0.144, n = 151). There was also no difference when transients were compared with residents (Md = 0.133, n = 245).

5.3.2 POSTURES AND VOCALIZATIONS

A total of 36 animals were observed feeding or attempting to feed during the ten nights of observation, for a total time of 1005 minutes (16.75 hours). I observed 28 distinct postures and vocalizations used by either the initiator or the recipient on 305 occasions. These are described below.

5.3.2.1 Vocalization

A total of 7 sound forms were readily identifiable in the field (Table 5.2) and where applicable, these were classified according to the system of Eisenberg *et al.* (1975). The 'snort' sound appeared to be produced by expulsion of air through the nostrils and the mouth. The 'humf growl' sound observed in the field corresponds most closely with the type IV hiss of Eisenberg *et al.* (1975). This is a low intensity call of low frequency, short duration and is often repeated. The 'bark' type was short in duration, high in energy, of a low frequency and seldom repeated. The 'clap' sound was produced by the animal snapping its jaws together. There is a gradation of 'growl-whines' which form a sequence starting with the 'monotone' type and increasing in intensity through the 'vibrato' to the 'crescendo'. These are the same as the type I calls described by Eisenberg *et al.* (1975). Two sound forms were observed which were not described by Eisenberg *et al.* (1975). The 'screech' call was observed twice and was associated with the defeated devil fleeing and being pursued. This could possibly be a variation of the type IIL growl of the devil, not observed in the field during this study, but observed in the laboratory by Eisenberg *et al.* (1975). 'Sneezing' was also observed but never initiated a response from the feeding animals.

5.3.2.2 Postures

A total of 20 postures were identified during interactions between initiators and recipients (Table 5.3) and these are described below.

Head and Tail Position

A total of 7 postures were all variants on the position of the tail and head relative to the horizontal plain running across the back of a standing devil. These varied from the often used 'Head Up-Tail Down' posture to the less frequent 'Head Up-Tail Straight' posture (Table 5.3). Although not included in the postures described here, the intensity of these postures seemed to be reflected by the degree of erection of the fur on the tail.

TABLE 5.2
Comparison of types of vocalization recorded in this study with the classification system of of Eisenberg et al. (1975)††

This study	Eisenberg
Snort	Snort
Humf growl	Hiss
Bark	Bark
Clap jaws	Clap
Monotone	Growl whine
Vibtrato	Growl whine
Cresendo	Growl whine
Screech	*
Sneeze	*

* indicates the call was not directly comparable with the classification systems of the two studies.

†† Through lack of equipment, sonograms are not presented in the present study. Frequency modulations, therefore, are not discussed but are treated by Eisenberg et al. (1975).

TABLE 5.3

Frequency of occurrence of postures and vocalizations relative to the distance between the recipient and the initiator.

POSTURES AND VOCALIZATIONS (*)	TOTAL	IN BUSH		15 m - 5 m		< 5 m		CONTACT		FEEDING
		I	R	I	R	I	R	I	R	RECIPIENT #
SNORT *	»	6	0	6	7	2	5	1	1	>>
MONOTONE *	»	5	0	12	25	9	14	1	3	>>
HEAD UP, TAIL DOWN	64	0	12	15	24	6	6	1	0	0
GAPE	39	0	0	23	4	4	2	2	2	2
HUMF GROWL *	38	2	0	16	9	1	5	1	0	4
TAIL UP, HEAD UP	26	0	0	6	10	5	3	0	1	1
VIBRATO *	17	4	0	0	0	3	4	4	5	1
TAIL UP, HEAD DOWN	12	0	0	1	4	4	0	2	1	0
HORIZONTAL	11	0	0	4	4	0	1	0	0	2
NECK THREAT	10	0	0	0	0	0	0	4	4	2
BARK *	9	0	0	2	6	1	0	0	0	0
TRIPOD	8	0	0	5	3	0	0	0	0	0
SITTING	8	0	0	7	1	0	0	0	0	0
CRESCENDO *	8	4	0	0	0	0	1	1	2	0
LYING DOWN	7	0	0	7	0	0	0	0	0	0
URINATING	7	0	0	5	0	2	0	0	0	0
BIPEDAL	5	0	0	3	0	0	0	1	1	0
ANO-GENITAL DRAG	5	0	0	5	0	0	0	0	0	0
BROADSIDE	4	0	0	0	0	0	0	1	3	0
CLAP JAWS *	4	0	0	2	0	0	0	0	2	0
TAIL DOWN-HEAD DOWN, EARS FLAT	4	0	0	3	0	2	2	2	1	2
STIFF LEGGED	3	0	0	1	2	0	0	0	0	0
LOPE APPROACH, BOUNDING	3	0	0	0	0	0	0	0	0	0
TAIL UP FLEEING	3	0	0	0	0	2	0	0	0	1
HEAD UP, TAIL STRAIGHT	2	0	0	0	0	0	0	0	0	0
HEAD DOWN, TAIL DOWN, EARS FLAT	2	0	0	0	0	1	0	0	0	2
SCREECH *	2	0	0	0	0	1	1	1	0	0
SHOULDERING	2	0	0	0	0	0	0	1	1	0
STABBING WITH FORE FEET	0	0	0	0	0	0	0	1	0	0
TOTAL NUMBER OF DISTINCT POSTURES USED	305	21	12	123	99	43	44	23	27	17
TOTAL NUMBER OF POSTURES OBSERVED	28	5	1	18	12	14	11	14	13	11
TOTAL UNIQUE TO EITHER I or R	24	5	1	6	0	5	2	3	2	
TOTAL UNIQUE TO THE DISTANCE OF I FROM R	11	0		6		1		4		0

These postures and vocalizations occurred between devils feeding together. I = initiator, R = recipient. * indicates vocalization.

For example, when the tail was raised the hairs on the tail were flat when the animals were far apart, but as they approached each other the same posture was maintained but the hairs on the tail would become fully erected. The horizontal posture was the result of the head and tail being held on the same plane as the bac.In some circumstances the legs would be bent sufficiently for the belly to scrape on the ground.

Gape

The jaws of the animals were often opened and held open for a few seconds as interactions took place. This was described as a 'Gape' posture.

Neck Threat

When the dyad was in close proximity one of the animals would nip at the neck area of the other, but never make contact. These nips would be repeated and the recipient would respond by either shouldering the initiator or attacking it face on.

Tripod

The animal would raise one front paw off the ground whilst facing the other animal. The head of the animal was held up and the tail down. On one occasion the 'tripod' posture developed into a 'bipedal' posture.

Sitting

Low intensity interactions often culminated in the initiator sitting and staring in the direction of the recipient. This posture was often integrated with 'gaping' and 'lying down'.

Lying Down

The initiator lay down in view of the recipient with their bellies on the ground and with the fore and hind feet extended anteriorly and posteriorly respectively. This should not be confused with animals that had fed to satiation and would then leave the carcass and lie down within the study site. These animals never interacted with the possessor of the carcass.

Urinating

The initiator urinated within full view of the recipient, sometimes in conjunction with a 'stiff legged' gait or 'gaping'. This action may also fascilitate a chemical signal to the recipient.

Bipedal

There were two forms of bipedal postures. The initiator, when far from the recipient, would support itself on its tail and hind legs with the fore paws held in a relaxed mode

and facing the recipient. When the dyad was in contact and the degree of interaction escalated, both the animals would raise themselves onto their tails and hind legs and place their fore paws onto each others shoulders. This was accompanied by crescendo calls and although not observed during this observation period, devils have been seen to interlock jaws and wrestle while bipedal.

Ano-genital Drag

The ano-genital area is pressed against the ground and the animal drags itself along with its fore paws, whilst holding the anterior region of the body above the ground. This posture was shown by both sexes and hence is better described as an ano-genital drag (Eisenberg *et al.* 1975) rather than a cloacal drag (Buchman *et al.* 1977). The posture was sometimes accompanied by gaping and an erect tail position. This posture may also be associated with the transmission of chemical signals.

Shouldering

When the dyad is in physical contact, the neck threat posture of one animal invokes the recipient to offer a shoulder in place of the neck. The pair may then proceed to move in a circle with continuous attempts at 'neck threats' which are usually thwarted by the position of the recipients shoulder.

Stiff legged

This posture was conspicuous because the animal moved forwards without flexing the joints of the legs. The posture was of short duration with the animal moving less than one meter. The associated position of the head and tail varied.

Lope Approach

Although rarely observed, this mode of approach to a carcass was always successful in terms of the initiator displacing the recipient from the carcass. The initiator would approach the carcass from outside the study site at a rapid pace and run straight up to the recipient without hesitation.

Broadside

The initiator would orientate its side to the recipient with the head and tail in various positions.

Stabbing with the fore feet

This was observed on one occasion when an animal leapt from behind a tussock at another animal stabbing at the recipients chest with its forefeet.

Examples of some of these postures are shown in Figure 5.2.

FIGURE 5.2

Top photograph

This shows two devils in close contact. Both animals have their tails down, hairs on the tail erect and ears up. The devil on the left is reacting to a neck threat. Both devils were using vibrato calls.

Bottom photograph

This shows three juvenile devils feeding on a Bennett's wallaby. The middle devil has a radio collar carrying an LED. The devil is displaying a Head up-tail down posture and is about to lift its front leg thus showing a Tripod posture. Note also the erect ears.

Photographs by M. Egawa.

5.3.2.3 The frequency of postures with respect to the distance between the members of the dyad

Interactions between devils in the bush and, therefore, out of sight of the recipient on the carcass were only discernible to the recipient via their calls. When the recipient responded, it was always with a 'Head Up Tail Up' posture. The number of postures observed relative to the distance between the initiator and recipient is shown in Figure 5.3. This excludes the postures associated with the position of the initiator in the bush, as the full range of postures could not be observed. There is a clear decrease in the frequency with which postures were used as the distance between the initiator and recipient decreased. The total number of postures used also decreased with proximity, but the number of postures unique to the distance between the two animals did not. This is not surprising, as the postures used when the animals were in contact, such as 'shouldering' and 'neck threats' cannot, by definition, be performed unless the animals are in very close proximity. The initiator tended to display more frequently and use more unique postures than the recipient at the onset of the interaction when the animals were furthest apart, but with decreasing distance, both initiator and recipient used similar postures at a similar frequency. When devils were feeding together they were almost constantly vocalizing. Snorts and monotones were the most common sound forms used.

5.3.2.4 Interactions that resulted in physical damage to either member of the dyad

Of the total of 119 bouts of interactions observed during the feeding trials, only one resulted in physical damage to an animal. In this case the initiator of the interaction approached the recipient, made contact, squealed and turned and fled with its tail up with the recipient chasing it and biting the rump of the fleeing animal. The animal was pursued across the paddock for ≈ 100 m in a zig zag path with both animals constantly vocalizing. Opportunistic observations were also made of two encounters where agonistic interactions between two devils led to jaw wrestling. These animals were both in a bipedal stance with their fore paws on each others shoulders or chests and their jaws interlocked. The animals vocalized constantly using 'vibrato' and 'crescendo' sound forms whilst they shook their heads from side to side. During this stage, although there was no obvious physical damage to either of the animals, the nature of the interaction appeared as if it could have caused extensive damage to the muzzles or jaws of the animals. Again, the defeated animal ran off into the bush with its tail in the air and fur fully erect, with the winner pursuing it and biting its rump whenever it was close enough.

Retrospective examination of the animals trapped during the study showed that out of 150 animals, only 6 % had suffered extensive physical damage and 29.5%

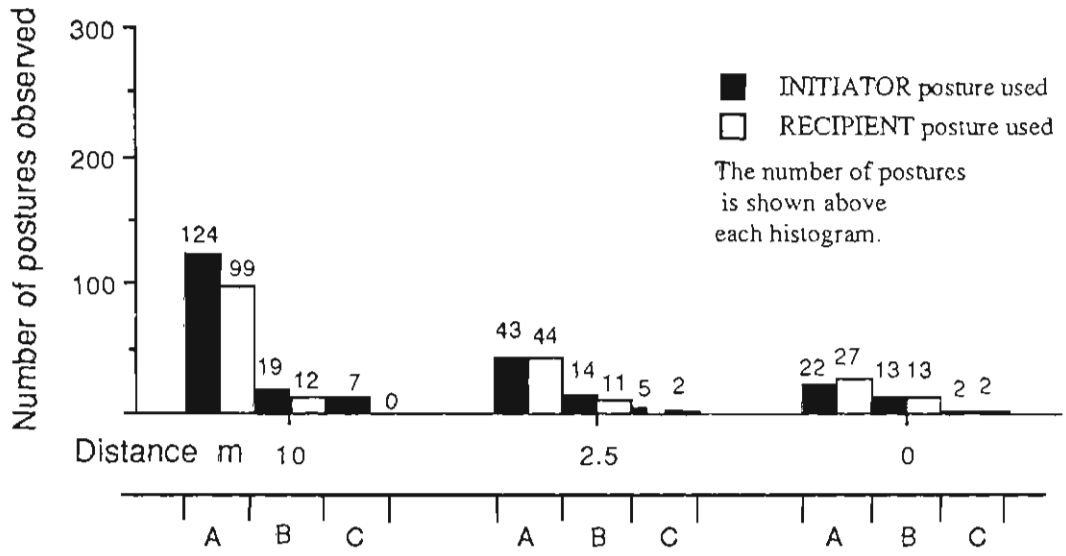


FIGURE 5.3

The frequency with which all postures were used (A), the number of individual postures that comprised this frequency (B) and the number of postures unique to either the initiator or the recipient (C), with the data scored throughout for iniators and recipients and plotted against distance of the initiator from the recipient.

showed some form of wounds (Table 5.4). The wounds were most commonly located on the muzzles (48.4 %) and the rumps and tails (28.7 %). The damage to the tails resulted in short (3 to 6 cm), furless tails. These should not be confused with animals showing fur loss on their tails and rumps as a result of sarcoptic mange. The damage to the rump and back often took the form of puncture holes. The most extensive wounds were located on the jaws and muzzle and in the worst cases loss of flesh made the teeth visible (Table 5.4).

5.3.3 FEEDING ACTIVITY

5.3.3.1 The temporal nature of feeding

Of the 31 feeding bouts observed, 22 were continuous and 9 were discontinuous. The discontinuous feeding bouts were interrupted by interactions with other animals whereby the recipient or feeder was displaced by the initiator of the interaction. The mean time spent feeding by continuous feeders was 29.6 ± 21.8 minutes and by discontinuous feeders was 45.0 ± 39.3 minutes. There was no significant difference between these feeding times ($t = 1.61$, $DF = 29$, $p > 0.05$) so the data were pooled giving a mean feeding duration of 34 ± 25.2 minutes. The only group of animals that were readily distinguishable by observation at the carcass site were adult males. This was because of their relative size difference to the rest of the population and the presence of scars in this group of animals (see Chapter 2). The time spent feeding by this age group was compared with the time spent feeding by the rest of the animals (adult and juvenile females and juvenile males) Adult males fed for an average of 57.1 ± 29.1 minutes ($n = 9$) whilst the rest fed for 24.7 ± 15.3 minutes ($n= 22$), a significantly shorter period ($t = 4.087$, $DF = 29$, $p < 0.01$).

There were a total of 119 interactions recorded, involving 36 animals. Interactions were only recorded between the possessor of the carcass (the recipient) and the challenger (the initiator). Of the 36 animals, 31 actually fed from the carcass. There were a total of 199 postures by the recipient and the average posture lasted for 23 ± 19 seconds ($n = 25$ interactions with $n = 165$ postures). Therefore, the 'average devil' was involved in 3.8 interactions (119/31) with 1.7 postures per interaction (199/119) during a feeding bout. Using this data it was calculated that the average devil spent 2.5 minutes defending the carcass from challengers per average feed [3.8 (interactions) x 1.7 (postures) x 23 seconds (time for a posture)=2.5 minutes].

On four separate nights of observation, an average of 7.5 ± 1.5 devils consumed all the food provided. Although 20 kg of food was provided during these trials, devils did not consume the entire carcass, leaving the skin and the more dense bones such as the vertebrae, pelvis, skull and long bones. All the muscle, fat, organs, intestine and contents of the intestine were consumed. Devils were observed chewing

TABLE 5.4 Frequency of occurrence and location of scars and wounds on male and female devils (A) and description of facial wounds observed on adult residents (B)

A

Wound and scar location	Number of devils with scars	
	Males	Females
Muzzle	43	16
Ears	4	4
Shoulders	2	0
Claws missing	3	2
Legs	1	0
Back	7	5
Rump	15	4
Tail	12	4

B

ID	Sex	Description of wound
L145	male	Left jaw muscle missing, teeth visible
L47	male	Lips torn and pieces removed
L84	male	Lips and nostril torn
L88	male	Side of jaw muscle gone, teeth visible
L123	male	Jaw muscle torn
L27	male	Left jowl torn
L144	male	Right jowl missing, teeth visible
L117	male	Right jowl torn
L118	male	Right jowl torn
L116	female	Top lips torn

TABLE 5.5 Group size of devils at and away from carcass

Group size of devils at carcass	Frequency of occurrence	
	n	%
1	42	53.2
2	29	36.7
3	5	6.3
4	2	2.5
5	1	1.3

Group size of devils away from carcass	Frequency of occurrence	
	n	%
1	95	100

the epiphyses off the long bones, the distal ends of the vertebrae and pelvis and the nasal bones of the skull. The edible proportion of the carcass has been estimated as 90 % of the carcass. This figure translates to 18 kg per 7.5 animals per night or 2.4 kg per animal per night.

5.3.3.2 The number of animals feeding simultaneously

The number of animals feeding on the carcasses varied from one to five with solitary feeders being the most common (Table 5.5). However, in contrast to observations of the group size of devils away from food, where only solitary animals were seen (n = 63), 46.8 % of observations on carcasses showed that more than one animal fed together.

5.3.3.3 Feeding activity through the night

The number of animals feeding per hour relative to the total number that fed on the carcass is shown for summer and winter and compared with the foraging activity of the animals in Figure 5.4. In summer and winter the majority of animals fed within the first two hours of the first arrival at the carcass, followed by a fairly constant decrease in the numbers feeding after this initial burst. The decrease in numbers feeding is not surprising, as the feeding rates of the animals in the first two hours (2.4 kg per animal) would deplete the resource available for subsequent feeding. In both winter and summer the animals started to forage within half an hour of sunset. However, the lag time between animals starting to forage and initiation of feeding on the carcasses was two hours in winter and less than half an hour in summer.

5.3.3.4 Food consumption rates of free-ranging devils

Using ^{22}Na influx rates from devils from Kempton (B. Green unpubl. data, n=35) and Mt.William (n=36) rates of food consumption were calculated. Intra-sexual comparison between the study sites showed that there was no significant difference between the two localities so the data were pooled (ANOVA, ns). When the data are split by age groups (see Chapter 2), adult males ate a mean of 107 g $kg^{-1}day^{-1}$ and adult females 146 g $kg^{-1}day^{-1}$ (Table 5.6). Juvenile males ate a mean of 140 g $kg^{-1}day^{-1}$ and juvenile females ate 108 g $kg^{-1}day^{-1}$ (Table 5.6). There was no significant difference between the sexes of adults or juveniles (t-tests, ns). Similarly, there was no sex-related difference in the amount of food consumed by male (73 g $kg^{-1}day^{-1}$) and female weaners (77 g $kg^{-1}day^{-1}$) (Table 5.6). The mass specific data for males were pooled and compared across the ages and again there was no significant difference. A similar process was applied to the females and showed no significant difference. Further, there was no difference between all males and all females in rates of food consumption (ANOVAs, ns). Therefore, all the data were pooled, giving a mean food consumption for devils of 120 g $kg^{-1}day^{-1}$ with a range of 17 g $kg^{-1}day^{-1}$ to 443 g kg^{-1}

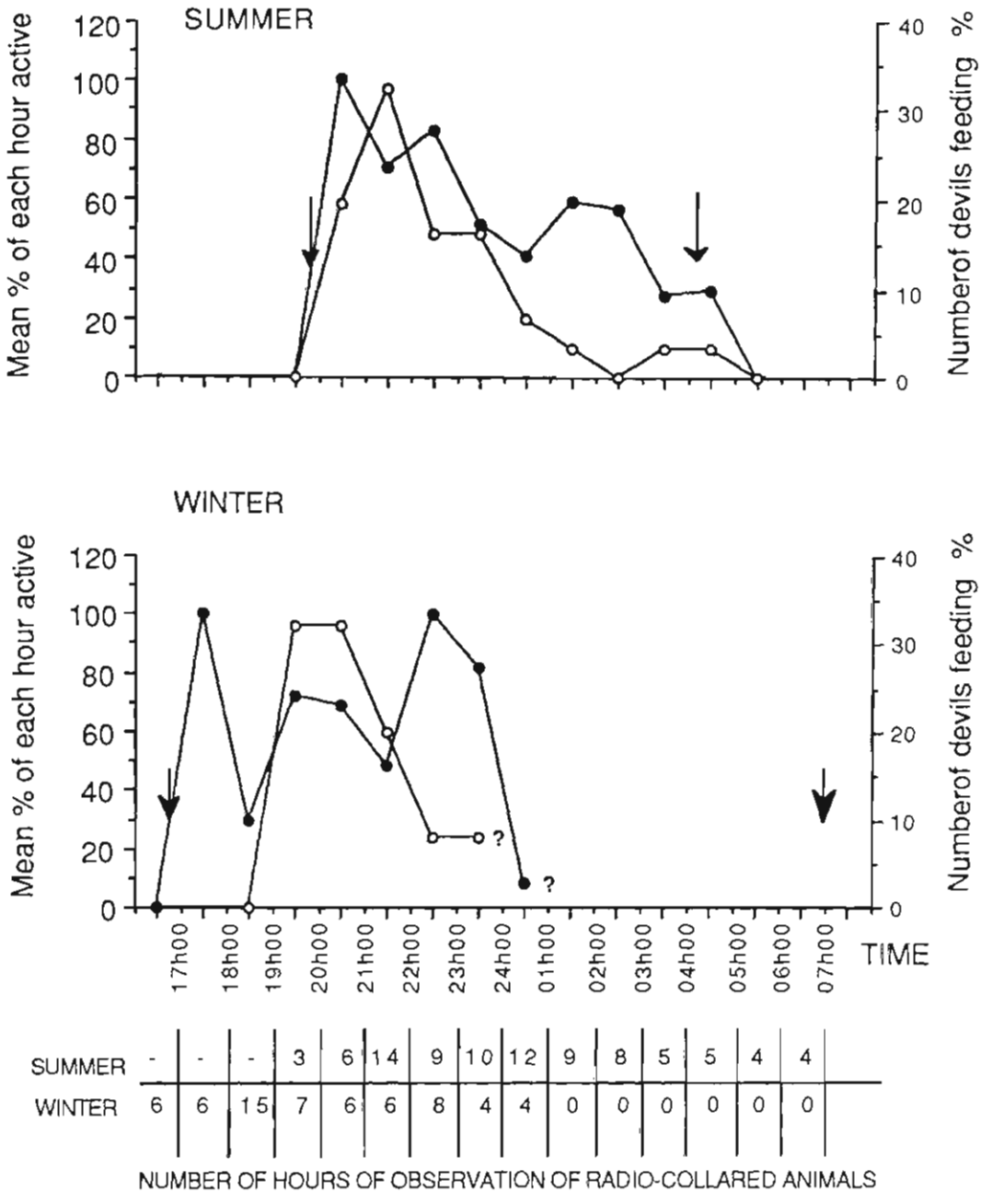


FIGURE 5.4

Percentage of each hour of the day that adults were active (•) in summer and winter. The number of animals feeding per hour relative to the total number that fed on the carcass is also shown (∘). Arrows indicate time of sunset and sunrise respectively.

? indicate end of data set prior to sunrise (winter).

TABLE 5.6 Rates of food consumption as determined by isotope turnover

Age class	Sex	Body mass kg	Food consumption rate g/kg/day		
		mean ± SD	mean ± SD	n	range
Adult	male	10.2 ± 0.9	107.4 ± 99.8	16	32 - 443
	female	7.1 ± 0.4	145.8 ± 95.3	23	27 - 386
	pooled		130.0 ± 97.7	39	27 - 443
Juvenile	male	6.2 ± 1.2	140.2 ± 87.7	15	28 - 354
	female	4.9 ± 0.4	107.8 ± 30.5	4	74 - 142
	pooled		133.4 ± 79.5	19	28 - 354
Weaner	male	3.3 ± 0.7	72.7 ± 54.7	4	17 - 138
	female	3.4 ± 0.8	76.9 ± 40.8	9	23 - 156
	pooled		75.6 ± 43.1	13	17 - 156
TOTAL	ALL DATA	6.7 ± 2.4	120.5 ± 86.6	72	17 - 443

$^{1}day^{-1}$ (Table 5.6). These figures translate to food consumption rates of 12 % body mass in food per day, with a range of 2 % to 44 %.

The sequential food consumption rates for animals at Mt.William are shown in Figure 5.5. The amount of food consumed per day varied dramatically depending on the time period between turnovers. When turnovers were more than 10 days apart the consumption rates per day decreased towards the mean, whilst those turnovers that were between 3 (the minimum time required for sufficient depletion in Na activity for accurate calculations) and 10 days gave food consumption rates as high as 40 % or as low as 3% body mass.

5.4 DISCUSSION

5.4.1 COMMUNICATION DURING AGONISTIC ENCOUNTERS AT FOOD

The Tasmanian devil has a well developed repertoire of comunicatory behaviour associated with aggression around food. This involves visual (18 postures), vocal (7 sound forms) and probably chemical signals (2). It has been suggested that visual signals are limited in dasyurids due to their nocturnal behaviour (Croft 1982), but the results of this and other studies (Buchman *et al.* 1977 , Eisenberg *et al.* 1975) indicate that in dasyurids visual signals are both frequent and varied in their structure during agonistic interactions. As an example, the varying position of the head and tail results in at least 7 varieties of posture. These postures elicited a response from the recipient whether they were used in conjunction with vocal signals or not. Buchman & Guiler (1977) suggested that this repertoire of visual displays was as a result of the devil being so conspicuous because of their white markings, use of facial expressions and the tendency for vasodilation of the ears during interactions. Buchman & Guiler (1977) went on to suggest that the white markings exhibit a high degree of variability and therefore may be useful in social recognition of con-specifics. The results of the present study do not support this hypothesis, as many of the animals in the Mt William population were black (13%) and for every animal with white markings, on average there was at least one other animal which was indistinguishable from it. If the recognition of conspecifics was based on the specific colour patterns of individuals, then none of the black animals could be recognised by this method, and up to 50% of the animals with markings could be misidentified. It is therefore doubtful that devils would rely solely on colour and markings to identify each other.

The white colouration was common on the chest or rump and, as pointed out by Eisenberg *et al.* (1975), the markings would demarcate anterior and posterior regions of the body during encounters. During agonistic interactions, most of the postures and vocalizations were made whilst the animals were orientated with either

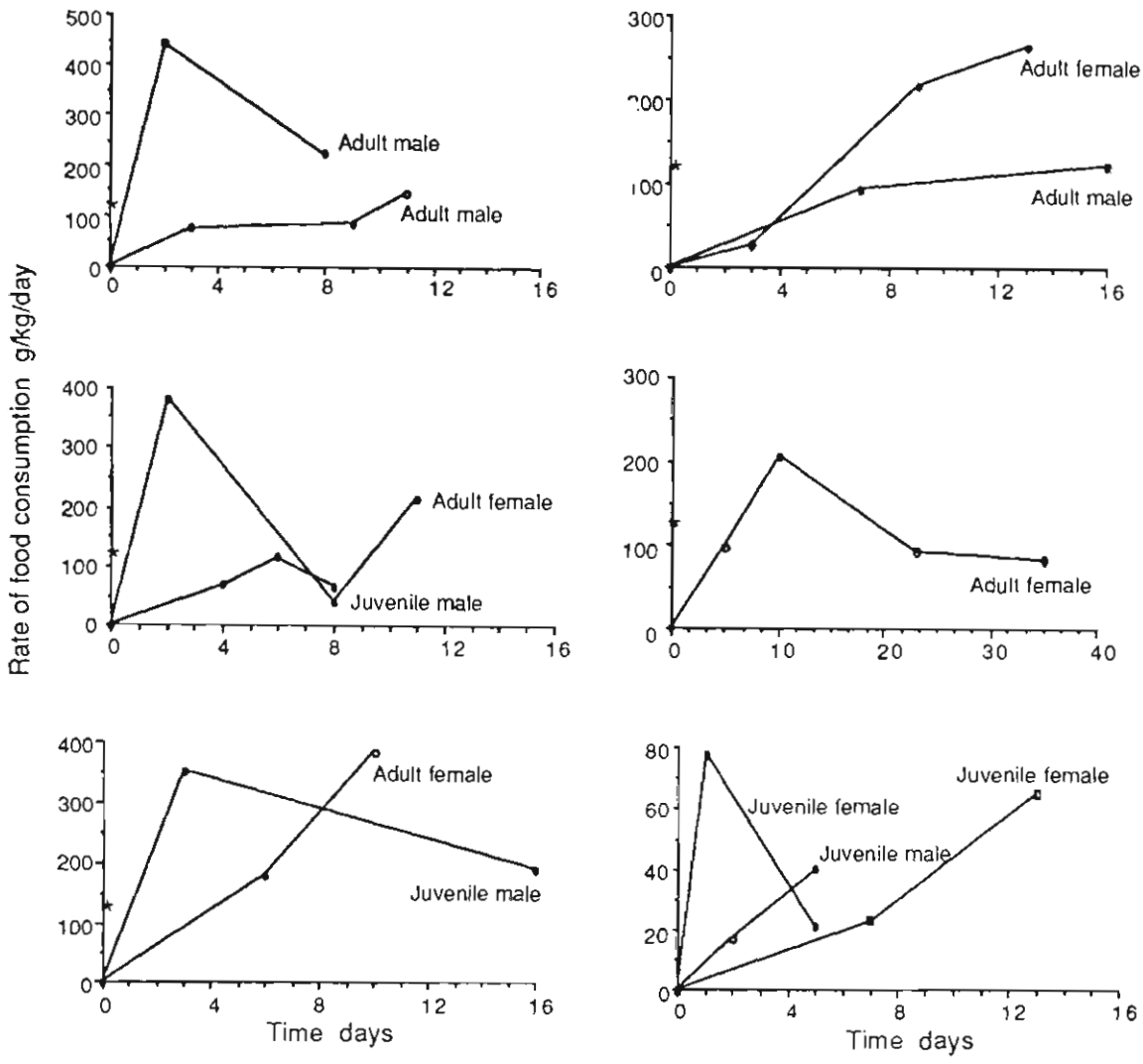


FIGURE 5.5

Examples of sequential food consumption rates. * on y axis indicates the mean food consumption rate for all devils sampled

their anterior or posterior ends towards each other. A few of the postures such as 'broadside', 'neck threat' postures and 'stiff legged' walking involved the sides of one of the dyad, but white markings on the rump and shoulder could serve to orientate animals to these postures. It is therefore possible that the position and extent of colouration has a bearing on the information transfer during interactions. If this is so, then it would follow that those animals that had less white colouration would have a different level of information transfer for a specific posture when compared with a marked animal. If the level of information transfer was significantly different it should manifest itself in the social status of the animal. For example, if an animal without markings was to display its approach to a carcass but the recipient failed to detect the extent of the display, the recipient may consequently fail to respond in the appropriate fashion and so be displaced from the carcass. Constant repetition of this scenario would provide the black animal with an advantage over the marked animal. Hypothetically, the black animal could become more successful in obtaining food and therefore tend to remain in the area where it is procuring the food, whilst the marked animal would constantly be unsuccessful in obtaining food and may leave the area, becoming transient. However, in the present study, there was no significant difference in the position or extent of white markings of transient and resident devils, suggesting that there was no obvious affect of colouration on the residency status. However, this is only one of many possible outcomes that may result from the apparently large discrepancy in orientation marks that can exist between two devils competing for food. The adaptive significance of colouration patterns in the devil should be further investigated via experimental manipulation of these patterns.

5.4.2 AGONISTIC INTERACTIONS BETWEEN CONSPECIFICS AND PHYSICAL DAMAGE

The agonistic interactions around carcasses seldom resulted in physical clashes between the animals. The use of the analysis of scarring in the trapped sample relied on the assumption that the wounds were results of agonistic interactions between devils. The location of the majority of the scars was on the rump and face, sites of wounds which would be expected from fighting, as most of the postures associated with fighting involved the head and the rump. The presence of more wounds on the adult males (Table 5.4) may be explained by the fact that these animals have to feed for longer to attain an equivalent % body mass in food than do the smaller animals. Adult males are therefore exposed to more interactions and potential conflicts.

The adult male residents were the only devils that suffered extensive damage to the facial area where large portions of flesh were missing (Table 5.4). All these wounds were unhealed and the animals were never trapped again. No wounds of similar severity were seen to have healed. It appears therefore, as if these wounds were

concurrent with the demise of the male residents. The wounds were probably not the primary cause of death as they were never septic nor bleeding to such an extent that the animal would die from chronic infection or loss of blood. Two of the resident males which showed this form of wounding (L47 & L84) were lame in the hindquarters and had extensive fur loss on the rump and tail, suggesting a physical deterioration of the animals other than that caused by intra-specific aggression. Such physical deterioration has been linked to stress related diseases in association with mating strategies of male dasyurids such as *Antechinus* spp (for a summary of see Lee & Cockburn 1985) and "diseases of adaptation" in relation to population densities in rodents (see: Christian 1971). It may well be that a similar mechanism is operating to some degree in the demise of male devils. This rationale will be further developed in Chapter 7 .

5.4.3 THE RITUALISED NATURE OF THE AGGRESSIVE INTERACTIONS

The agonistic interactions between the possessor of a carcass and the challenger were usually carried out at a reasonable distance from each other (5 to 15 m) and so without physical contact. The postures used in these interactions were conspicuous and sufficient to settle disputes without physical clashes. Clearly then, the agonistic behaviour of the devil can be considered to be ritualised following the terminology of Huxley (1914) and Eibel-Eibesfeldt (1961). A similar conclusion was drawn by Buchman & Guiler (1977) based on laboratory studies of the behaviour of the devil.

5.4.4 THE PATTERN OF FEEDING AT CARCASSES

The observations of animals feeding at carcasses showed that feeding bouts lasted on average 34 minutes. Although some of the feeding bouts were discontinuous, the devils always returned to feed until they had fed for a similar time to those that fed continuously. The animals ate on average 2.4 kg per feeding bout or 39 % of the body mass of the average devil. The adult males were the only group readily discernible by remote observation and they fed for an average of 54 minutes. Assuming that they ate at the same rate as that calculated for the average animal, they ate 4.0 kg or 40 % of their body mass (mean mass 10.2 kg).

The food consumption rates of devils calculated by the ^{22}Na turnover method showed that devils ate on average 12 % (range: 2 % to 44 %) of their body mass per day. These data indicate that the consumption rates obtained via the observations at carcasses are the same as the maximum rates calculated via the turnover technique. If the average devil eats 39 % of its body weight in a feed, as calculated from the observations at carcasses, then, using the mean food consumption rate data from ^{22}Na turnover, devils would only need to eat approximately every 3 days (39/12). Adult males would only need to feed every 3.6 days (40/11) to maintain the average food

consumption rates as calculated in the field by the isotope turnover technique. This was indeed the case, as the pattern of food consumption rates relative to time obtained via the turnover technique shows that the animals were feeding in bursts within the shortest accurate turnover periods of 3 to 8 days.

The animals were therefore maintaining an average food consumption of 12 % body weight per day by gorging themselves every 3 to 4 days. This consumption rate compares favourably with that of the theoretical food consumption rate of 9 % body mass predicted by Nagy (1987) for marsupials.

The ability of carnivores to gorge themselves has also been recorded in lions *Panthera leo* (Schaller 1972) and spotted hyaenas *Crocuta crocuta* (Kruuk 1972, Tilson & Hamilton 1984, Frank *et al.* 1985). Lions were recorded eating between 17 and 23 % of their body weight in one meal and spotted hyaenas between 18 and 27 %. These values are lower than the 40 % body weight engorgement capability of the devil, but this is not suprising as the lions and hyaenas are social animals with complex intra-group competition limiting the amount of food available to any one member of the group (Schaller 1972, Kruuk 1972). Further, hyaenas unlike the devil, cache food and so engorgement to the degree observed in the devil is probably unnecessary.

Although many animals would assemble in the area of the carcass, most feeding bouts observed involved one (53 %) or two animals (36.7 %), although up to 5 animals have been observed on the carcasses (Table 5.5). When more than one animal was at the carcass they would feed continuously with constant monotonal calls. If another animal arrived and approached the carcass only one of the feeders would respond to it. The number of animals feeding on a carcass is probably related to the size of the carcass as on one occasion when a cow was shot in the study area, 22 devils were observed feeding on it simultaneously. Tilson (1984) found similar results for spotted hyaenas, where the number of hyaenas feeding was related to the size of the carcass. Unlike devils however, the feeding patterns of hyaenas have been related to a dominance hierarchy where the dominant animals gained access to the carcass over the subordinates (Tilson 1984).

5.4.5 THE RELATIONSHIP BETWEEN FEEDING AND DOMINANCE

Buchman & Guiler (1977) showed that devils formed stable dominance-subordination relationships in captivity. They go on to suggest that in the wild "truce relationships" are established within feeding groups and that such groups are closed to "outsiders". However, in the present study the relationship between the feeders and non-feeders was related to the length of time the feeders had been at the carcass and

therefore not to any preconceived status of the feeder by the non-feeder. The interaction between feeders and non-feeders was in the form of a ritualised contest with the feeder obtaining sufficient food to gorge itself and to sustain it for another three days, before succumbing to the challenge of the non-feeder. The larger the devil the longer it has to feed for .

5.4.6 AGONISTIC INTERACTIONS AND SOCIAL BEHAVIOUR

It has often been argued that agonistic interactions between animals, particularly those like the devil that can inflict considerable damage, are diminished by safer methods such as threat displays, which have evolved to communicate intentions (Tinbergen 1951, Geist 1971). The 'War of Attrition ' model however predicts that the information about the Resource Holding Potential (RHP) will be transferred via agonistic interaction (Maynard Smith 1979) and that where fighting does occur its occurrence and intensity will depend on the costs and benefits to the contestants (Parker 1974, Maynard Smith & Parker 1976). Information on the RHP of the contestants needs to be transferred when the contest is possibly asymmetrical and as yet unknown to the contestants. Both these arguments rely on the assumption that conflict yields considerable benefits and can have considerable costs.

The aggressive interactions of feeding and non-feeding devils around a carcass involves the benefits of eating and the costs of being bitten. It is hypothesised that the ritualised contest enables the initiator, or non-feeder, to establish the tenacity of the feeder. The tenacity of the feeder can be viewed as a form of dominance over any contestant for the food and the strength of this dominance should wane as the feeder approaches satiation. There would therefore be an element of asymmetry to the feeders dominance which a non-feeder would not immediately know as it would have no idea of when the feeder commenced feeding. The ritualised interactions would therefore enable the non-feeder to gauge the degree of dominance (satiation) the feeder may have over rivals. The interactions are graded in that the amount of sound energy produced and the physical nature of the postures tends to increase as the dyad approaches physical clashes. This grading allows an economical assessment of the RHP of the contestants as would be expected from the War Of Attrition model (Maynard Smith 1979).

The occurrence of discontinuous feeding bouts is probably a reflection of a variation in the strategy of the non-feeders whereby instead of testing the degree of dominance of the feeder, the non-feeder attacks regardless and displaces the feeder. The direct bounding approach is an example of this strategy. On the three occasions this was observed it was associated with discontinuous feeding bouts. It is suggested that this form of aggression conceals the attack intention of the contestant, as would be expected in the 'War of Attrition' model (Maynard Smith 1974). It is obvious that a

devil bounding into physical contact is not concealed *per se*, but relative to the ritualised transfer of RHP, the devil being attacked has little time to assess the RHP of the attacker and therefore the attack intention is effectively concealed in terms of retaliation.

I hypothesise that the ritualised encounters between devils when in competition for food can be explained via the "War of Attrition" model of Maynard Smith (1974). The relative ease with which devils can be enticed into group feeding situations makes the testing of this hypothesis feasible.

5.5 SUMMARY

1. A total of 18 postures, 7 vocaliations and 2 possible chemical signals were observed during agonistic encounters.

2. Devils have a variety of white markings located on the chest, shoulders and rump. The position and extent of these markings varied considerably, and the patterns of markings were not unique to individuals. These markings are unlikely to be critical in conspecific recognition.

3. Adult males showed a higher degree of scarring and open wounds than any other age group or sex. This is explained by the relatively longer time they needed to feed than the smaller animals to attain suffincient food per body mass, and hence their increased exposure to conspecific interactions.

4. Agonistic interactions are interpreted as ritualised encounters which seldom resulted in physical contact.

5. Feeding bouts were either continuous or discontinuous. Animals that fed in a discontinuous fashion fed for a similar time to those that fed continuously. Feeding bouts lasted on average for 34 minutes. During the average feeding bout there were 3.8 interactions which occuied 2.5 minutes of the feeding time.

6. From feeding trials at carcasses it was found that devils gorged themselves on the carcasses eating about 40% of their body weight. This consumption rate was similar to the maxima obtained via the isotope turnover technique which showed that devils fed at approximately 3 day intervals.

7. The result of agonistic interactions at the carcass was related to the amount of food consumed and therefore probably not to any form of dominance hierarchy.

8. The interactions between the feeder and non-feeder are interpreted as a transfer of information of the Resource Holding Potential (RHP model) by the feeder to the non-feeder. The frequency of interactions prior to displacement of the feeder probably reflects this transfer of RHP information.

CHAPTER 6

SPATIAL ORGANISATION AND FORAGING METHODS OF THE TASMANIAN DEVIL

6.1 INTRODUCTION

An understanding of the spatial organisation and foraging methods is integral to a description of the social organisation of a species (Brown & Orians 1970). It has been shown that there is a close relationship between the spatial organisation of a species, the foraging method, its food and the dispersion of this food (Wilson 1975, Bradbury & Vehrencamp 1976b, Kruuk & Parish 1982). This Chapter describes the spatial organisation and foraging methods of the Tasmanian devil and relates this to the dispersion pattern of its potential food.

The spatial organisation is described principally in terms of the home range of the animals. The definition of home range followed in this study is that of Burt (1943): " that area traversed by the individual in its normal activities of food gathering , mating and caring for young". Guiler (1978) showed that devils were capable of roaming over large areas (16 km per night). Consequently, for this species traditional capture recapture methods of home range determination are logistically impractical in terms of number of traps necessary to adequately cover a home range and the time taken to clear these traps. Therefore a radio tracking study was initiated, specifically designed to determine the home range of the devil, the spatial nature of the home range with respect to conspecifics and the foraging methods used by the devils within its range. The decision to use this technique was vindicated after the first few days of radio tracking animals when it was found that maintaining contact with the devils, which traveled extensively throughout the night through dense bush, was even a challenge to state of the art telemetry gear.

6.2 METHODS

6.2.1 RADIO TRACKING

Initial attempts to radio track devils between February 1985 and March 1986 every three months to assess the seasonal variation in home range size were unsuccessful due to failure of radio transmitters and receivers.

Adult residents of both sexes were fitted with radio collars after capture on the trapline. Radio collars were attached to the animal using a nylon tape (1.5 cm wide) neck collar. These were fitted to each individual by trimming excess length of collar until two fingers could be fitted between the neck and the collar. The collars were then

secured with rivets. AUSTEC transmitters were the first units to be deployed. These, after being potted in beeswax and dental acrylic weighed ≈ 100 grams, or less than 2 % of the average animals body mass. The transmitter antennae was incorporated within the collar. The transmitters operated on a 150 MHz band with each of the 10 transmitters having a distinct frequency. Transmissions were monitored on an AUSTEC receiver. Triangulation was carried out with a null-peak (5 element Yagi) antennae which was mounted on a rotating hub on the top of a vehicle. This could be rotated by the driver from within the vehicle. A hand-held 2 element Yagi was used to approach animals in the bush at night and to locate dens. After the failure of all the AUSTEC transmitters and receivers, Customs Electronics LA-12 receivers and BIOTRACK transmitters were purchased. These transmitters weighed ≈ 140 grams, or 2 % body mass, and were attached in the same way as the AUSTEC transmitters, except that they had whip antennae protruding 15 cm from the side of the collar.

Dens were located during the day from the top of Mt.William (216 m elevation). where up to 6 km range could be achieved with the 5 element Yagi antennae. Compass bearings were taken on the signals and the distance judged by the angle of declination of the bearing and the signal strength. This bearing was followed until the den was located. The precise location was determined by gradually reducing the reception of the apparatus by replacing the 5 element Yagi with the hand-held antennae as the signal strength increased until this could in turn be removed and the den located via reception without any antennae. After locating each den they were classified as burrows or surface dens and the substrate in which they were found was described. Radio collars were removed from the devils by trapping or hand-capturing animals.

Pilot studies with transmitters carried in the field at a height similar to that of a devil and through all habitat types showed that the telemetry system was accurate to within 100 metres. This observation was verified by the ease with which dens were located on bearings from up to 6 km away from the top of Mt William (Fig. 6.1). At night however locational data of foraging animals could not be collected by conventional triangulation via two or more receiver systems spaced at sufficient distance to cover the foraging range of the animals. This was because of the limited reception distance of the system relative to the distance covered by devils in one night. Although this could be achieved for approximately half of the foraging range of the study animals from the top of the mountain, the failure of receivers negated using more than one receiver station at any one time. Therefore, the locational data were obtained from a vehicle equipped with the receiving system. A bearing was obtained of the animal being tracked and then the vehicle driven approximately 1 km to the

FIGURE 6.1

Radio tracking from the top of Mt William to locate dens during the day. Note the use of a 5 element Yagi antennae and the woodland scrub and pasture distribution in the background. (Photograph by V. Monamy).

nearest vantage point and another bearing taken. These bearings were plotted on a 1:15000 map.

In addition, the locations were further refined by assessing the approximate position of the animal from the signal strength, read off the strength dial on the receiver, along both bearings. Maximum signal strength was usually associated with animals which were within 200 m. A signal of less strength, but still easy to detect and obtain a bearing was associated with a devils at a distance of between 200 m and 1 km. Faint signals were usually difficult to triangulate with and the best reception was gained from the nearest elevation point. These signals were from devils which were over 1 km away from the receiver system.

Signal strength also waxed and waned as animals traveled through sparse habitat such as pasture or heathland and into dense tea tree creeks or forests. It was found that this variation in strength contributed to the location of the animal as the predicted variation in habitat from the signal strength could be verified by checking it with aerial photographs showing habitats. Aerial photographs were taken in 1979 (TASMAP) and printed for this study at a scale scale of 1:10 000. Using the photographs distinct patches of habitat could be identified as the radio tracked animals traveled through them. These conclusions were verified by direct observations. The accuracy of triangulation was therefore variable, depending on the habitat within which the animal was moving and the inherent accuracy of the null peak receiving system. A conservative estimate of the location of the devil was made and the location point was recorded in the centre of the appropriate 0.5 x 0.5 km cell of a grid placed over the 1:15000 map of the study area.

The accuracy of the locations therefore could also vary with the time between bearings used to triangulate if the animal was moving, as was usually the case. It was predicted that the average speed of a devil would be less than 5 km/hr based on allometric relationships of the cost of moving in the Mammalia (Gordon *et al.* 1977) and the running speeds of devils on treadmills in the laboratory (S. Nicol pers comm). A devil traveling at this speed would cross the 0.25 km^2 cell in 6 minutes. All triangulations were therefore made within this time frame.

To facilitate direct observations of animals, Beta lights (Roe Saunders, Britain) and Light Emitting Diodes were attached to two and four animals respectively. For direct observation, 7 X 50 binoculars were used.

Individual devils were generally tracked for two to four weeks (Table 6.1). One animal, L24 could not be recaptured after tracking in August 1985 and hence

carried a radio collar through to December of that year providing data on den fidelity. Animals were followed from dawn to dusk where possible and triangulations carried out every 30 minutes or when the animal was moving rapidly, every time it left a 0.5 km^2 cell and entered another. Thirteen animals were radio tracked in this manner.

6.2.2 HOME RANGE SIZE

There is a plethora of models with which to analyse the range size of an animal (for summaries see: Kenward 1987, Macdonald *et al.* 1980, Worton 1987). The Minimum Convex Polygon method (MCP) of range size determination (Dalke & Sime 1938, Mohr 1947) was the principal method used to analyse home range in this study. MCP has been widely used in the past (see summary: Harestad & Bunnell 1979) and so use of the method in this study facilitated comparison of results with other studies . However, as with all models, the MCP method has several drawbacks such as its dependence on sample size which, when increased, does not decrease the variance. Also the MCP model assumes that the entire home range is used with equal intensity thereby possibly including much non-utilised space (Worton 1987). Therefore, the nonparametric Dixon and Chapman model which incorporates centres of activity and is relatively robust to small sample sizes (Worton 1987, Kenward 1987, A. Cockburn pers comm) was used as a second measure of home range size. The results from the two models were then compared.

The relationship between home range size and sample size was analysed by examining the data from the first animal for which successive nights of location points were available. In this way the sample size required for accurate assessment of home range size was determined early in the study. The criteria established from this analysis was applied to all animals tracked subsequently.

In the assessment of home range from the MCP model all location points were plotted in the centre of the appropriate cell on a 0.25 km^2 grid and the MCP drawn around these points. The area of the home range was calculated by totaling the number of cells within the MCP boundary. All cells lying in non-useable areas (e.g. ocean) were excluded thus reducing the potential error of the calculation. To gain a measure of the potential variation that may be induced by an actual location being in 1) the middle of the cell (where it is assumed to be and referred to as the mean) 2) on the boundary closest to the next MCP enclosed cell (the minimum) or 3) on the boundary furthest from it (the maximum), the MCP was measured at three scales. The minimum MCP estimate was calculated by ignoring all cells actually dissected by the MCP boundary so that the only cells counted were entire cells within the MCP. The mean MCP was calculated by adding 0.125 km^2 (1/2 cell) and the maximum by adding 0.25 km^2 (1 cell) for every cell dissected by the MCP boundary. The degree of overlap

between the home ranges of the tracked animals was calculated by plotting all the MCPs on the same grid and measuring the area of each animals home range that did not overlap with another. This was then calculated as a percentage of the home range of the respective animals.

The Dixon and Chapman model was run by Dr. A Cockburn, Australian National University. The use of this nonparametric technique relies on the location points being independent of each other and hence only those points separated by three hours or more were used (Worton 1987, Jaremovic & Croft 1987). The home range was calculated as the area containing 95 % of the location points, considered to be a close approximation of the home range area (Dixon & Chapman 1980, Jaremovic & Croft 1987, A. Cockburn pers comm). This method was used to calculate the home range of three male and three female devils.

6.2.3 FORAGING MODE

Continuous observations were used to calculate the foraging mode of the devil with respect to the distance covered in a set time in relation to the time from when the devil first left the den. The distance and time records were extracted from field notes of the movements of the continuously tracked animals. These were transcribed onto the 0.25 km^2 grid and the distance calculated by direct measurement when cells were adjacent to each other or with Pythagoras' theorem when the successive locations were diagonally opposed to each other. Hence calculations could only be made on animals that traveled out of one cell and into another. Again, the accuracy of the calculations depends on the validity of the assumption that the animals were located in the centre of either cell. Where absolute data are used, rather than means, interpretations should take into account the potential bias. Analyses of pooled data which produce trends for the 'average devil' should be valid as there is no reason to expect the distribution of localities to be biased to any one side of the cell and therefore provide a skewed distribution in the data. On the contrary, the locational deviations within the cell would be randomly distributed across the sample and taking into account the large sample size of the pooled data, the results are assumed to be sufficiently accurate.

The start and finish of a bout of activity was defined as the period bounded by no movement and these in turn were called bouts of inactivity. All bouts were analysed in terms of their duration and the distance covered during the bout.

The average nightly bout was described with respect to the time taken and the distance traveled. Only those animals that were tracked from leaving the den in the evening to entering the den in the morning were used in these analyses. The percentage activity per hour through the night was calculated and plotted against time.

This was done separately for data from summer and winter. The summer sample constituted data from those devils which were tracked for the entire night. The winter sample however, due to a smaller sample size, included data from any devil which was tracked past midnight, but not necessarily for the entire night. In these analyses of individual movements I have interpreted records of activity as foraging as the devils could not be directly observed.

The distance, speed and direction of of travel by each animal that was tracked for more than half the night were plotted against time and the mode of foraging interpreted. Interpretation was based on the presence of active versus inactive records sequentially through the night. Thus animals could be described as either foraging continuously and at a regular pace all night, not foraging at all, or some intermediary between these extremes. The time to commencement or cessation of foraging with respect to sunrise and sunset was calculated.

6.2.4 LATRINES

Latrines were located on an opportunistic basis throughout the study period. The position of the latrines relative to the local topographic features were noted and the number of fresh scats counted.

6.3 RESULTS

A total of 13 animals were radio tracked with varying degrees of success with respect to reliable locational data during the day or night. Locational data during the day was obtained for 139 animal days and 263 animal hours in total (Table 6.1). Animal number L66 was tracked at the beginning of 1985 and again from December 1985 through to January 1986 and is therefore listed twice.

6.3.1 THE USE OF DENS

The 13 radio collared individuals were located in a total of 50 dens during the day. The number of dens per individual varied from 1 to 10 with a mean of 3.8 ± 2.1 dens per animal (Table 6.2). There was no significant difference between the number of dens held by females or males. The den which was most frequently used by each individual was referred to as the primary den (Table 6.3). The apparent difference between the sexes where males used one den on 45 % of occasions and the females on 64 %of occasions, is probably the result of the denning characteristics of one female L210 and one male R273 (Table 6.3). The animals usually changed dens every day or within three days of occupying a den (Table 6.4). There was marked intra-animal variation of this trend with one animal occupying a den for 25 consecutive nights and three others for 8 consecutive nights (Table 6.4).

The presence of dependent young in the dens was shown by trapping during late lactation. Traps were set at the entrance of two den sites which had only one

TABLE 6.1 The identification number and sex of the animals radio-tracked and the time they were tracked for.

I.D.	Sex	Duration radio-tracked	
		Period	Days triangulated
L214	Female	6 Feb to 14 March 1985	18
R236	Male	9 Feb to 14 March 1985	13
L210	Female	11 June to 26 June 1985	13
L36	Male	9 Feb to 6 March 1985	6
L66	Female	22 Feb to 12 March 1985	6
L128	Female	14 Aug to 23 Aug 1985	5
R372	Male	9 Aug to 24 Aug 1985	11
L24	Female	15 Aug to 11 Dec 1985	14
L216	Female	12 Dec to 12 Jan 1986	22
L66	Female	12 Dec to 3 Jan 1986	9
R384	Male	8 Jan to 19 Jan 1986	8
R273	Male	12 Feb to 16 March 1986	19
L88	Male	13 March to 26 March 1986	10
L107	Female	25 March to 29 March 1986	3

TABLE 6.2 The number of dens per devil for males and females.

Sex	1	2	3	4	5	10
Males			1	2	2	
Females	1	1	3	3		1
Total	1	1	4	5	1	1
%	7.7	7.7	30.6	7.7	7.7	7.7

TABLE 6.3 The number of dens and the fequency with which specified dens were used by devils as determined by radio-tracking.

Sex	I.D.	Dens n	No. of days in a specified den*							
			A	B	C	D	E	F	G	H
Females	L214	4	25	2	1	1				
	L216	4	7	5	4	2				
	L66	3	7	4	1					
	L66	4	1	1	1	1				
	L210	10	3	2	1	1	1	1	1	1
	L24	1	12							
	L128	2	4	1						
	L107	3	1	1						
	Total n		60	16	8	5	1	1	1	1
	%		64.5	17.2	8.6	5.3	1	1	1	1
Males	L88	4	1	1	1	1				
	R384	4	1	1	1	1				
	R273	5	8	5	2	2	1			
	R236	3	4	3	1					
	R372	3	4	1	1					
	Total n		18	11	6	4	1			
	%		45	27.5	15	10	2.5			
Total n			78	27	14	9	2	1	1	1
%			58.6	20.3	10.5	6.8	1.5	0.4	0.4	0.4

* Dens designated as A-H are specific to each individual devil and are not shared by other devils.

TABLE 6.4 The frequency with which devils used the same den in consecutive days

Sex	I.D.	No. of consecutive days in the same den								
		1	2	3	4	5	6	7	8	25
Female	L214	2	1							1
	L216	9	3							
	L66	6	2	1						
	L66									
	L210	6	1							
	L24	1					1		1	
	L128								1	
	L107	3								
	TOTAL	26	7	1			1		2	1
Male	L88	1								
	R384	2								
	R273	4	2			1			1	
	R236	1	1							
	R372	1	2	1						
	TOTAL	9	5	1		1			1	
TOTAL n		35	12	2		1	1		3	1
%		63	22	4		2	2		5	2

entrance per den. On three separate occasions the young were trapped suggesting that they were tenacious to den. The presence of young in the dens of L24 and L128 in August was indicated by fresh puncture marks on the radio transmitters of the females. Young were never seen traveling on or with the females as has been reported in the literature (Strahan 1983). The dens containing the young were always the primary den of the female.

Most dens (89 %) were in burrows in the soil, the remainder being on the surface or in log heaps (Table 6.5). The dens in log heaps could not be verified as being surface dens or burrows because of the size of the log heaps and the density of logs within them. Burrows are certainly found in the soil under log heaps when the log heaps are cleared (D. Pemberton pers obs), and wombats, which always den in burrows, were seen to emerge from log heaps in the study area. The uncertainty of the type of dens within the log heaps is not of major importance as there were relatively few dens situated within log heaps.

The most common burrow type used for denning was located in the parallel longitudinal Quaternary dunes which traverse the northern portion of the National Park. These burrows were usually in the form of a warren and were used by other devils and wombats. They were all located above the surrounding wetlands.

The animals that were found denning on the surface seldom moved when the observer was attempting to locate them and on three occasions the animals lay quitely while the condition of the whip antennae and collar was checked. One devil found on the surface moved around the observer in thick ferns, but never ran off and when last seen was within 10 m of its original den site. These surface dens did not contain any bedding material although this has been observed in devil dens in caves in other parts of Tasmania (D. Pemberton pers obs, N. Mooney pers comm). The surface dens in the forests were located under thick *Lomandra* tussocks and those in the tea tree creeks in thick coral fern (*Gleichenia* sp).The animals were well concealed in these dens and could only be located with the aid of radio tracking equipment. No animals denning in hollow logs were ever found .

One animal, R273 an adult male was observed inhabiting a den continuosly for a period of 8 days from 24 February to the 3 March. Because of the duration of the occupancy a small hole was excavated into the den after 5 days of den occupancy. There was a female present in the den with the male. These animals appeared to be involved in courtship as evidenced by the duration of occupancy of the den and the occurence of the event within the copulation period for devils. Nine days later the same male occupied another den for 5 days.

TABLE 6.5 Classification of den types used by devils

	Burrows				Surface		Log heap
	Warren	Single					
	Fossil dunes	Exposed hill	Forest	Tea tree	Forest	Tea tree creek	
n	25	7	6	3	2	3	4
%	54.3	15.2	13	6.5	4.4	6.5	8.7
% per den type		89				10.9	8.7

6.3.2 HOME RANGE SIZE

The relationship between home range size as determined by the MCP method and sample size is shown in Figure 6.2. Home range size was dependent on sample size, that is, the number of location points, until the number of fixes exceeded 40. Therefore, at least 40 fixes collected over a period of 5 days were necessary before home range area was independent of sample size. The data from one animal (L66) did not meet this criteria and therefore were not used in the analyses. Nonparametric methods of home range determination typically need between 20 and 100 independent locations per animal for accurate analyses (Cameron & Spencer 1985, Worton 1987, Kenward 1987). In attempting to satisfy the requirement of independent locations, this sample size was not achieved for two animals used in Dixon & Chapman estimate (Table 6.6). These data were treated with caution.

The home range sizes as calculated by the MCP method were similar to those calculated by the Dixon and Chapman model (Table 6.6). Of the three estimates of MCP (minimum, mean and maximum) the maximum estimate showed closest agreement with the Dixon and Chapman estimates. In light of these corroborative data, the maximum MCP area estimate was accepted as the measure of home range size in the devil and referred to as the home range size.

The mean home range size was 13.3 $km^2 \pm 7.0$ (range 4 - 26.7, n = 9). The smallest home range size was 4.0 km^2 measured in August for the female L 24. This animal denned its young for the first time during the tracking period. The largest home range area was that measured for L210, a resident adult female. There was no significant difference between the range sizes of males and females calculated by the MCP method ($t=0.13$, $DF=7$, $p> 0.5$). There were insufficient data to test for seasonal differences in home range size.

The overlap between home ranges of the tracked animals is considerable (Fig. 6.3). Five of the animals overlapped totally with the other animals whilst four others had a portion of their home range which was exclusive (Table 6.7). The mean home range overlap for the 9 animals was 84.1%. The total area covered by the home ranges of the radio tracked animals and calculated by pooling all location points and drawing a maximum MCP around them was 46 km^2 (Fig. 6.4).

6.3.2.1 Home range location and habitat

The MCP boundaries for all the animals in Table 6.6 are shown as overlays of the habitat boundaries in Mt. William (Figures 6.5a to 6.5i). Most of the area covered

TABLE 6.6 The home range size (square km) as calculated by the MCP method and the Chapman and Dixon model. (n=no. of location points)

I.D.	Sex	MCP				Chapman & Dixon	
			home range				
		n	Minimum	Mean	Maximum	n	home range
L214	Female	28	7.25	10.00	12.75	27	15.10
R236	Male	58	4.75	7.50	10.25		
L210	Female	79	18.25	22.50	26.75	35	32.01
L24	Female	30	0.75	1.63	4.00		
L66	Female	46	5.25	9.63	14.00		
R384	Male	56	5.50	8.25	11.00	20	6.17
R273	Male	46	14.25	18.38	22.50	12	13.84
L88	Male	31	3.50	5.88	8.25	17	6.84
L216	Female	38	5.25	7.75	10.25	56	19.80
Mean			6.7±5.43	9.59±6.31	13.3±7.09		15.63±9.56

TABLE 6.7 The area of each home range that overlaps with another *

I.D.	Range size	Area overlapping	% overlapping
L214	12.75	12.75	100.0
L24	4.00	4.00	100.0
L66	14.00	10.25	73.2
R384	11.00	4.50	41.0
R273	22.50	20.50	91.0
L88	8.25	8.25	100.0
L216	10.25	10.25	100.0
Mean			84.1

* The index of overlap refers to that area common to two or more daily home ranges.

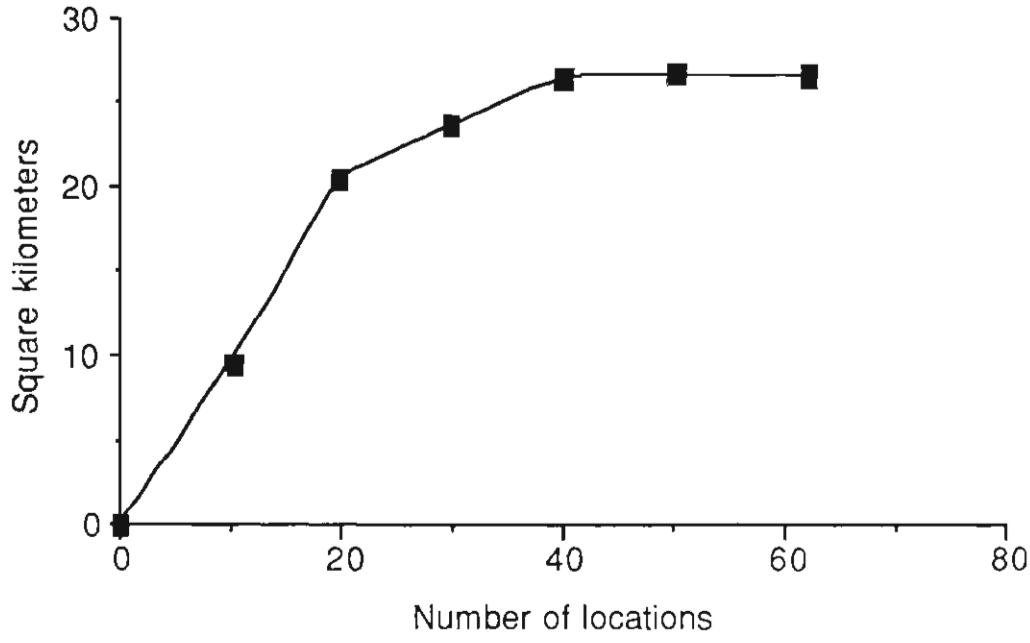


FIGURE 6.2 Size of the home range in relation to the number of locations collected.

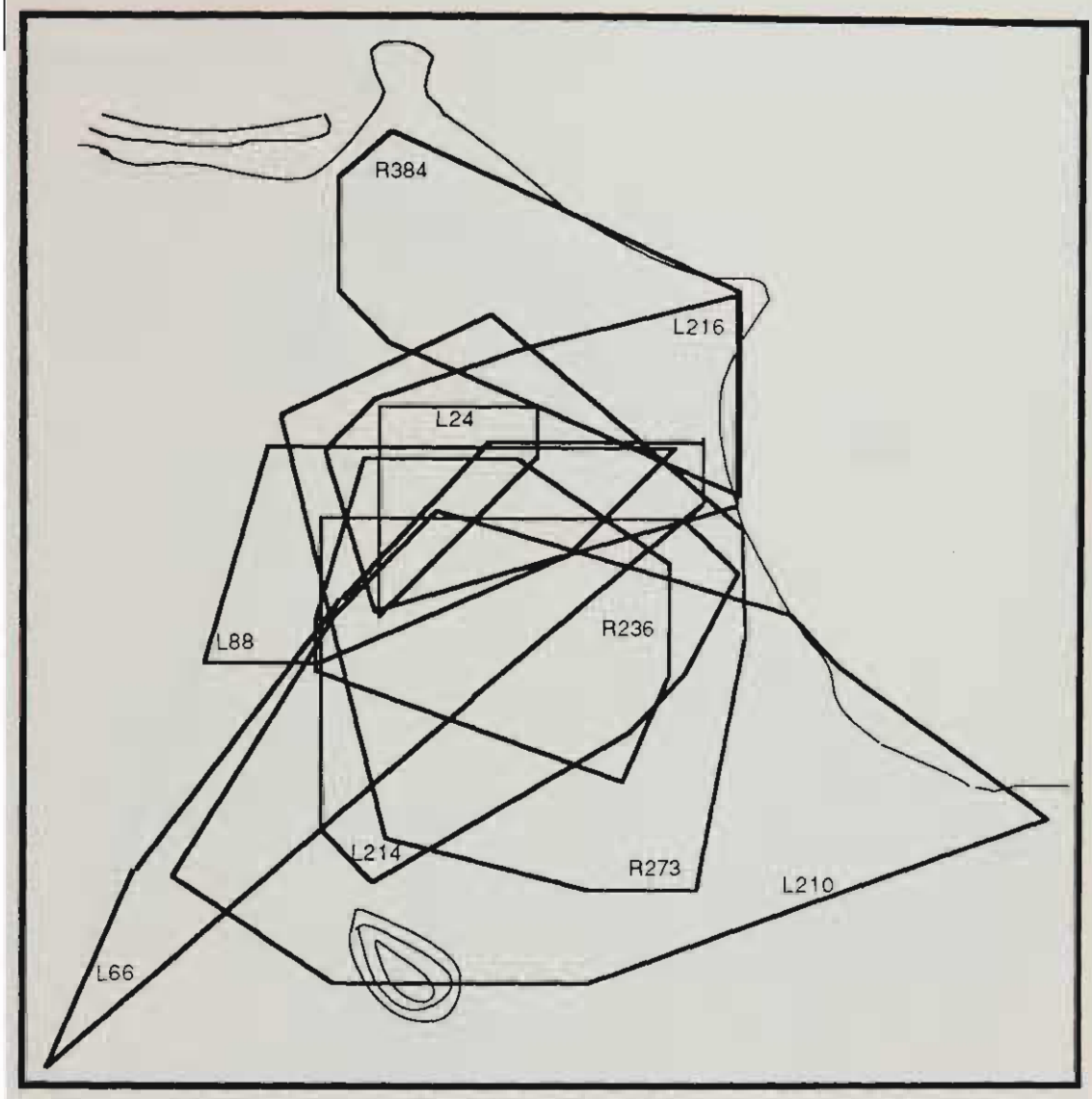


FIGURE 6.3 The ranges of all devils as determined by radio tracking showing the degree of overlap of the ranges. Devil ID numbers are shown alongside the estimated home range. Coast and Mt. William are shown for orientation.

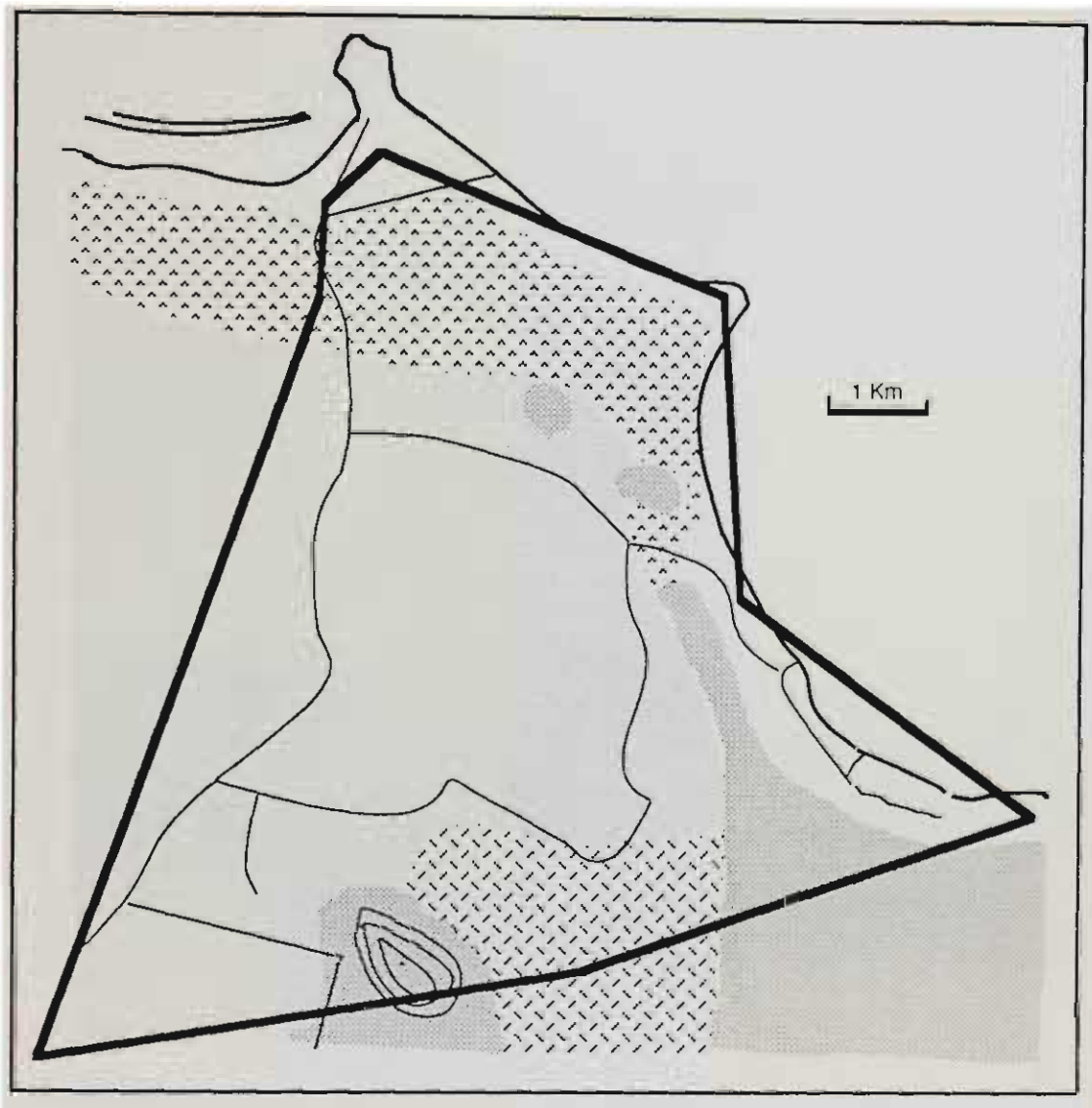


FIGURE 6.4 The range of the resident population as interpreted from individual home ranges. Vegetation types shown in Figure 1.2.

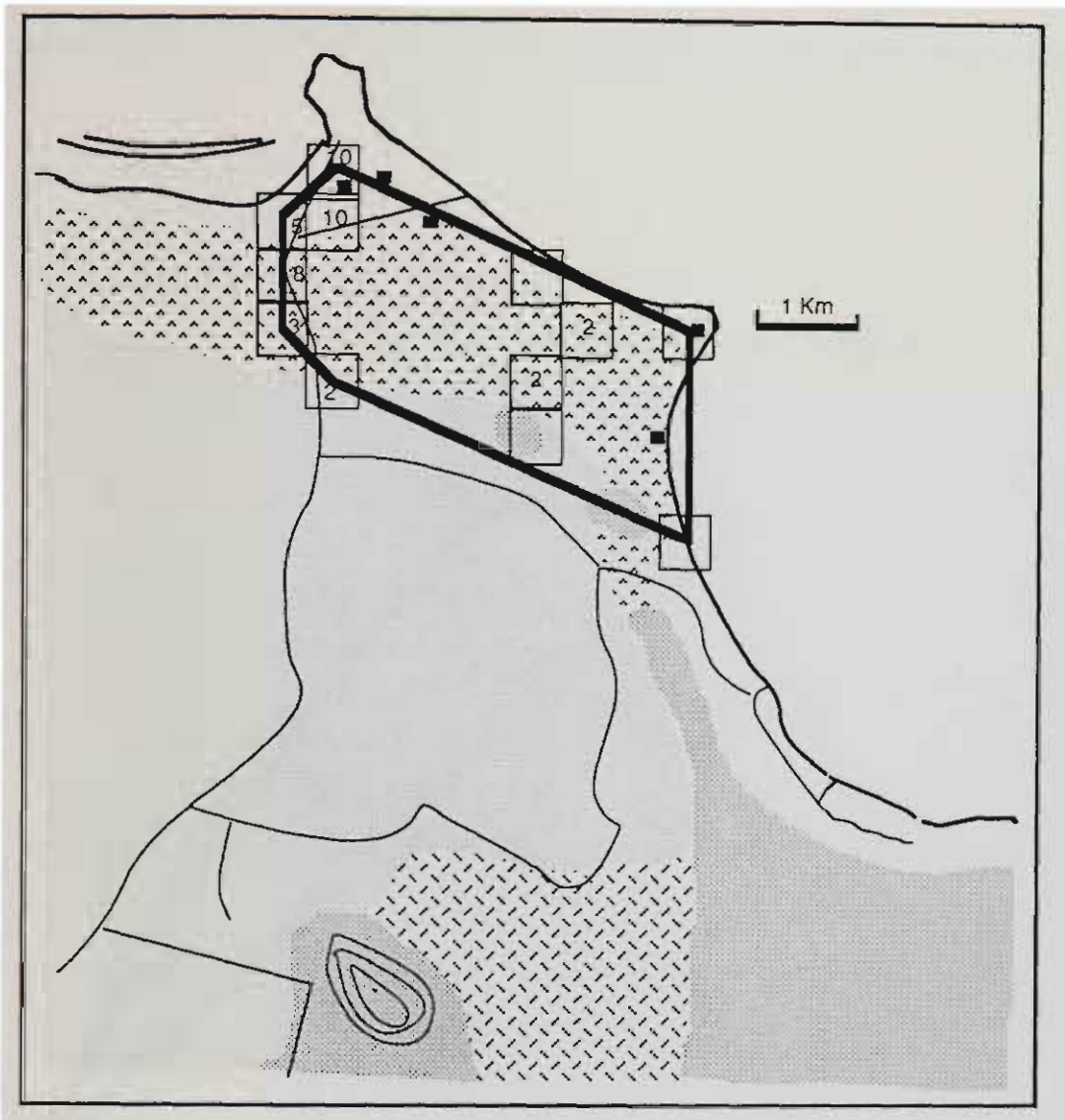


FIGURE 6.5a

Range of male no. R384, observed by radio-tracking. Stippling indicates habitat as per key on Figure 1.2. The black squares indicate the locality of dens used by the animal. The open squares are the cells in which the animals were located by triangulation and the numbers in the cell frequency with which animals were located in the cell if they were caught in a cell more than once.

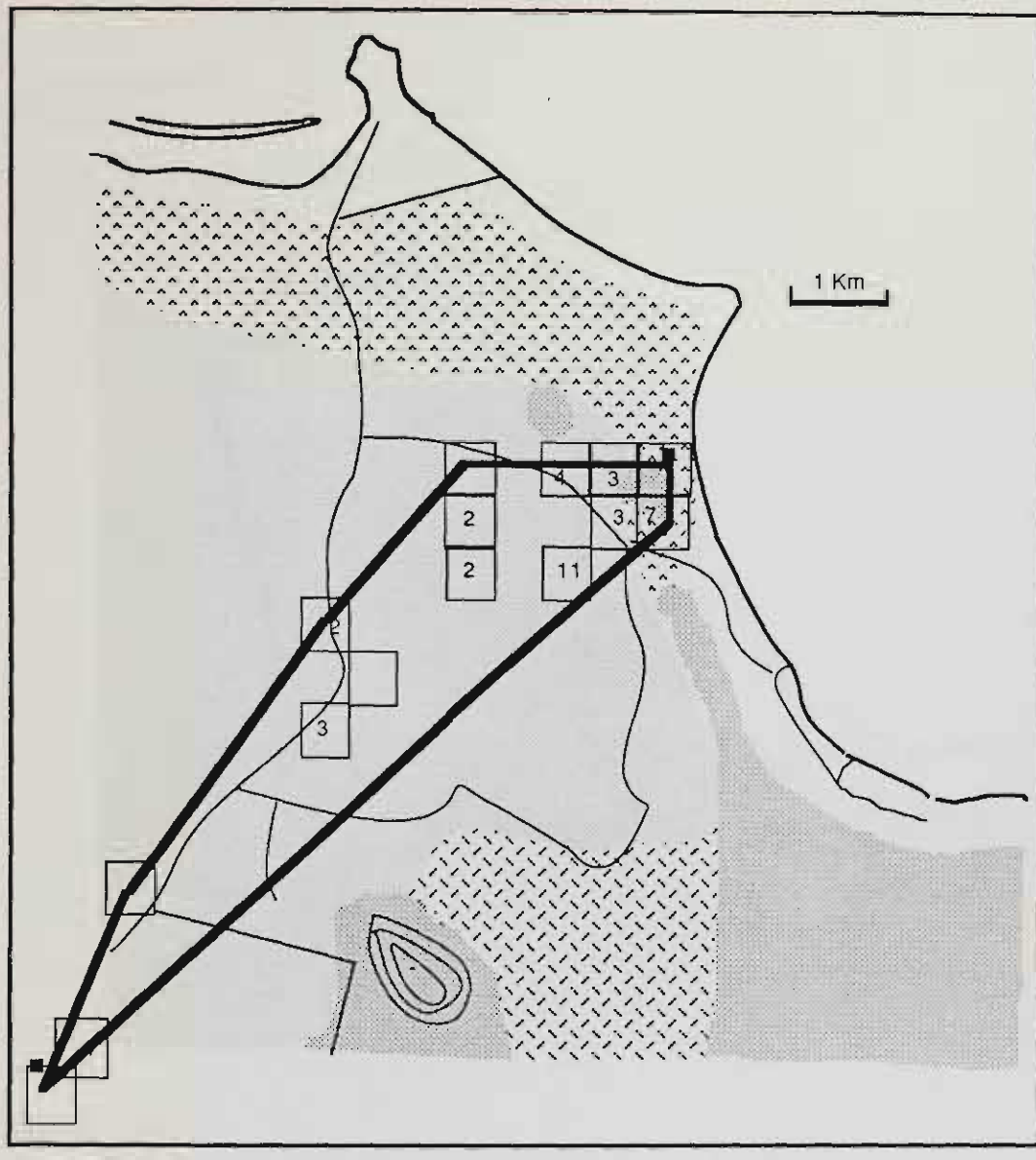


FIGURE 6.5b

Range of female no. L66, observed by radio-tracking. Stippling indicates habitat as per key on Figure 1.2. The black squares indicate the locality of dens used by the animal. The open squares are the cells in which the animals were located by triangulation and the numbers in the cell frequency with which animals were located in the cell if they were caught in a cell more than once.

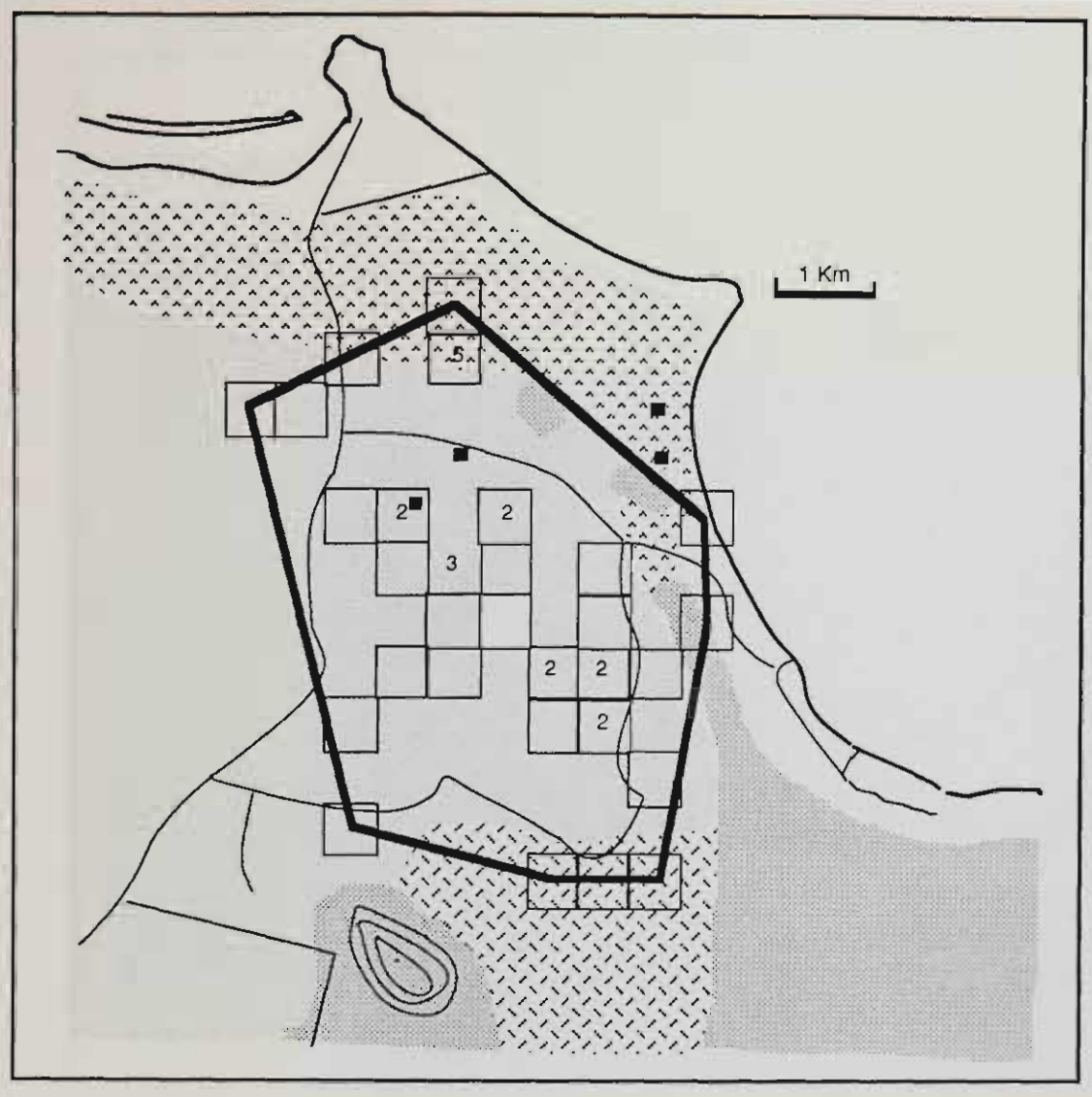


FIGURE 6.5c

Range of male no. R273, observed by radio-tracking. Stippling indicates habitat as per key on Figure 1.2. The black squares indicate the locality of dens used by the animal. The open squares are the cells in which the animals were located by triangulation and the numbers in the cell frequency with which animals were located in the cell if they were caught in a cell more than once.

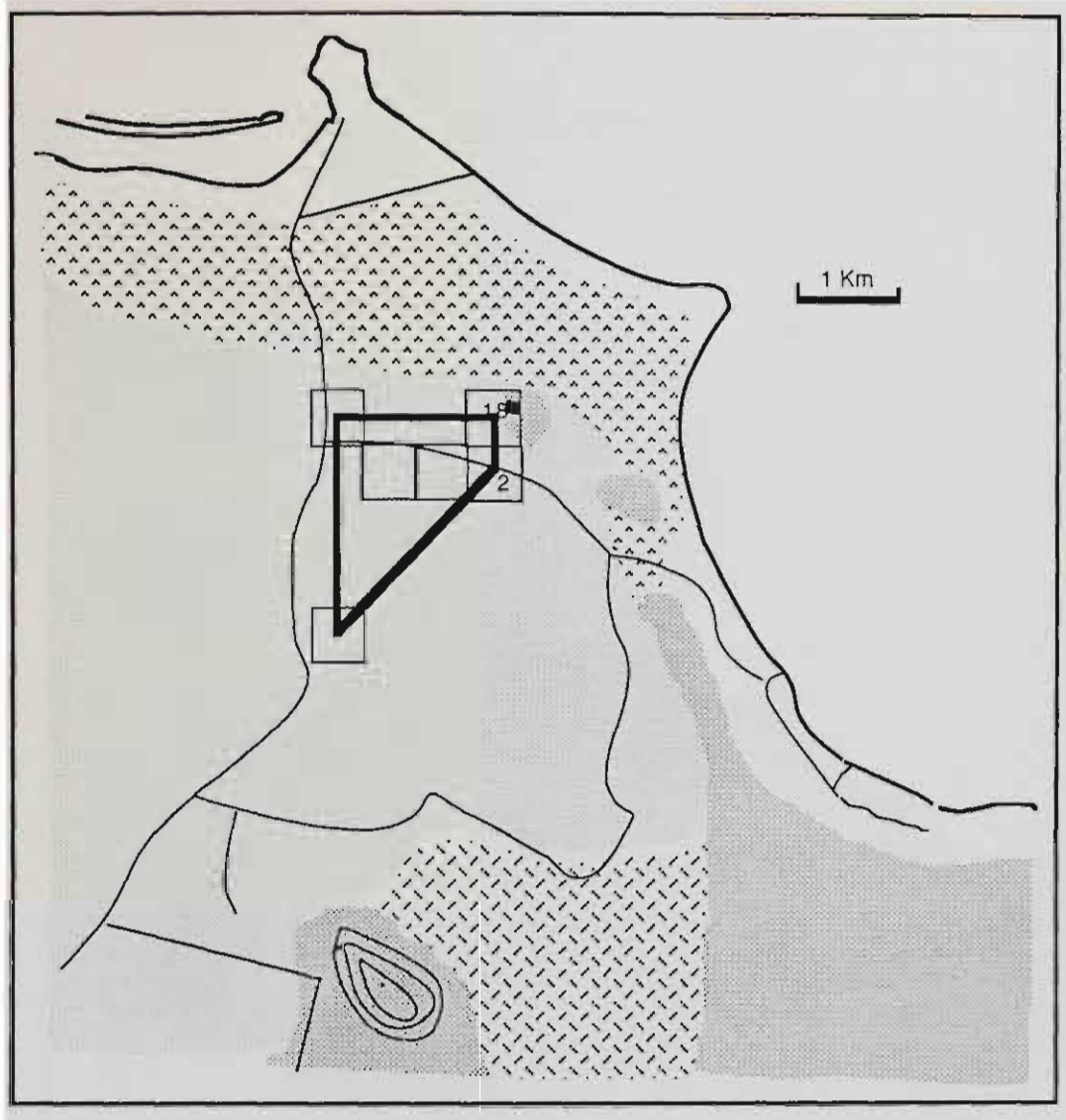


FIGURE 6.5d

Range of female no. L24, observed by radio-tracking. Stippling indicates habitat as per key on Figure 1.2. The black squares indicate the locality of dens used by the animal. The open squares are the cells in which the animals were located by triangulation and the numbers in the cell frequency with which animals were located in the cell if they were caught in a cell more than once.

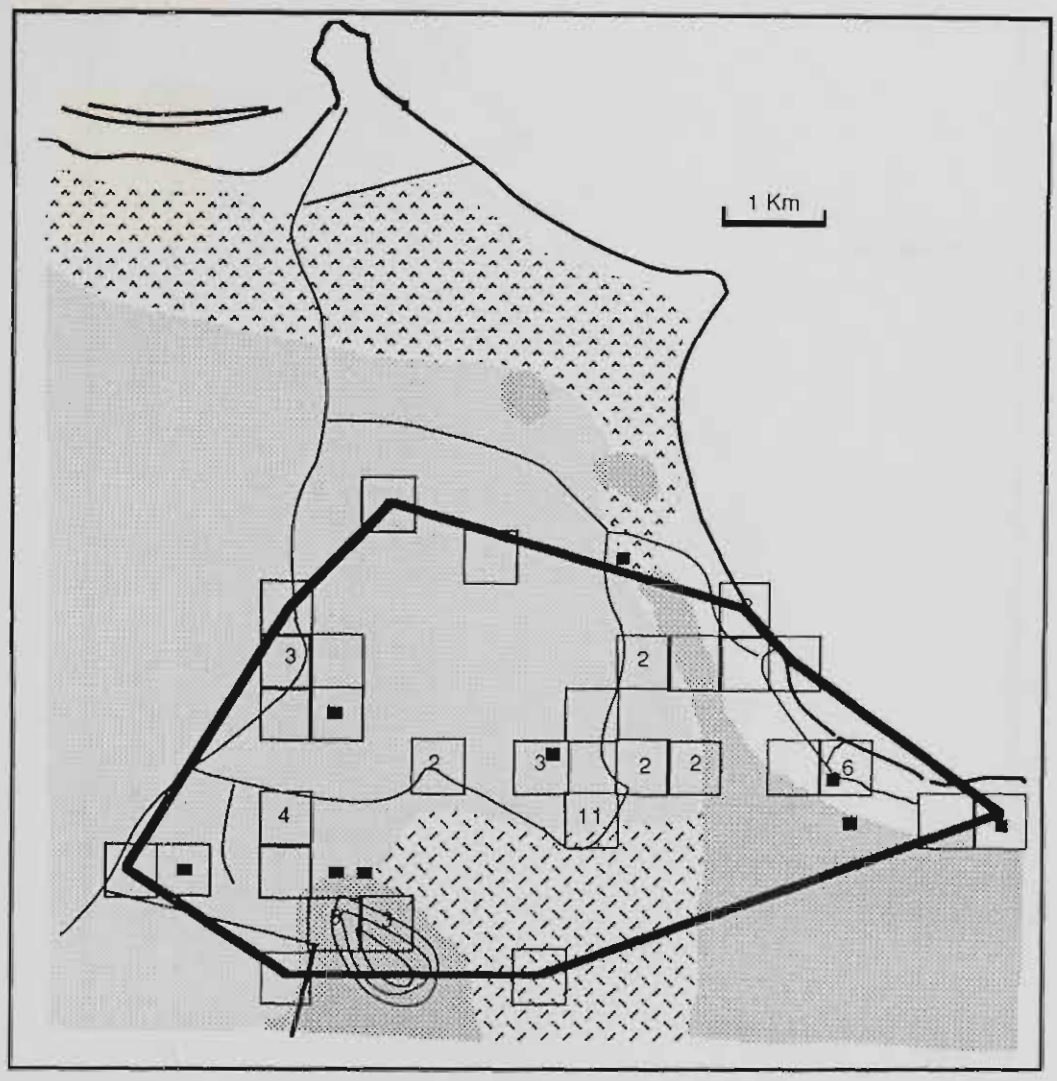


FIGURE 6.5e

Range of female no. L210, observed by radio-tracking. Stippling indicates habitat as per key on Figure 1.2. The black squares indicate the locality of dens used by the animal. The open squares are the cells in which the animals were located by triangulation and the numbers in the cell frequency with which animals were located in the cell if they were caught in a cell more than once.

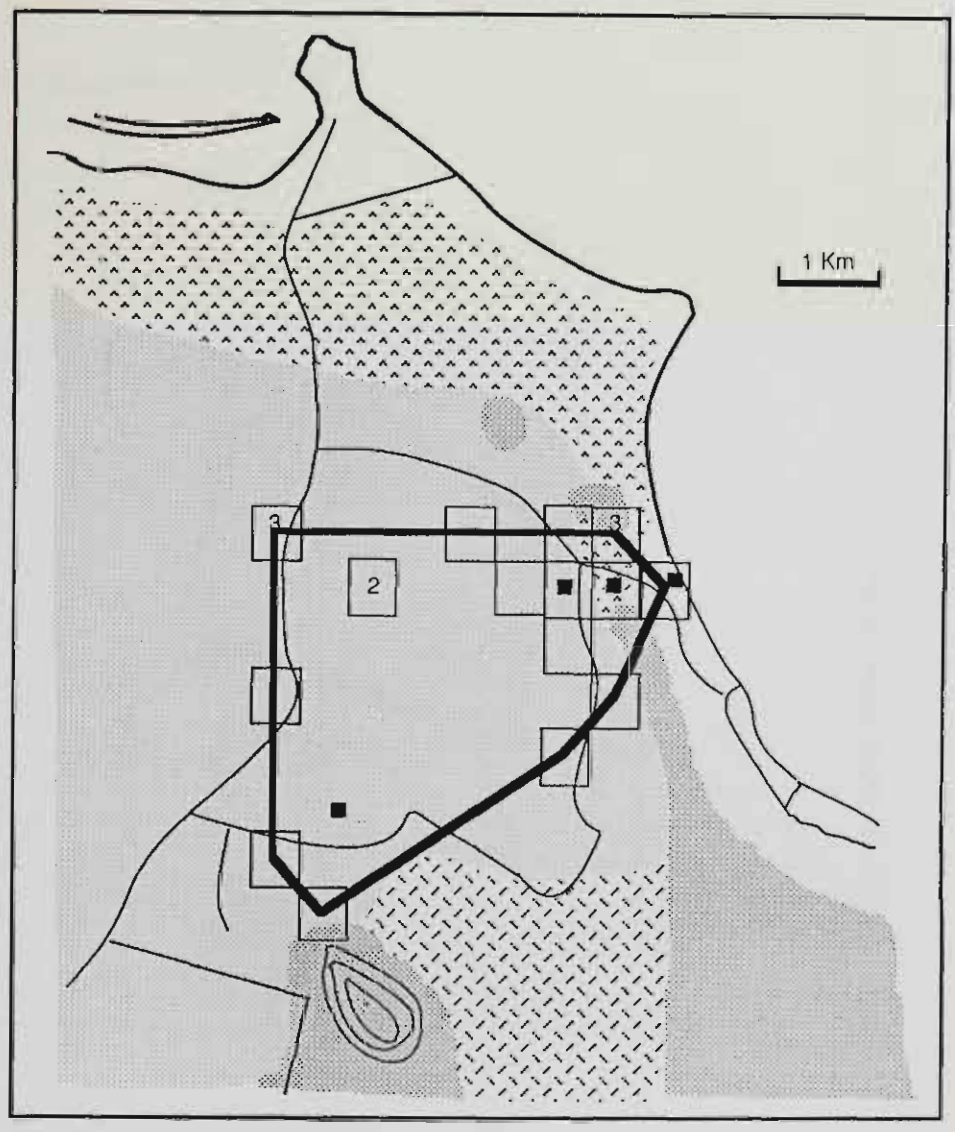


FIGURE 6.5f

Range of female no. L214, observed by radio-tracking. Stippling indicates habitat as per key on Figure 1.2. The black squares indicate the locality of dens used by the animal. The open squares are the cells in which the animals were located by triangulation and the numbers in the cell frequency with which animals were located in the cell if they were caught in a cell more than once.

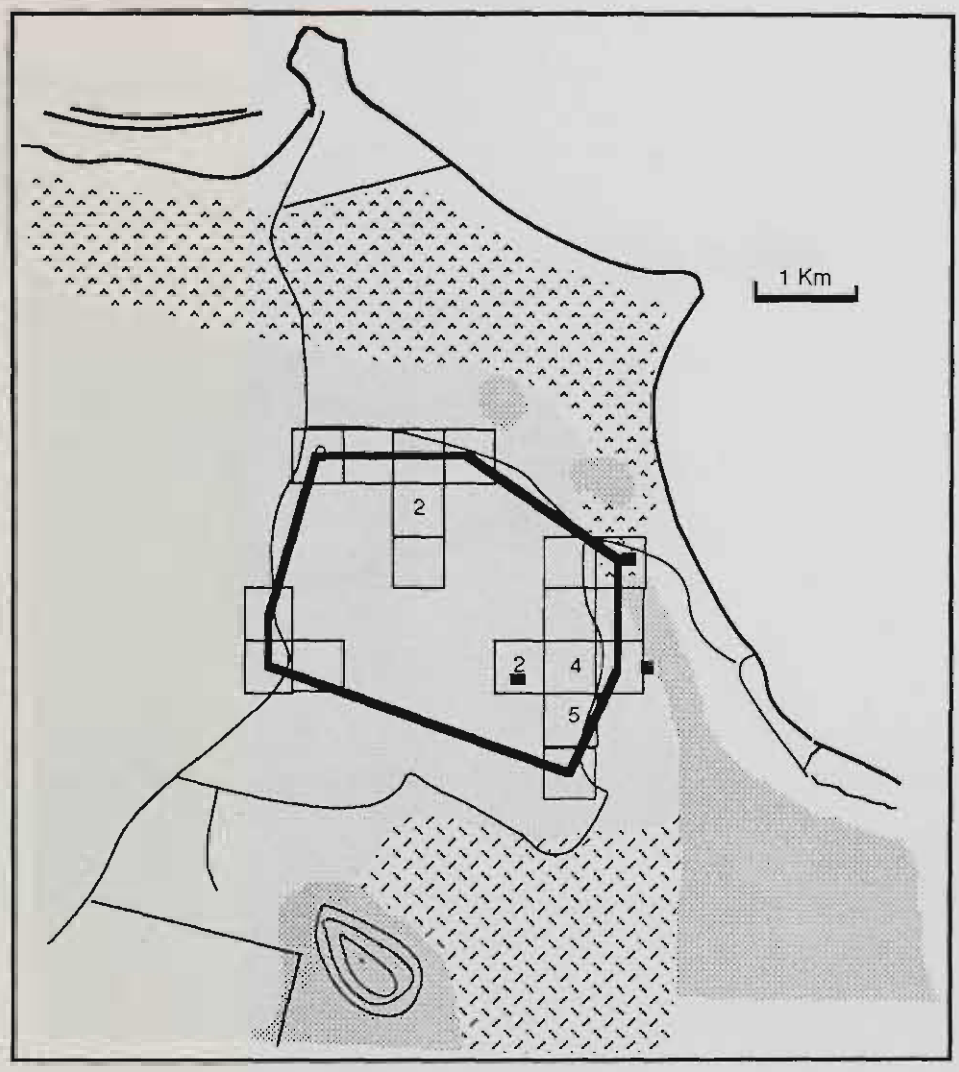


FIGURE 6.5g

Range of male no. R236, observed by radio-tracking. Stippling indicates habitat as per key on Figure 1.2. The black squares indicate the locality of dens used by the animal. The open squares are the cells in which the animals were located by triangulation and the numbers in the cell frequency with which animals were located in the cell if they were caught in a cell more than once.

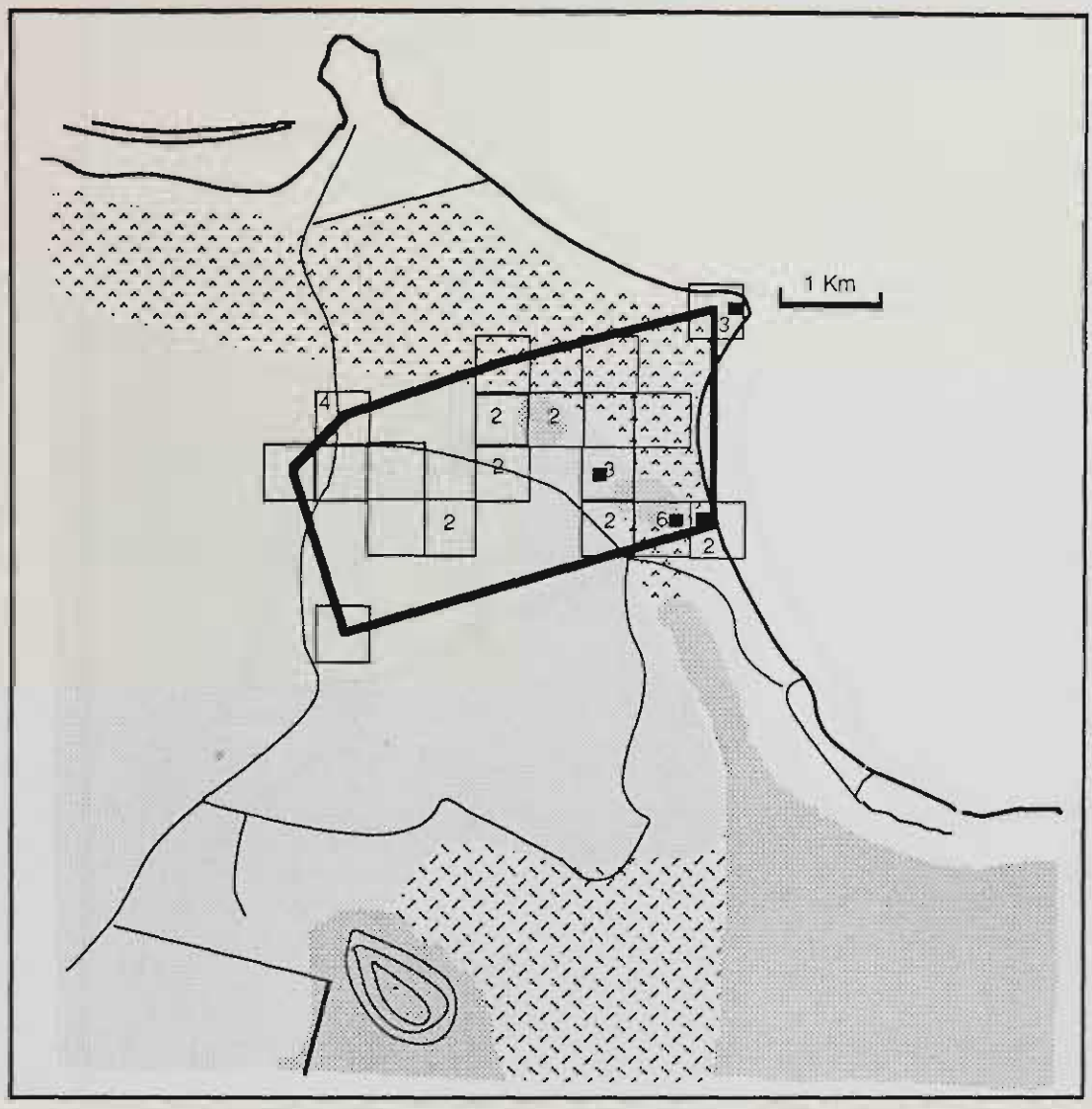


FIGURE 6.5h

Range of female no. L216, observed by radio-tracking. Stippling indicates habitat as per key on Figure 1.2. The black squares indicate the locality of dens used by the animal. The open squares are the cells in which the animals were located by triangulation and the numbers in the cell frequency with which animals were located in the cell if they were caught in a cell more than once.

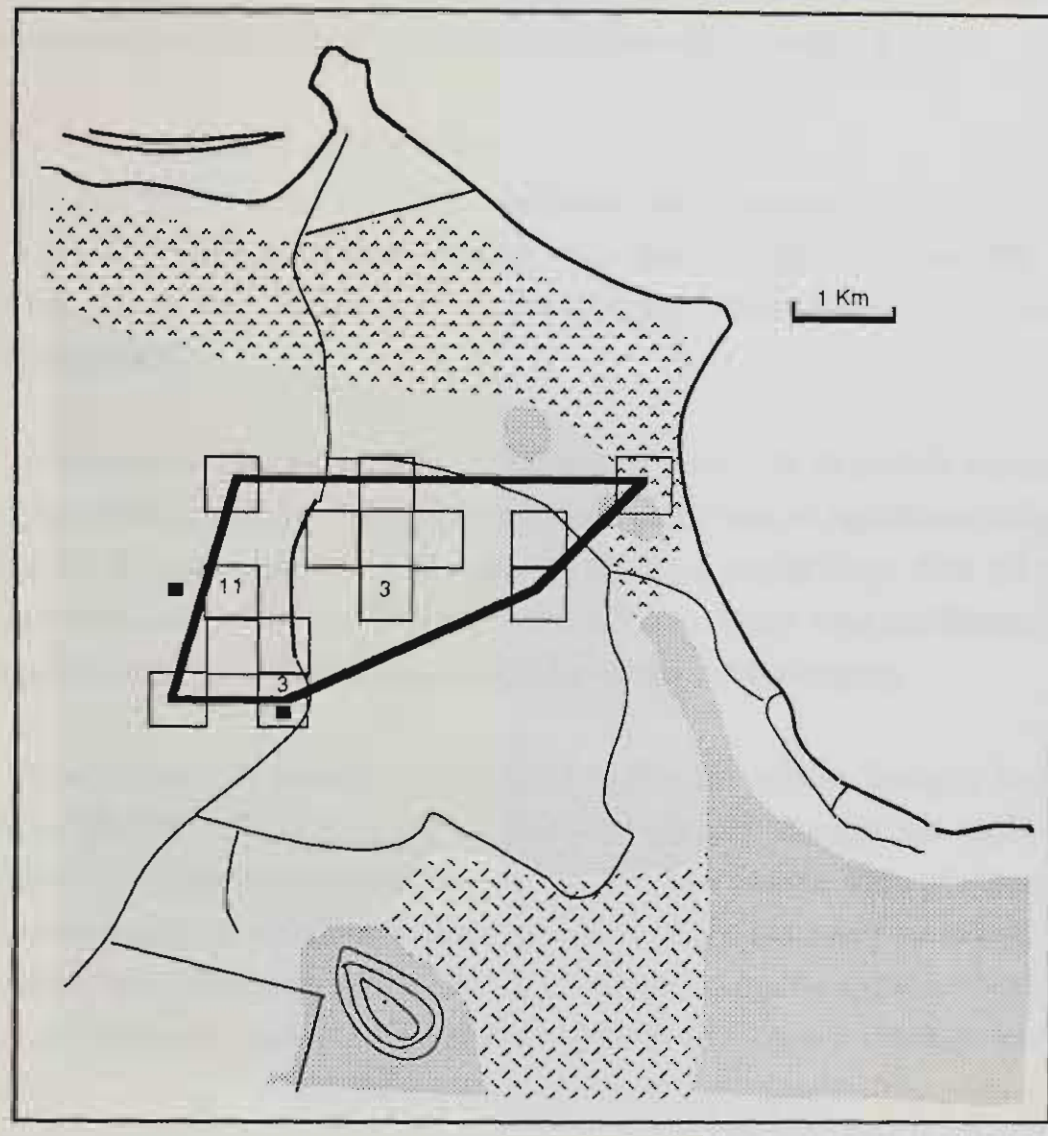


FIGURE 6.5i

Range of male no. L88, observed by radio-tracking. Stippling indicates habitat as per key on Figure 1.2. The black squares indicate the locality of dens used by the animal. The open squares are the cells in which the animals were located by triangulation and the numbers in the cell frequency with which animals were located in the cell if they were caught in a cell more than once.

by the home ranges was located within Mt. William national park. The home ranges of all the devils, except R384, were predominantly charaterised by the pasture forest habitat. The home range of R384 was located in the wetlands at the north of the Park and incorporated the Musselroe Bay holiday village and tip site (Fig 6.5a).

6.3.3 FORAGING STRATEGY

Of all the 244 bouts recorded, the devils were stationary (inactive) for 75 (30.8 %) bouts. Of the active animals most were speeds of up to 2 km/hr (Fig. 6.6). Devils can however reach speeds of 10 km/hour and can travel up to 8 kilometres without stopping.

Eight devils that were tracked from den to den on 19 occasions traversed a mean distance of 8.6 km in a mean of 7 hr 40 min. There was no significant difference between the distance and time of a complete foraging period from dusk till dawn between males and females ($t = 0.122$, $DF=14$, $p > 0.5$). These time and distance data translate to a mean speed 1.1 km/hr during the average nights foraging.

Examples of the patterns of the bouts within the nightly foraging bout are shown in Figures 6.7a to 6.7j. Three patterns of bouts through the night were identified: Exponential, Linear and Stepped. The first two take the form of exponential and linear regressions whilst the Stepped strategy includes stationary periods of more than half an hour. The speed with which devils foraged supports this classification as the speed increased from the Stepped strategy to the Linear strategy with the Exponential strategy having the most consistently high speeds. The plots of the foraging route (Fig. 6.7a - 6.7j) show that the devils usually returned via a loop to the starting area, and in some cases to the original den. The area encompassed by the loop varied but circular to square formats were common.

The activity pattern calculated from all the radio tracking records was shown in Figure 5.4 (Chapter 5) and the results are pertinent here. In summer there was burst in activity at the start of the evening that subsequently decreases until the devils return to dens at dawn. The data for winter is not as detailed, but the trend appears to be for a more sporadic pattern. The start of activity in the evening was similar for the two seasons with a mean of 74 ± 31.2 minutes ($n = 34$ range = 13 to 128) between sunset and the start in activity. In summer the devils remained foraging until 5 ± 50.1 minutes ($n = 14$, range = -127 to 56) after sunset. There are insufficient data to assess total foraging time of devils during the winter months.

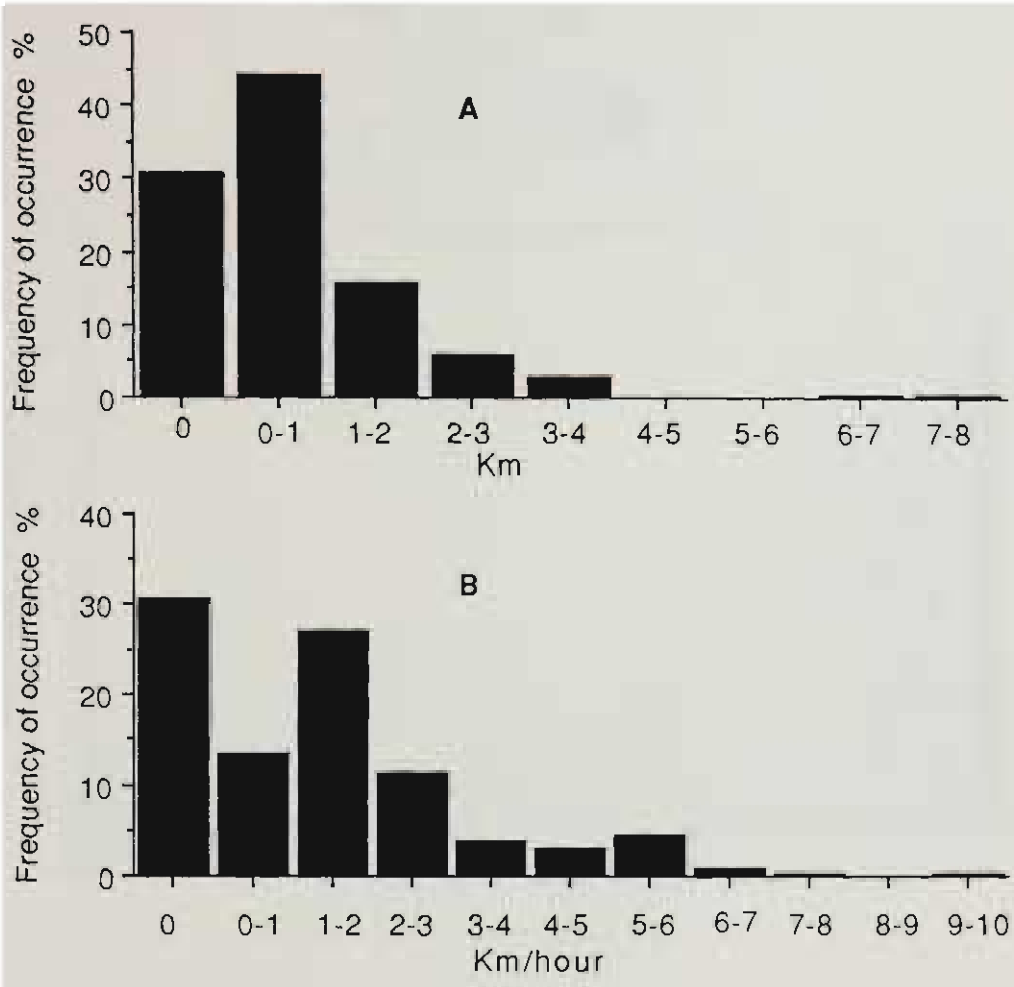


FIGURE 6.6 The frequency of occurrence (%) of distances covered (A) and speeds traveled (B) during foraging bouts (n=244 bouts). See section 6.2.3 for a definition of foraging bouts. Data based on continuous tracking from den to den.

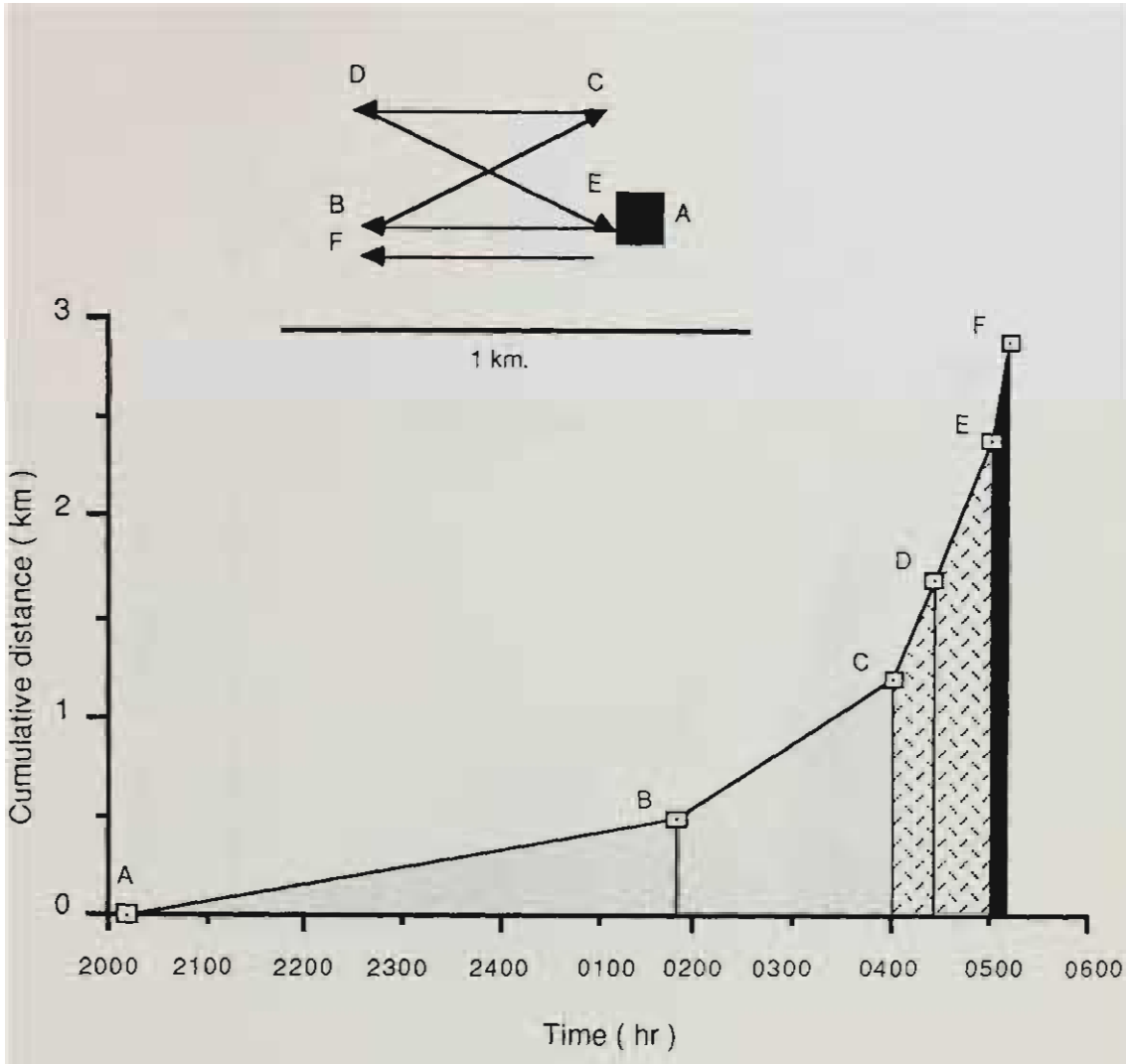
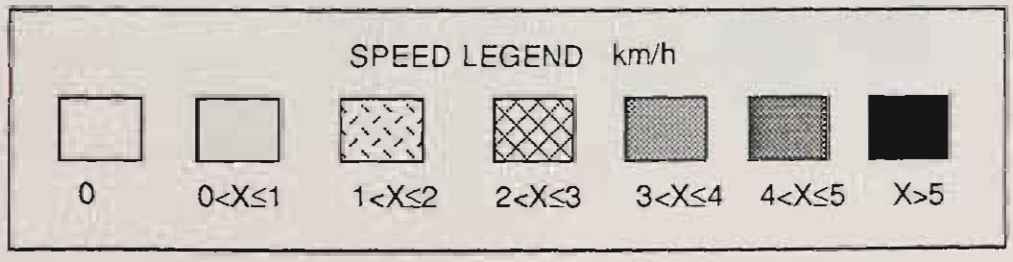


FIGURE 6.7a

Graph shows cumulative distance traveled by L214 during one night of radio tracking. The speed for each foraging bout (A - F) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " exponential " pattern.



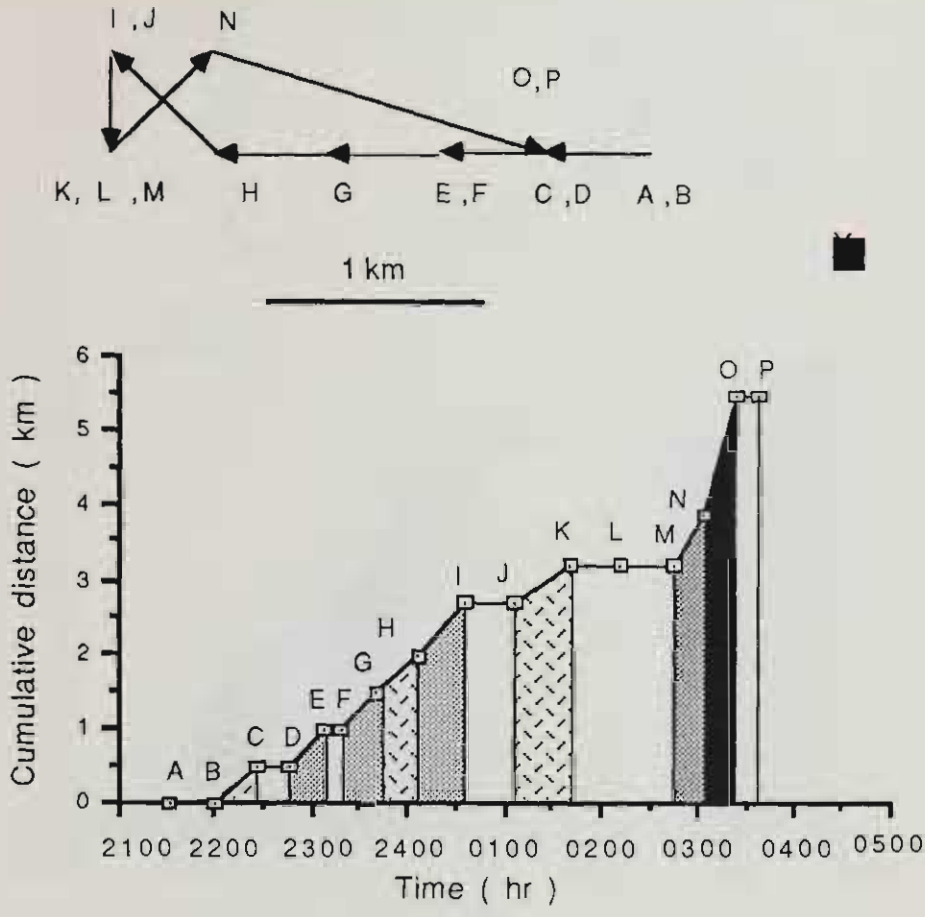
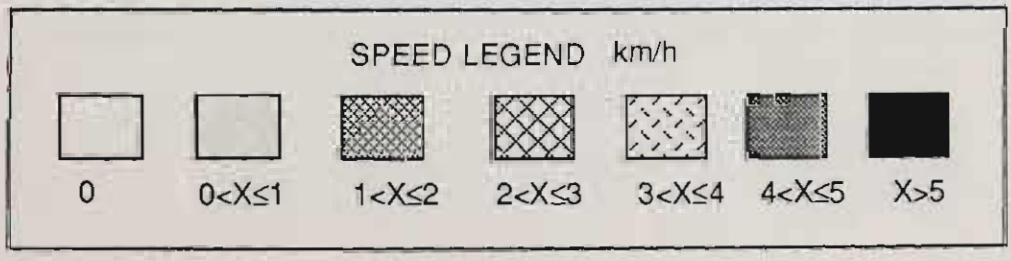


FIGURE 6.7b

Graph shows cumulative distance traveled by L216 during one night of radio tracking. The speed for each foraging bout (A - P) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " stepped " pattern.



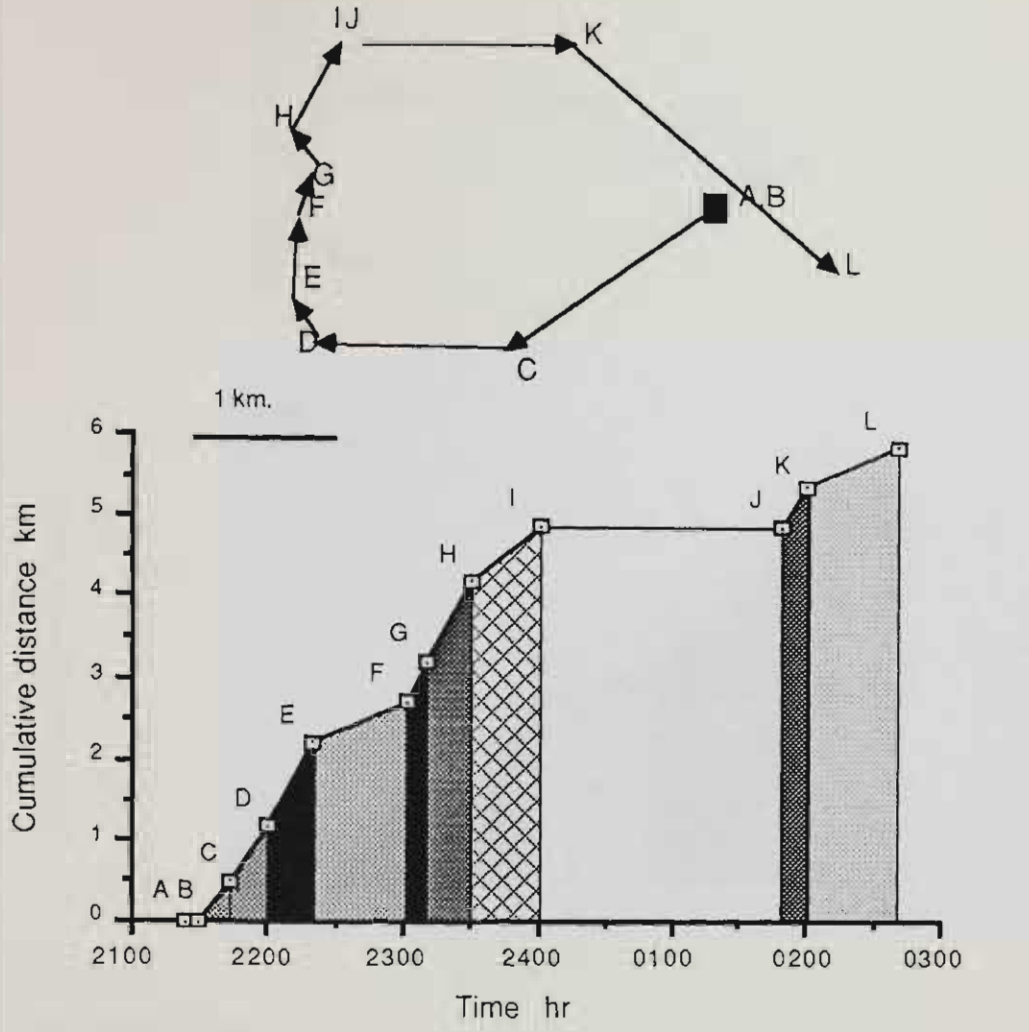
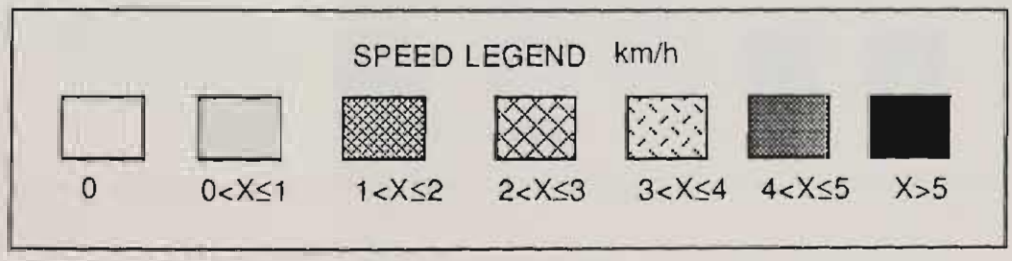


FIGURE 6.7c

Graph shows cumulative distance traveled by L216 during one night of radio tracking. The speed for each foraging bout (A - L) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " stepped " pattern.



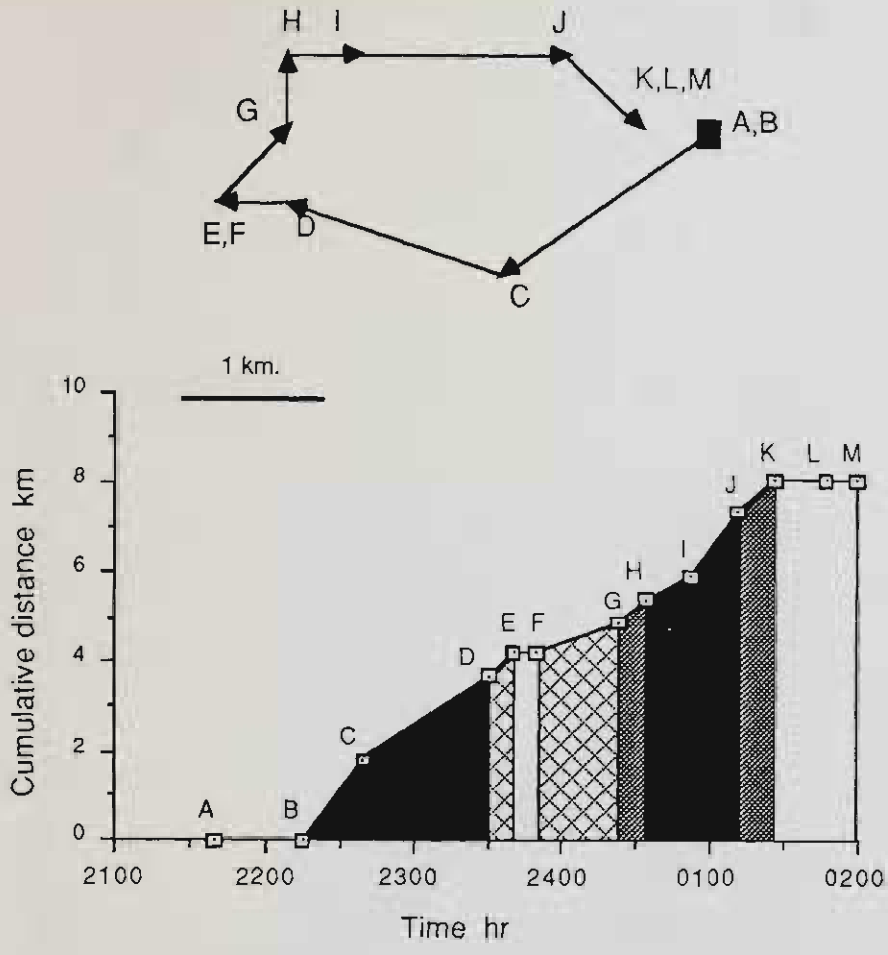
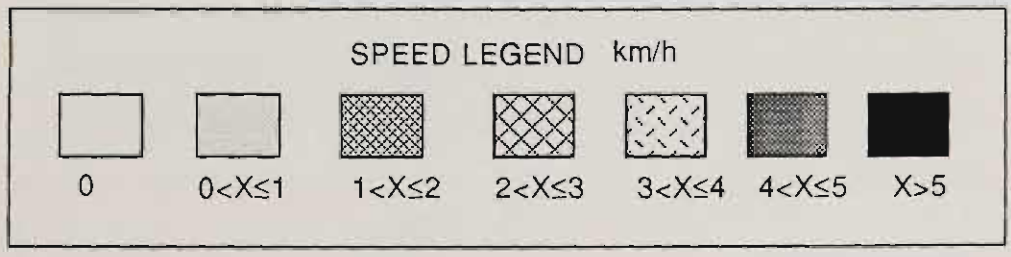


FIGURE 6.7d

Graph shows cumulative distance traveled by L216 during one night of radio tracking. The speed for each foraging bout (A - M) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " linear " pattern.



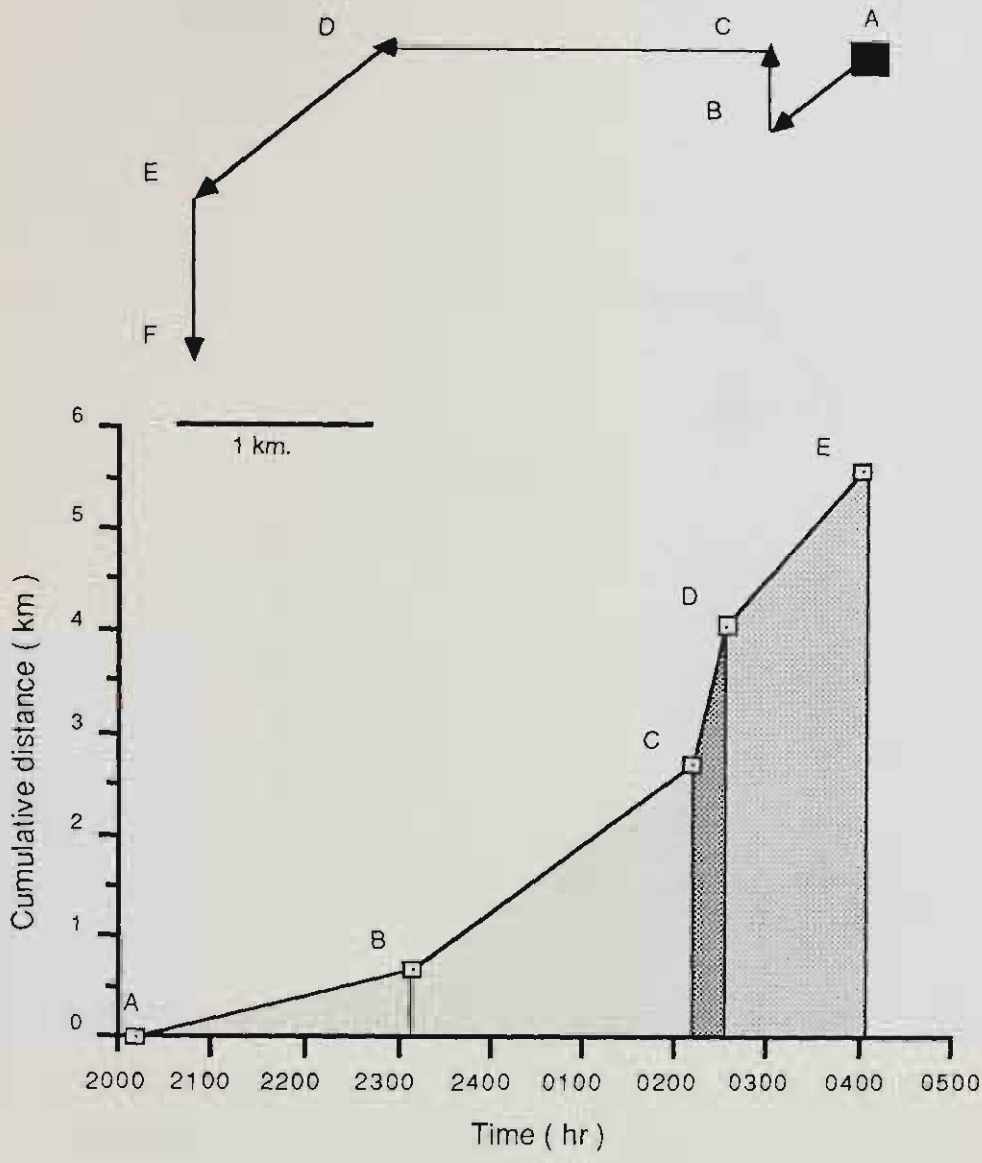
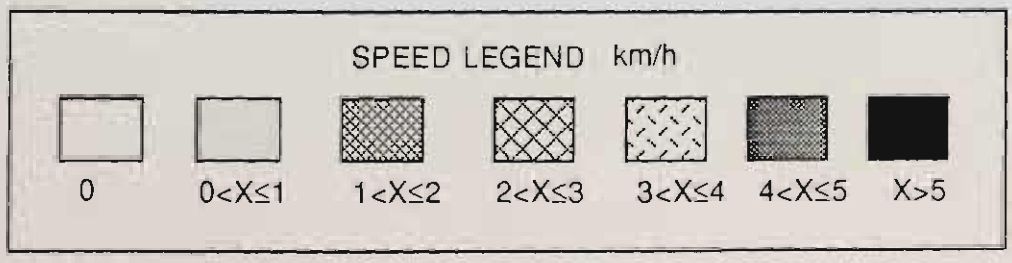


FIGURE 6.7e

Graph shows cumulative distance traveled by L214 during one night of radio tracking. The speed for each foraging bout (A - E) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " linear " pattern.



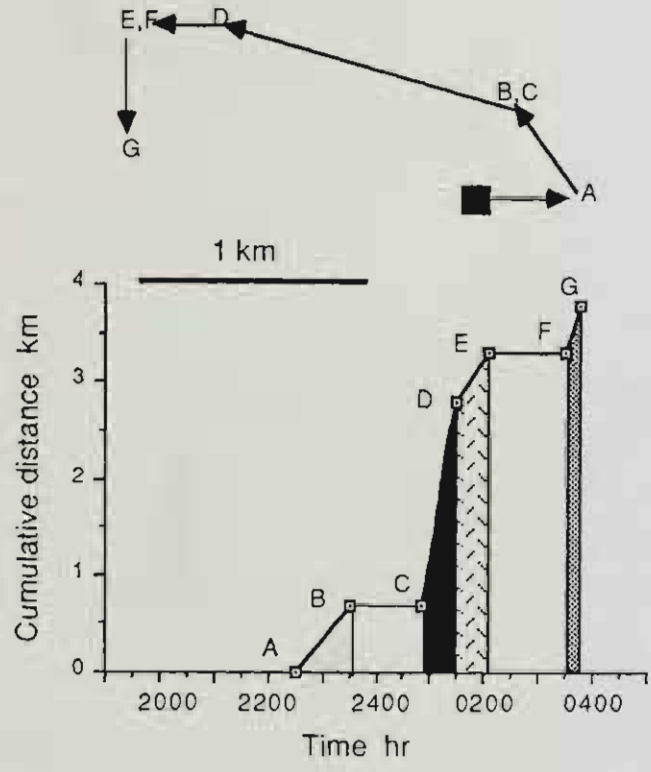
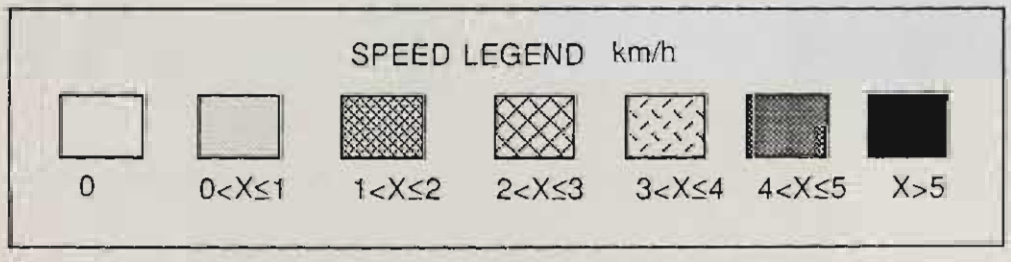


FIGURE 6.7f

Graph shows cumulative distance traveled by L216 during one night of radio tracking. The speed for each foraging bout (A - G) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " stepped " pattern.



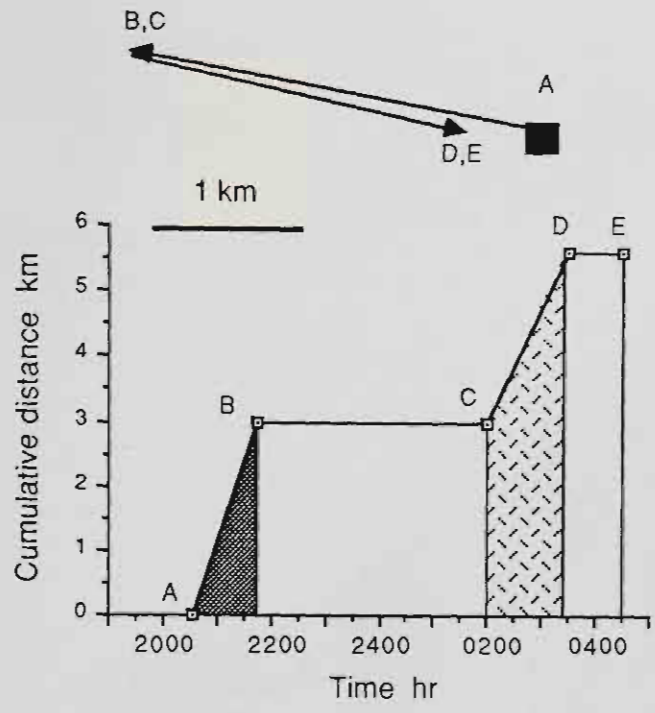
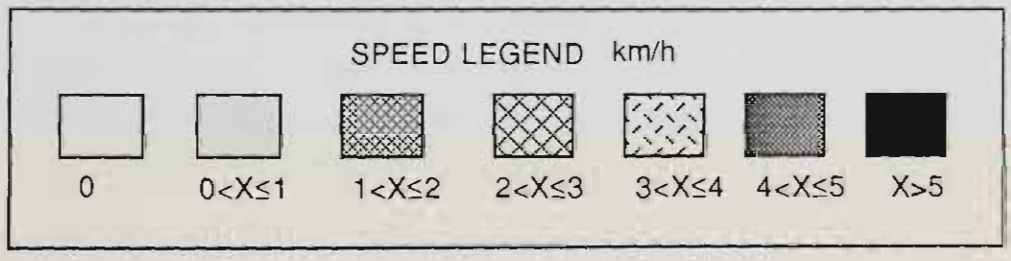


FIGURE 6.7g

Graph shows cumulative distance traveled by L216 during one night of radio tracking. The speed for each foraging bout (A - E) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " stepped " pattern.



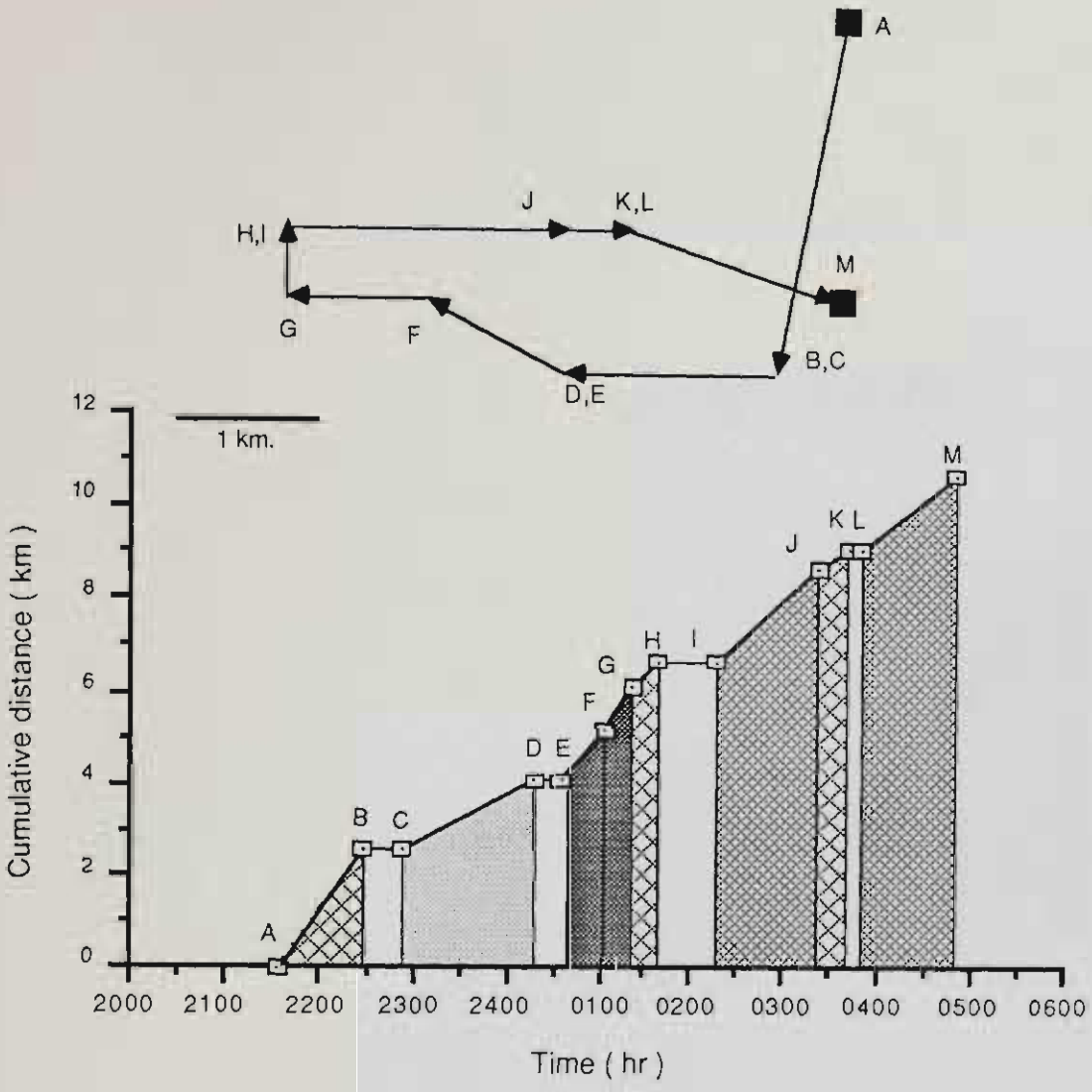
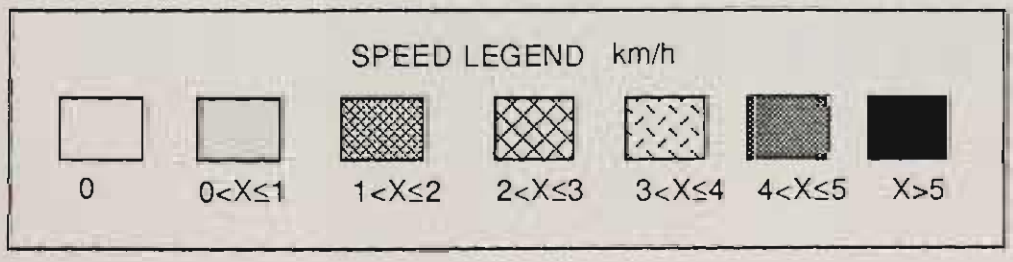


FIGURE 6.7h

Graph shows cumulative distance traveled by L216 during one night of radio tracking. The speed for each foraging bout (A - M) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " linear " pattern.



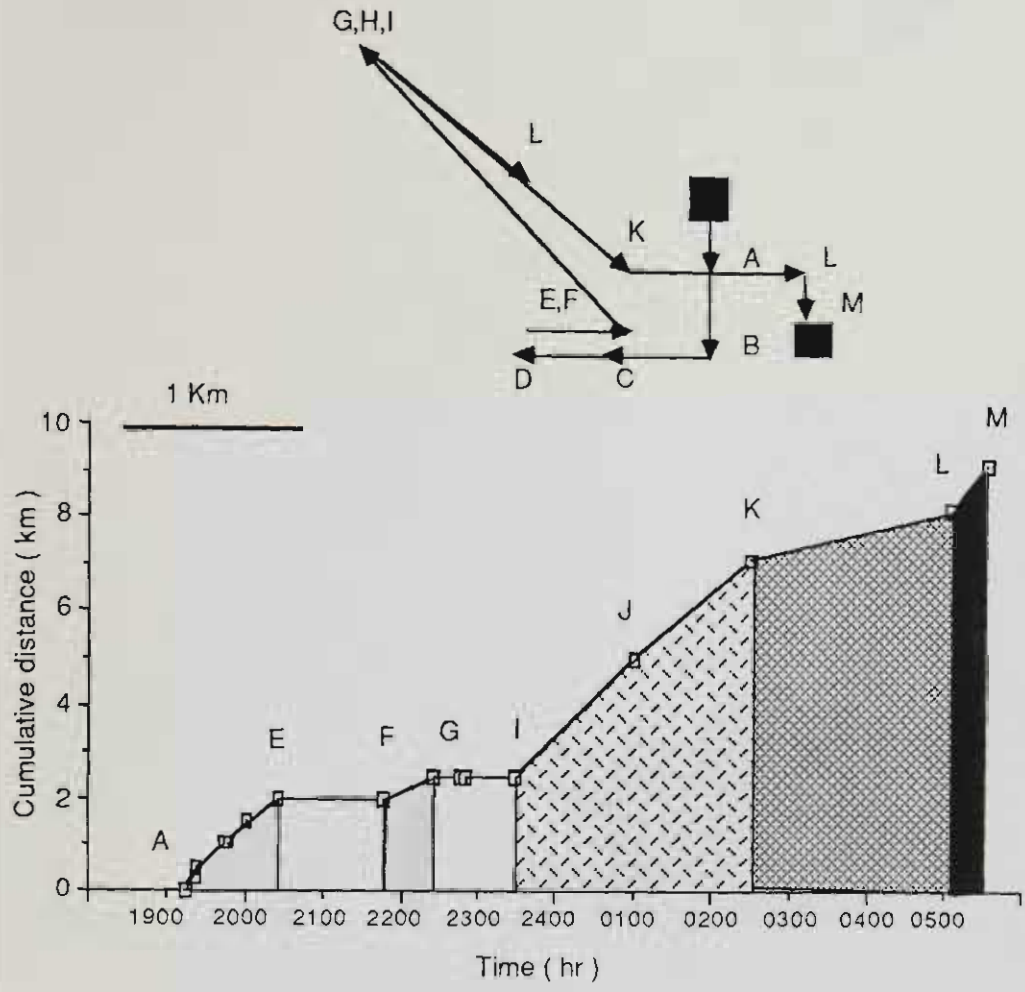
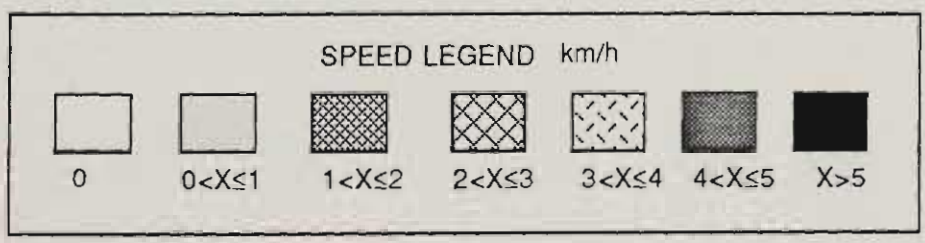


FIGURE 6.7i

Graph shows cumulative distance traveled by R236 during one night of radio tracking. The speed for each foraging bout (A - M) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " stepped " pattern.



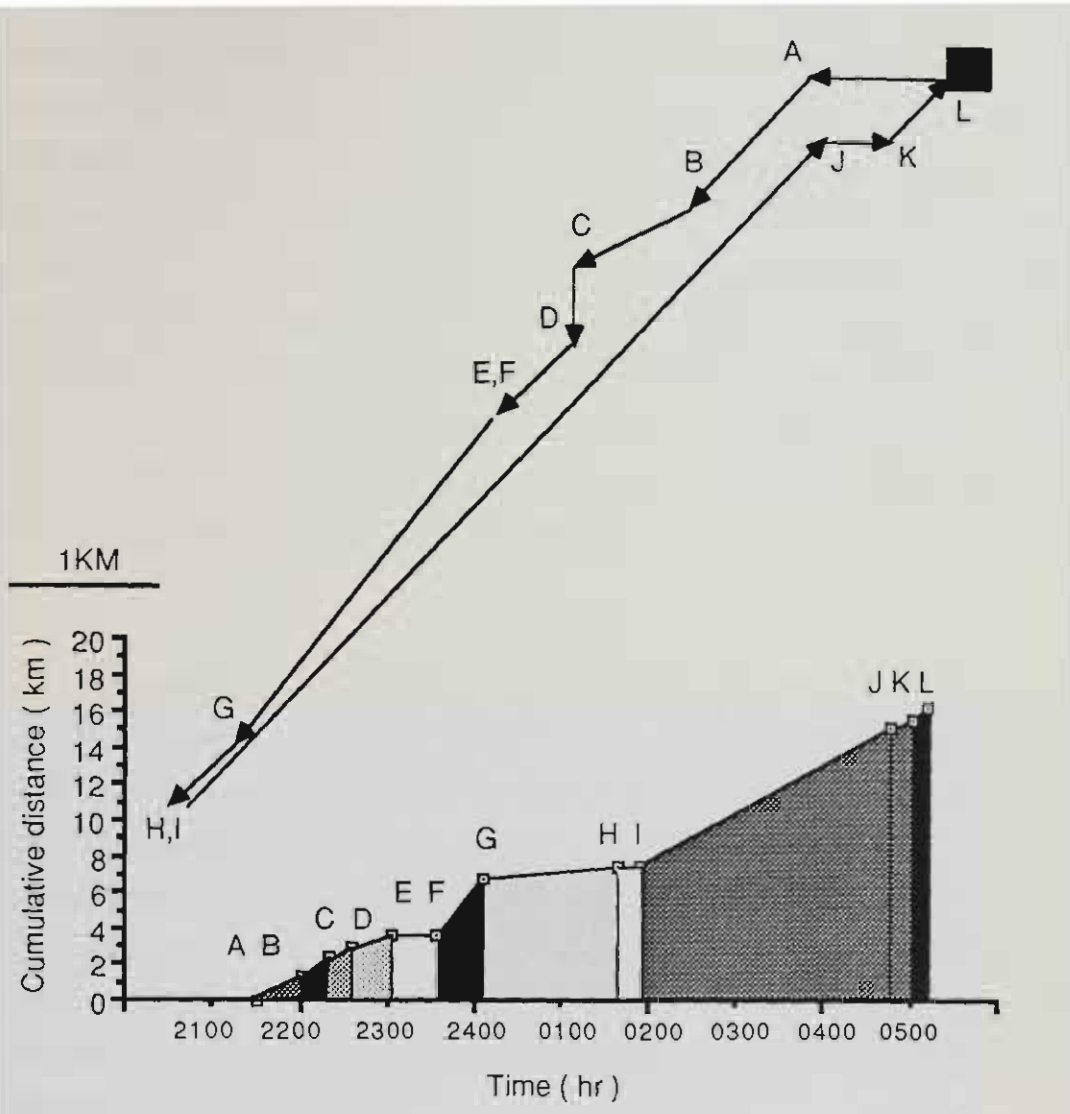
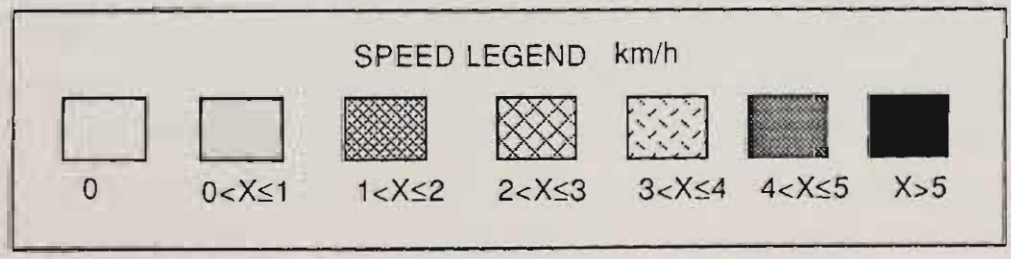


FIGURE 6.7j

Graph shows cumulative distance traveled by L66 during one night of radio tracking. The speed for each foraging bout (A -L) is shaded (see legend). The path to and from the den is also shown with each of the discrete foraging bouts indicated. The den is indicated, where known, by a black square. This foraging strategy shows the " linear " pattern.



6.3.4 DIRECT OBSERVATIONS

Radio collared animals were seen on only 14 occasions. Animals were seen crossing the road (n = 5), at the Musselroe tip (n = 1), at the shacks(n = 1) and on one occasion sniffing around the dustbins at a camp site. On two occasions animals were observed crossing paddocks. Both these animals loped at an even pace in an erratic direction, scattering wallaby as they went. On another occasion I observed a devil with a beta light on the collar moving down the road towards the vehicle. It loped up to the vehicle, looked at it then carried on up the road suggesting that the animal stuck to its chosen path regardless of the vehicle. Another animal, with a LED on the collar, was observed traveling along the edge of a tea tree forest then crossing a paddock and entering the forest. This took 5 minutes and the animal kept moving in an erratic fashion throughout the period of observation.

6.3.5 LATRINES

A total of 20 latrines which were used by devils for the duration of the study were located in the study area (Table 6.8). The latrines were mainly associated with paths or tracks crossing creeks. Other latrines were located at sights of permanent water, namely dams, on tracks, firebreaks and on the granite slabs on Mt.William. At these sites scats were restricted to an area of less than 15 m^2 and the area receiving faeces remained constant. The latrines varied in shape from longitudinal at sites such as latrine number six that was located on a track winding through a disused quarry to those at dams and on the granite slabs that were roughly square. Latrines were located throughout the park (Fig. 6.8).

6.4 DISCUSSION

6.4.1 SPATIAL ORGANISATION

A description of the spatial organisation of a species is effectively a description of the relationship between the individuals of the species and their interaction with the environment. There are several important facets of social organisation of the Tasmanian devil which have been described in this study and which warrant discussion. I have shown that at Mt.William, Tasmanian devils were solitary foragers occupying an overlapping home range and that they traversed these ranges at various speeds from sunset to sunrise in a series of bouts of activity interspersed with inactivity. They had a primary den but used more than one and most dens were located in burrows which in turn were usually located in Quarternary fossil dunes. The animals used latrines which were located throughout the study area.

The term "solitary" is usually used to describe animals that are spatially separated, show active avoidance of conspecifics and/or are antagonistic towards these conspecifics when they do meet (Leyhausen 1965, Waser 1975). "Solitary" is the

TABLE 6.8 The maximum number of fresh scats found at a latrine site and the physical description of the latrine. The latrine numbers refer to Figure 6.8 which shows locality

Latrine No.	No. of scats	Physical description
1	15	Granite slab on top of mountain
2	10	Granite slab in forest
3	12	Fire break with loose granite gravel
4	6	Road at creek crossing
5	17	Vehicle track at creek crossing
6	44	Track through quarry
7	46	Gravel next to dam
8	4	Track next to creek and dam
9	29	Sand next to dam
10	8	Track through scrub
11	6	Road in copse of scrub
12	3	Track over creek
13	3	Track over creek
14	2	Road crossing creek
15	3	Road crossing creek
16	9	Track across habitat boundary
17	26	Road crossing creek
18	30	Road crossing creek
19	15	Gravel next to pond
20	26	Track crossing erosion gulley

TABLE 6.9 The density of Bennett's wallaby in the different habitats of the Park. (from Hocking & Pemberton unpubl. data)

Habitat	Density during day (n per square km)
Pasture	27.9
Heath and wetlands	23.4
Woodland	104.1
Open Forest	24.0
Scrub	34.5

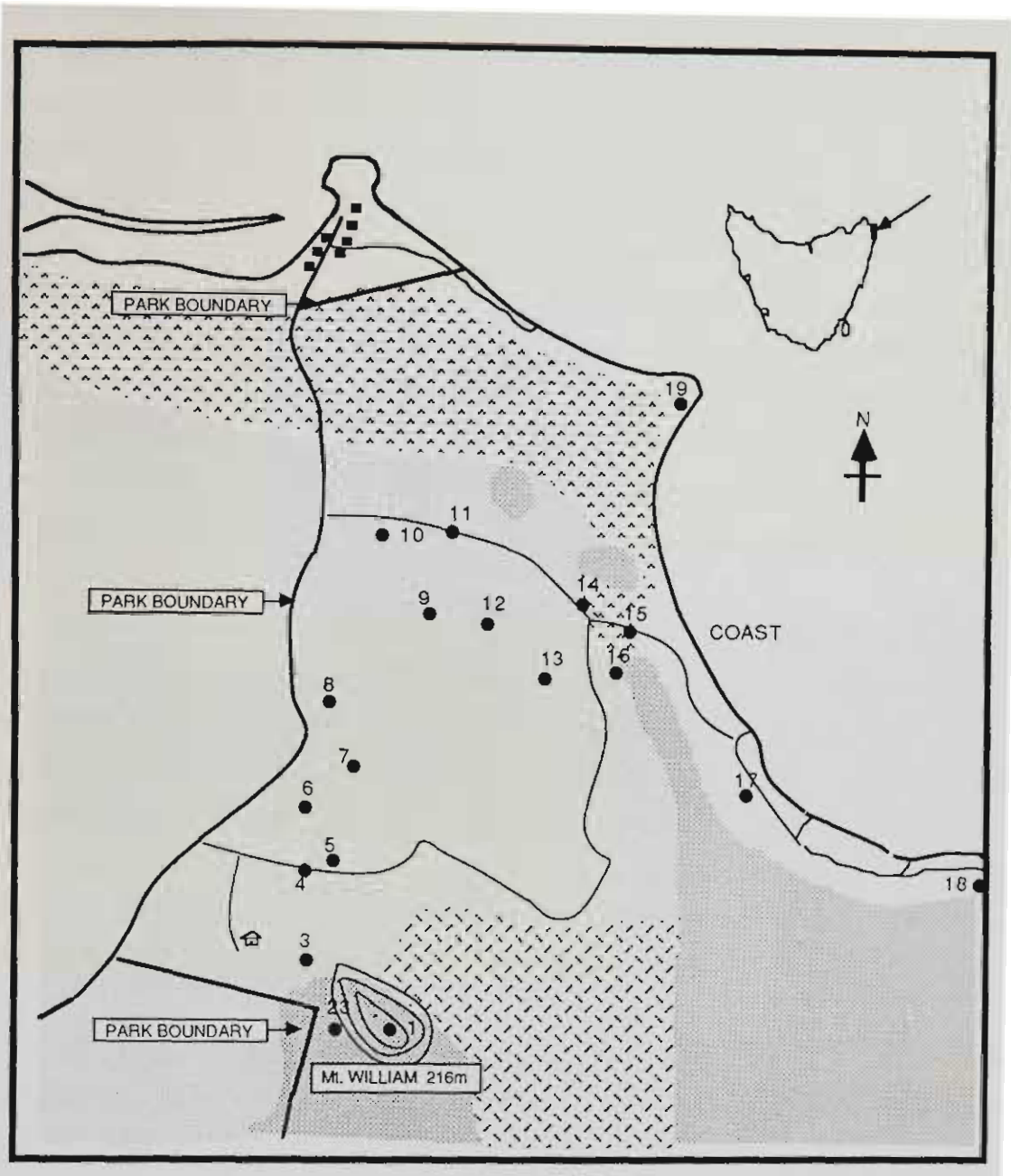


FIGURE 6.8

The locality of latrines in the study area. ● denotes the latrines and other notation is shown in the legend to Figure 1.2. Numbers refer to Table 6.8 where the latrine sites are described.

opposite of "gregarious", not of "social" (Charles-Dominique 1977). Devils do not satisfy all these criteria. They have overlapping home ranges and are then, in the broad sense, spatially integrated. They are however antagonistic towards each other when they meet as indicated by the feeding trials (Chapter 5). While this study has not proved that they actively avoid each other whilst foraging, they were never seen traveling together (Table 5.5), suggesting that encounters if they occurred would be brief. This hypothesis is supported by the observations of agnostic vocalizations made whilst radio tracking on 16 occasions. These vocalizations were dyadic in their nature, but short relative to those observed at feeding trials, suggesting that the encounter between two devils foraging had been brief and intense, and whilst the animals had not avoided each other, the encounter was antagonistic. It follows therefore that devils can be categorised as solitary in terms of their sociality and that the interactions that take place as a result of their spatial organisation are, therefore, antagonistic.

There did not appear to be any difference between the home range size of male and female devils, contrary to what would be expected from the established positive correlation between body mass and home range size in other mammals (Harestad & Bunnell 1979, Cameron & Spencer 1985, Swihart *et al* 1988).In general, males are expected to have larger territories than females as found for the Eastern quoll (*Dasyurus viverrinus*) (Godsell 1983), the closest relative of the devil in terms of phylogeny and body size which has studied to date. This is not the case with devils at Mt. William, although they show marked sexual dimorphism.

The home ranges although measured over a month for most animals were interpreted as being stable over the majority of the life-span of the animals for the following reasons. All animals radio tracked were adult residents and had a capture history of at least two years in the study area (Figs. 4.8 and 4.9, Chapter 4), the location of the trap line (Fig. 2.1, Chapter 2) lies well within all but one of the home ranges and in one case, a devil occupied the same den sites for at least three months. The latter also indicates that devils probably have a strong tenacity to their dens. It was observed that the animals seldom occupied the same den on successive nights, but that they did use one den, the primary den, more often than the others. Examination of the patterns of foraging (Fig. 6.7 a - 6.7 j) show that most devils returned to the den or at least the area in the proximity of the den. It appears, therefore, that the den site is very significant in the movements of the animals. Those dens that were occupied less frequently were interpreted as being used after excursions away from the core areas of the home range.

The most common choice of burrows as den sites is probably related to provision of shelter and a relatively stable microclimate. Even surface dens afforded

some shelter and no exposed dens were ever located. As devils have no predators it is likely that the requirement for shelter in dens is related to their physiology. Devils have the ability to conserve energy by decreasing their metabolic rate when resting (Nicol 1982). The use of sheltered dens may assist in the facilitation of this shallow torpor. Further, the burrows used by most animals were located in Quaternary fossil sand dunes restricted to the north of the Park. The apparent benefits of dens, and the restriction within the Park of the most favoured dens, supports the hypothesis that the movements of devils, and therefore their range size and orientation, is partly controlled by the position of the primary den sites with respect to the potential feeding area.

The primary dens were the only dens in which the females denned their young, although they continued to use other dens during the lactation period. The young, therefore, were not fed every day. As the identification of the primary den relied on the frequency with which it was used, and the fact that the young are never observed outside the dens until near weaning, it follows that the female will be returning to one den i.e. the primary den, to provide her young with the necessary food i.e. milk. The alternative option would be to move the young from den to den. This was never observed at Mt. William, although it has been reported that this occurs both with devils (Guiler in Strahan 1983) and Eastern quolls (Godsell 1983).

There is limited data with which to make a comparison across the period of lactation, but the evidence suggests that females may be more tenacious to their primary den when young are first denned. Two females occupied the same den for 6 to 8 (n = 3) consecutive nights after denning their young in August. In contrast all the lactating females radio tracked towards the end of lactation in December occupied the primary den, where it is believed the young were, for less than three days consecutively and usually for only 1 day resulting in the young missing feeds (Table 6.3). Further, one female tracked in June showed a very erratic pattern of occupancy of the primary den whilst her young were in the pouch and therefore suckling regardless of where she denned. The daily tenacity of a mother to a den during lactation is therefore probably related to the stage of lactation. The erratic pattern of visits to the weaners in the maternity dens may be a precursor to the weaning of the young either by inducing cessation of lactation or by the weaners leaving by necessity to procure food.

The observations of an adult male occupying a den for extended periods during the copulation period suggests that one male may mate with more than one female and in addition that there is a consort period during copulation. This was the only observation of conspecifics associating for a period greater than that found during agonistic enounters around food.

Whilst it is hypothesised that the den sites, and in particular the primary den, exerts an influence on the home range size and orientation with respect to the distance traveled, this influence would not affect the shape of the home range. The observed home range and movement patterns (Fig. 6.3 and 6.7) can be explained in terms of the habitat and potential food availability of the habitat covered by the home ranges. I suggest that the axes of the home range are restricted by tenacity to den sites and the potential foraging sites. The controlling influences exerted by these features would not be static and would change in their intensity, relative to each other, over time.

The greatest overlap between the radio tracked devils was located in the the habitat described as pasture bounded by woodland and scrub. Transect counts of Bennett's wallaby (*Macropus rufogriseus*)were carried out in co-operation with officers of the Dept of Parks Wildlife and Heritage across the northern end of the park (Hocking, Dept. Parks, Wildlife & Heritage internal report). These show that the scrub and woodland habitats contained the highest densities of Bennett's wallaby during the day (Table 6.9). These habitats were bounded by pasture where the animals grazed at night. Similar analyses showed that this area of the park contained higher densities of Forester kangaroos (*Macropus giganteus*) and pademelons (*Thylogale billardierii*) than the denser forests, wetlands, heathlands and kunzea scrub. Wallaby and wombats (*Vombatus ursinus*)were major prey items of devils in a study by Guiler (1978) in the nearby sheep station at Cape Portland.

The pattern of movement of devils has been shown to have a circular element. This pattern, in conjuction with the mean distance covered of 8.6 km would allow the devils to cover a fair proportion of not only their home range (13.3 km^2), but also much of the pasture woodland habitat which had the highest potential foraging yield (≈ 20 km^2). The association between home range size and the highest densities of wallaby is interpreted as a reflection of the potential foraging yield of the habitat and therefore the shape of the home range was affected by the foraging potential of the habitat.

6.4.2 FORAGING STRATEGY

According to the theory of optimal foraging behaviour, devils would be expected to show a foraging strategy which maximises the net energy gain per unit time spent foraging (Krebs & Davies 1984). Three patterns of foraging were identified for the devil and these have been interpreted as three strategies. The 'Stepped strategy' was one in which activity, namely movement greater than 0.5 km, was interspersed with periods of inactivity of greater than half an hour. In contrast animals using a 'Linear strategy' of feeding never had extended inactive periods and had a relatively

constant speed throughout the foraging trip. The 'Exponential strategy' was similar except that the there was an increase in speed with duration of the foraging trip. Many of these foraging trips (e.g. Fig. 6.7a) resulted in the animal traveling to its den at high speeds, thereby producing the exponential shape. The energetic cost of moving a given distance decreases with increasing speed (Taylor *et al.* 1970, Gordon *et al.* 1977). Therefore, the Exponential strategy is interpreted as a derivation of the Linear strategy where the devil involved is traveling at a minimum cost to itself to its den site at the end of its foraging trip, after using the Linear strategy during foraging. Consequently, in further discussion I will refer only to the part of the foraging trip which reflected the Linear strategy so as to concentrate on that part of the foraging trip that was more likely related to food acquisition and not travel associated with dens.

The stationary periods common to the Stepped strategy of foraging are similar to the length of time that devils feed off carcasses (Chapter 5). However twice when animals were stationary for one hour they were tracked down on foot and found to be lying down in the scrub with no evidence of feeding. In addition, in the previous Chapter it was shown that feeding bouts are characterised by extensive vocalization. No vocalizations were heard whilst radio collared animals were stationary. Constant fluctuations of the radio signal indicated that these stationary periods were accompanied by restricted movement, unlike the constant signals received from animals in dens that were presumably sleeping. Therefore, during the stationary periods the animals could still be involved in active foraging and may have been feeding on items to small to induce intra-specific aggression and hence vocalization. Another explanation would be that they were foraging via auditory recognition of food sources, namely listening for other devils squabbling over a carcass.

The relatively constant periods of activity associated with Linear and Exponential foraging strategies indicate a different foraging mode from that described above. These animals moved constantly all through the night and hence covered a larger range through potential foraging habitat, than that covered by animals using the Stepped strategy. By nature of the extra energy expended for locomotion by constant activity it could be interpreted that, in terms of energy balance, the Stepped strategy is a more optimal strategy with respect to the costs and gains of the strategies if they all resulted in acquisition of similar amounts of food. The Na^{22} turnover data (Section 5.3.3.4) showed that all animals gained sufficient food to at least remain in energy balance and thus maintain body mass. These data also indicated that there were feeding bouts every 4 to 8 days. It is tempting to speculate on the possibility of these feeding bouts being reflections of the different foraging strategies proposed here.

It is conceivable that the Stepped strategy may result in an animal feeding on a carcass which an animal using a Linear strategy has located, thereby reducing its cost for equal gain. This however relies on the assumption that Linear strategy feeders procure carcasses large enough for many animals to feed on. If this was so there would be a constant selection for this strategy with its obvious efficient energy conversion of maximal gain from minimal cost relative to the Linear feeders. This strategy could not survive in an evolutionary sense as the Stepped feeders would soon out number Linear feeders to find their food. In addition, one individual, L216 showed both feeding strategies in consecutive nights. Hence it appears as if animals utilise both strategies over a continuum of days. It is hypothesised that the Linear strategy animals are feeding on smaller carcasses which are consumed quickly before intra-specific aggression alerts Stepped strategy feeders to the presence of food. Although it is beyond the scope of this thesis, this hypothesis could be tested by investigating the food consumption rates of devils in relation to wether they were adopting Stepped or Linear strategies.

There is no evidence from this study to show that devils can predate on live prey. During this study I raised a young devil and some of the behavioural observations are relevant to this subject. On one occasion she found a rabbit maternity den, dug into it and ate the young. She would also catch and kill mice by pursuing them until she caught them and killed them with a neck bite and shaking. Similar observations of captive devils were made by Ewer (1969) although Buchman & Guiler (1977) state that devils are inept at killing. Ewer (1969) argues that this method of killing is similar to that employed by the felids, mustelids, viverrids and some canids. Although devils have never been recorded killing in the wild, there are three reliable observations by colleagues of devils pursuing pademelons and in two of the cases the pademelons were bitten by the devil (P. Naughton, N. Mooney, N. Brothers pers comm). In one of the cases the devil followed the pademelon into a creek and continued the attack. The outcome is unknown as further attempts by the devil to bite it were prevented by the observer chasing the devil away. It is possible that prey such as ringtail possums (*Pseudocheirus peregrinus*) when on the ground would be attainable prey for devils as implied by Taylor (1986). If predation does form a significant part of a devils diet I suggest there this would only occur in the absence of available carcasses of large animals, such as macropods. This situation could arise in wet forested areas where devils occur and where the marsupial population is comprised predominantly of small (e.g, ringtail possums) rather than large (e.g. macropod) species.

Olfactory communication in mammals has been reviewed by Ralls (1971), Brown & MacDonald (1985) and Gorman (1990)
Eisenberg & Kleiman (1972), Johnson (1973), Stoddart (1976), and for the

Dasyuridae by Croft (1982). Olfactory communication is achieved either via deliberate scent marking, such as cloacal dragging and sternal rubbing or passively via odour liberation as the animals move through their environment. The function of these scent marks, as summarised by Croft (1982) are: (1) a warning or deterrent to other conspecifics that a territory is occupied, (2) a sex attractant or stimuli, (3) an orientation mechanism within the home range for the individual marking, (4) an indicator of individual identity with regard to sex, age and perhaps dominance. In the Dasyuridae the use of deliberate defaecation as a form of olfactory communication is common (summarised by Croft 1982), as it is in eutherians such as the spotted hyaenas *Crocuta crocuta* (Kruuk 1972), brown hyaenas *Hyaena brunnea* (Mills 1983), maned wolf *Chrysocyon brachyurus* (Kleiman 1972), Himalayan musk deer *Moschus chrysogaster* (Green 1987) and badger *Meles meles* (Kruuk 1978b) to name a few. Defaecation by these eutherians is often associated with a distinct restricted site with respect to time and space and therefore scats accumulate and it becomes a predictable area of olfactory information. These sites are termed latrines. The defaecation sites of devils are restricted in a similar manner and are therefore described as latrines and considered to be of significant social importance via their ability to hold olfactory information. The interpretation of the function of the latrines relies on which animals defaecate at the latrines, which animals use it but do not defeacate at it, the position of the latrine with respect to the home range and the information content that can be held in the scats at the latrine. This information was not obtained in this study, therefore a definitive description of the function of the latrines is not attempted. The following can however be insinuated from the information available.

The latrines were used throughout the study period, fall within the home-range of the residents and lie on breaks in ecotonal boundaries which devils readily use during their foraging trips (Guiler 1978, Mooney 1988). They would therefore convey information in a predictable fashion both spatially and temporally to the users. The latrines are likely, therefore, to serve an integral function in communication within the population.

Croft (1982) suggested that the marking patterns of most dasyurids indicated that they probably label their home range with scent marks. This is probably the case with devils, but it is unlikely to be in the form of a territorial marker whereby the marker defends a fixed territory as found in many eutherian species (e.g. Kruuk 1972b, 1978, Mills 1983, Nel & Bothma 1983). The devils in this study occupied overlapping home ranges with at least 100 residents sharing the majority of their home range with each other. The information contained in the latrines would however facilitate the transfer of information, of this otherwise solitary animal, with regard to

the sexual status of the animals as is found in the dasyurid *Sminthopsis crassicaudata* (Ewer 1968). It is interesting to note that the latrines are used all year round and are therefore not restricted to the brief synchronised breeding season as would be expected if the information on sexuality of the users was paramount. This may, however, be the case as devils are facultatively monoestrous (Lee & Cockburn 1985) and thus the females have the potential to come into oestrous at any time. Indeed, two of the observations of out of phase breeding in devils have been made adjacent to this study area by Green (1967).

If a female did come into oestrus, which is predictably very brief (L. Hughes pers comm) how would these solitary animals communicate their state to the potential sires in the area? Latrines, with their spatial and temporal stability of information, particularly with respect to residents, may well serve to communicate this information to the the potential mates in the population, hence the presence of latrines throughout the year. This suggestion is supported by the observation that devils, the only facultative monoestrous dasyurid, is apparently also the only one with a latrine system of communication. This however does not negate the potential value of latrines for other forms of information transfer via oduors, nor is it implying a causal relationship between latrines and asynchronous breeding. Rather it is suggesting that latrines provide one of probably many behavioural mechanisms that facilitate interaction between these solitary animals when necessary, in this scenario for copulation.

The role of latrines in the spatial organisation of devils needs further investigation and may contribute to the use of marsupials as a baseline for understanding the evolution of mammalian behaviour as proposed by Eisenberg & Golani (1977).

6.5 SUMMARY

1. Devils use on average 3.8 dens of which one is more frequently than the others and is termed the primary den.

2. Dens were found both in burrows and on the surface with burrows been the most common.

3. Burrow dens were most common in fossil dunes located in the north of the Park, these were also the only dens identified as maternity dens.

4. The pattern of den use by the females was probably related to the stage of lactation where females attended young every night when they were first denned and sporadically at the end of lactation. It is hypothesised that this induced the weaning of the young.

5. Devils occupied overlapping home ranges of 13.3 km^2 on average. A combination of the ranges of all the tracked animals shows that the effective area sampled by trapping was 46 km^2.

6. The orientation and longitudinal dimension of the home ranges are influenced by the tenacity to den sites and their location. The width of the home range however is controlled by the location of the habitat with the highest potential foraging yield, namely the area of pasture woodland and scrub in the centre of the park. The den localities and distribution of macropods have a dual influence in the control of the size and shape of the home range.

7. Devils traveled at an average speed of 1.1 km/hr covering 8.6 km from sunset to sunrise. There was no difference between the times of den departure in summer and winter with the animals commencing foraging 73 minutes after sunset on average. In summer, the only season for which there is data, the animals returned to the den 5 minutes after sunrise.

8. Three strategies of foraging were identified, Stepped, Linear and Exponential. It is hypothesised that the costs and benefits of the strategies will be similar as a result of the Linear Strategy being associated with the consumption of small prey.

9. Latrines are distributed throughout the home ranges and are usually situated at breaks in ecotones. They remain in use for long periods of time and it is hypothesised that they are instrumental in facilitating interactions between members of this otherwise solitary species.

CHAPTER 7

STEROID LEVELS IN THE PERIPHERAL PLASMA OF TASMANIAN DEVILS: THE INFLUENCE OF SOCIAL FACTORS

7.1 INTRODUCTION

Social interactions have a rapid modulating effect on circulating hormones in many mammals (Edwards & Rowe 1975, Harding 1981, Kemper *et al.* 1987). Social interactions as the result of sexual behaviour are manifested in rapid but transient elevation of testosterone concentrations, whilst those resulting from increased population levels and dispersal manifest themselves in depressed testosterone levels (Harding 1981, Moberg 1985). Both forms of social interaction can produce elevated concentrations of corticosteroids. In addition, it has been shown that the in many species, dominant animals have a much higher level of testosterone than do subordinates (Moberg 1985). The measurement of these steroids can thus aid in the interpretation of social interactions in a population. Corticosteroid and testosterone concentrations in peripheral plasma of Tasmanian devils were measured in the field to contribute towards an understanding of the mating system, social interactions as the result of population fluctuations and the dominance status of devils with respect to their age, sex and residency status.

There is a trend among most mammals to display a polygamous mating system (Eisenberg 1981). Males can attempt to increase there reproductive potential, and therefore fitness, by mating with as many females as possible. Eisenberg (1981) found that 82 % of 59 mammalian species were polygamous. Included in this group were Tasmanian devils.

Polygamy is normally associated with some form of dominance hierarchy and territoriality amongst the breeding males (Kleiman & Eisenberg 1973, Wilson 1975, Eisenberg 1981). The mating system of the Tasmanian devil has been classified in various ways by different authors. Eisenberg (1981) placed them in the polygamous system where a dominance hierarchy exists amongst males. These males seek out females either singly or in groups, in an uncoordinated manner, with the dominant male gaining preferential access to the female. Lee & Cockburn (1985) included Tasmanian devils in a group of facultative monoestrous species where both sexes breed for more than one year. Their classification was devised to categorise dasyurids according to life history strategies and therefore did not take into account the behavioural relationships between individuals. Russell (1984) followed the classification system of Wittenberger (1979) and classified devils as an overlapping promiscuous species where there was no prolonged association. Buchman & Guiler

(1977) suggested that there was some form of dominance in feeding groups that were closed to "outsiders". If dominance relationships exist in devil society, then devils would fit into the category of hierarchial promiscuity where a male's dominance status would affect its chances of copulating with a female. If this is the case, then it can be expected that the dominance status will be reflected in the steroid concentrations, particularly with respect to the residents which would be expected to have the highest potential of attaining dominance.

The relationship between dominance, residence status and conspecific aggression is well established. The development of aggressive behaviour depends on the stimulation by androgens (Kemper *et al.* 1987). Frank *et al.* (1985) found that resident spotted hyaenas *C. crocuta* had higher levels of androgens than did transients. In addition, dominant animals had androgen levels seven times higher than that of subordinates. Rises in plasma testosterone levels have been associated with aggression during mating in many dasyurids, including the red-tailed phascogale *Phascogale calura* (Bradley 1987), dusky antechinus *Antechinus swainsonii* and yellow footed antechinus *A. flavipes* (Mcdonald *et al.* 1981), brown antechinus *A. stuartii* (Lee *et al.* 1977), Eastern quoll *D. viverrinus* (Bryant 1988) and the Northern quoll *D. hallucatus* (Schmitt *et al* . 1988). These observation have also been made for many other marsupials (for review see Tyndale-Biscoe & Renfree 1987). The testosterone profiles were investigated to gain an insight into the mating system of the devil, the largest of the extant dasyurids.

In the phascogale and the three species of antechinus mentioned above, there is a strong negative correlation between the testosterone concentration and maximum steroid binding capacity (MCBC), which results in the catastrophic die off of males after mating. Total plasma corticosteroid concentrations consist of three fractions, a small free fraction, a small fraction bound to albumin and approximately 80 % which is bound to transcortin-like high-affinity plasma proteins (McDonald *et al.* 1981). Only the free and albumin-bound fraction are biologically active and therefore a decrease in the concentration of the binding globulin results in an increase in the biologically active fractions. The MCBC, which gives a measure of the plasma transcortin concentration, decreased below the level of the plasma corticosteroids for these three species at the time of mating. As a consequence, plasma free corticosteroids rose dramatically just prior to males disappearing from the population. This increase in free corticosteroids suppresses both the immune and inflammatory responses. Autopsies carried out on these small dasyurids show that gastric ulcers with extensive hemorrhaging are the probable final cause of death (Bradley 1987). The death in these small dasyurids is therefore attributed to an androgen-dependent fall in plasma transcortin concentration, a suppression of the immune and inflammatory systems and pathological conditions

which result in mortality (Bradley *et al.* 1980; McDonald *et al.* 1981; Bradley 1987). A similar pattern of responses to stress around mating has been suggested by Godsell (1983) and Bryant (1988) although the relationship was not as strong. In addition both these studies showed responses in *D.viverrinus* steroid levels to population fluctuations. The corticosteroid profiles in devils were investigated to assess whether a similar response of steroid concentrations in peripheral plasma could be correlated with social interactions as the result of mating and population fluctuations.

7.2 METHODS

Blood samples were collected in the field from trapped devils at Mt. William between January 1985 and March 1986. All animals were bled between 0600 and 1000 hrs. Samples were collected from an ear vein by first smearing Vaseline on the ear to hold the blood in droplets and then nicking the vein with a scalpel. Only those samples which were obtained within 2 minutes were used to reduce the risk of elevated levels of testosterone as the result of aggression or stress by the devil due to handling (A. Bradley pers comm). Approximately 2 ml of blood was collected in a lithium heparanised vial. The samples were stored on ice until return to the field hut where they were centrifuged. The plasma was transferred to separate vials where they were frozen at - 20°C until analysis. All samples were analysed by Dr. Sally Bryant and Dr. Adrian Bradley at the University of Tasmania. Testosterone concentrations were measured by radioimmunoassay (Fletcher 1983; Bryant 1986, 1988). The testosterone assay was validated using blood samples from captive animals (Bryant 1988). Total corticosteroid concentration was measured by radioligand assay as described by Bradley *et al.* (1980). The maximum corticosteroid binding capacity was determined using equilibrium dialysis and, a gel filtration technique with a specific high affinity association constant applied for the devil (Bradley *et al.* 1980). To verify the testosterone levels, a series of duplicate plasmas were re-assayed by Dr. D Irby, Anatomy Dept, Monash University. These assays were consistent with the levels obtained from the samples run by Drs. Bryant and Bradley. Partitioning into CBG bound, Alb bound and free fractions were determined by Dr. Adrian Bradley.

The degree of stress suggested by the levels of free corticosteroids is inferred from Bryant (1988) where an experiment was carried out to determine the range of cortisol levels that occur in the Eastern quoll. Cortisol represents 86 % of the total peripheral plasma corticosteroid concentration in Eastern quolls (Bryant 1988) and similar values have been found in the Tasmanian devil (A. Bradley pers comm). The values used by Bryant (1988) were converted to total corticosteroid values using this percentage to allow for interpretation of the degree of stress indicated by the free corticosteroid concentrations found in devils in this study. Values of between 0 and 5 nM correspond with unstressed animals, 5 to 7 nM with moderately stressed animals

and greater than 7 nM with highly stressed animals. Interpretation of these data should be treated with some caution as the experiment of Bryant was carried out on male quolls and is here applied to both sexes of devil .

7.3 RESULTS

7.3.1 CORTICOSTEROIDS AND THEIR BINDING PROTEINS

There were variations in the corticosteroid binding capacity throughout the year, but in all months it was well in excess of the total peripheral plasma corticosteroid concentration (Fig.7.1). For both sexes changes in maximal corticosteroid binding capacity were mirrored by changes in total corticosteroid concentrations. Therefore, the biologically active fraction, or free corticosteroid, did not change dramatically despite changes in the total corticosteroid concentration. There was no significant correlation between male MCBC and plasma testosterone concentrations ($y = -7.839 x + 130.47$, $r^2 = 0.02$).

The mean levels of free corticosteroids of different age groups and residency status for both sexes are shown in Table 7.1. The adult resident males showed the lowest levels of free corticosteroid. There was a significant difference between adult and juvenile males ($F_{(1,89)}=6.885$, $p=0.01$) but no significant difference between resident and transients ($F_{(1,89)}=2.993$, $p=0.09$). There was no significant difference between the adult and juvenile females ($F_{(1,71)}=0.07$ $p=0.798$), nor between the residents and transients ($F_{(1,71)}=0.096$ $p=0.76$).

These data were further analysed by subdividing the data set into the various combinations of age and social status and testing for differences between all these groups by ANOVA. There was a significant difference between these groups ($F_{(7,161)}=2.747$, $p = 0.01$). The significant differences detected were all associated with the low level of free corticosteroids of the male adult residents (Table 7.2). This group showed a significant difference when compared with all the groups of females and male juvenile transients and were lower in all cases (Table 7.2). The only groups with similar low levels of free corticosteroids were the male adult transients and male juvenile residents. When the data of the latter two groups were compared to all other groups there were also no significant differences. The male adult residents were characterised by lowest levels of free corticosteroid relative to other groups.

7.3.2 ANNUAL VARIATION IN PLASMA FREE CORTICOSTEROID CONCENTRATIONS

The annual variation of free corticosteroids was not analysed for the groups shown in Table 7.2 because of the small sample size, so analyses were carried out on the different age groups and dispersal groups of males and females. Within these

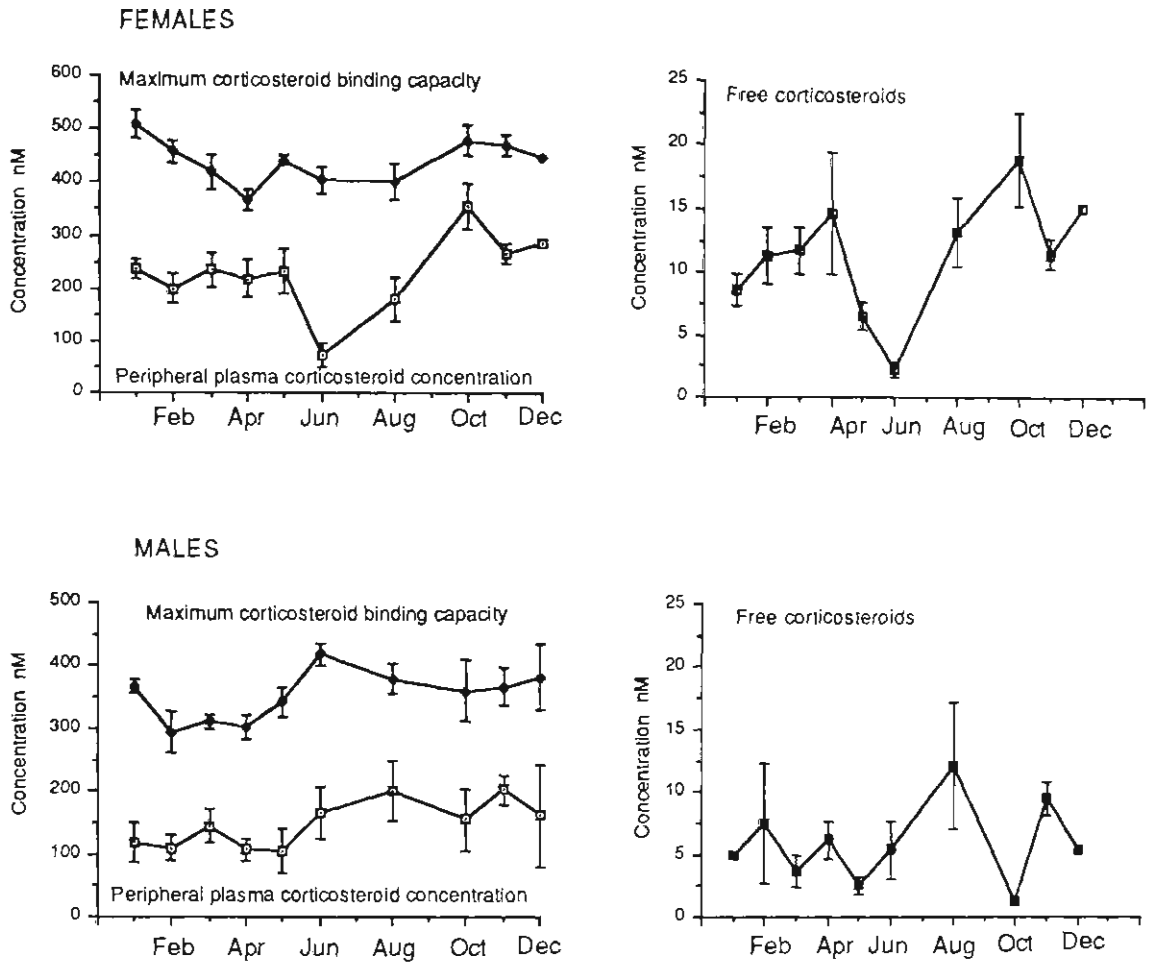


FIGURE 7.1

Mean monthly concentrations of peripheral plasma corticosteroids, the maximum corticosteroid binding capacity (MCBC) and the resultant free corticosteroids (± SE) Sample sizes shown in Table 7.3.

TABLE 7.1 Plasma-free corticosteroid levels (nM) for devils of different sex, age and residence status

	Male			Female		
	mean	SE	n	mean	SE	n
Adult	5.6	0.9	49	11.9	1.0	45
Juvenile	10.0	1.3	41	12.4	1.9	27
Resident	7.0	0.9	70	11.8	1.2	42
Transient	10.4	1.9	20	12.4	1.4	30

TABLE 7.2 Mean ± SE concentration of free corticosteroids for the various sex, age and social status groups. The F value and P level indicate the degree of difference from the value for male adult residents *

	mean	SE	n	F	P
male adult residents	5.8	1.0	45		
male adult transients	6.5	3.2	4	8.114	$P > 0.05$
male juvenile residents	9.1	1.7	25	3.879	$P > 0.05$
male juvenile transients	11.2	2.0	17	4.527	$P < 0.05$
female adult residents	11.4	1.1	29	3.703	$P < 0.05$
female adult transients	12.6	2.1	16	4.627	$P < 0.05$
female juvenile residents	12.6	3.4	13	4.897	$P < 0.05$
female juvenile transients	12.1	1.9	14	4.759	$P < 0.05$

* F value from Fisher's protected least significant difference test
$P < 0.05$ indicates statistical significance

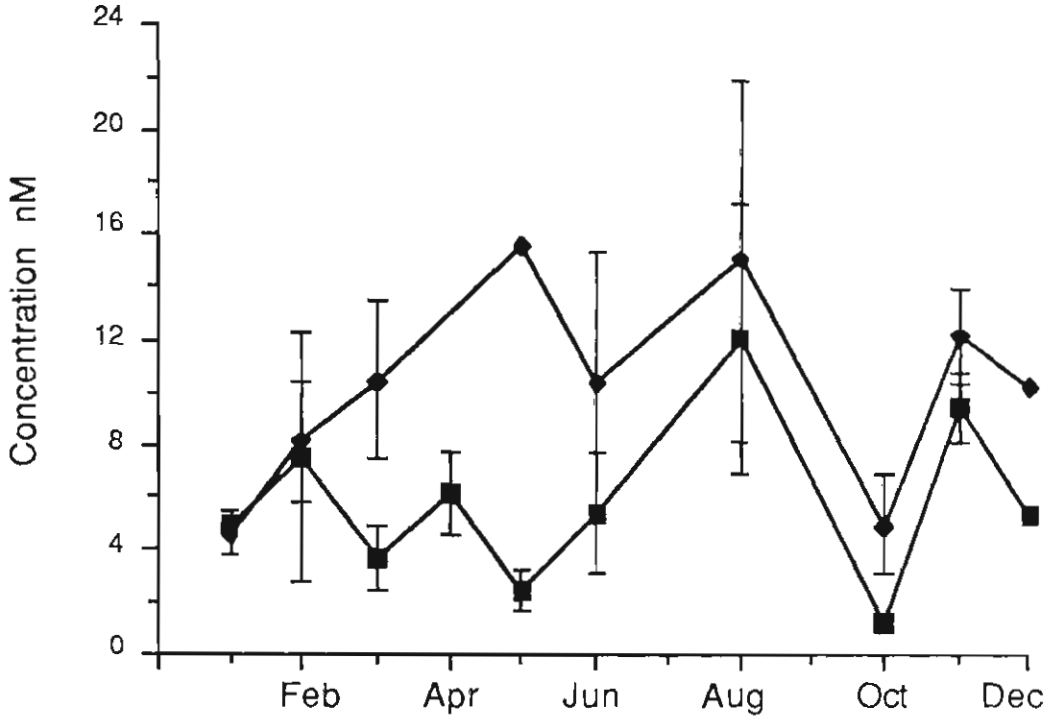


FIGURE 7.2

Mean (+SE) monthly free corticosteroid concentrations for adult (squares) and juvenile (diamonds) males.
Sample sizes in Table 7.3

categories the sample sizes of the male transients (n=22) and female juveniles (n= 27) were too small to do statistical seasonal comparisons. These data are shown in Table 7.3

The male devils showed no significant overall seasonal variation in free corticosteroid concentrations ($F_{(9,82)}$=1.267, p=0.267). In contrast, the females did show a significant seasonal variation in the concentration of free corticosteroids ($F_{(9,62)}$=3.203, p=0.003) (Fig. 7.1). There was a steady increase from January to April when the peak in births took place. The concentrations then decreased to a low of 2.2 nM in June which contrasted with a high of 22.5 nM in October (F= 9.841). Again there was a significant decrease from October to 12.6 nM in November (F= 7.623) when young devils started to emerge from their dens.

The male and females showed a significant difference when compared with each other across the year ($F_{(9,147)}$=2.837, $p < 0.001$). The April and October samples showed the maximum variation between the two sexes. In April females had a mean concentration of 15.375 nM compared to 6.154 nM for males. This difference was even more marked in October (females: 22.543 nM, males: 4.025 nM).

A detailed analyses of the subgroups showed that there was no significant seasonal variation in the free corticosteroid levels of male adults ($F_{(9,48)}$= 1.302, p=0.267), male juveniles ($F_{(8,40)}$= 0.695, p=0.693), male residents ($F_{(9,69)}$=1.172, p=0.33), female adults ($F_{(9,44)}$=1.943, p=0.08) and female transients ($F_{(9,32)}$=1.041, p=0.434). The resident females did show a significant difference with season ($F_{(9,41)}$=2.473, p=0.029).

The mean free corticosteroid levels for juvenile males remained consistently higher than those for adult males (Fig. 7.2) although there was considerable overlap in the standard errors. There was no significant difference in the free corticosteroid concentration of juvenile and adult males in January and February but this became significant when the juvenile levels rose to 10.6 nM in March and the adults fell to 3.6 nM ($F_{(1,18)}$=5.073, $p < 0.05$). The adult levels fell to low of 2.475 in May whilst the level in juveniles continued to rise. Although the sample size is small (Table 7.3) there was a significant difference between these values ($F_{(1,9)}$=16.935, $0.001 < p < 0.05$). This pattern was also evident in adult females which showed a decrease in free corticosteroids whilst the juveniles remained higher (Table 7.3). This period corresponds with the period of maximum population size (Chapter 3).

The adult females and resident females showed a similar pattern of change over the year (Fig. 7.3). This is to be expected as the data set contains 29 values that are

TABLE 7.3 Levels of free corticosteroids (nM) for males and females of different age and social status *

Month	Adult		Juvenile		Resident		Transient	
	mean ± SE	n	mean ± SE	n	mean ± SE	n	mean ± SE	n
MALES								
January	4.9 (5.5,4.4)	2	4.6 ±1.8	4	5.3 ±0.3	4	3.6 ± 1.6	2
February	7.5 ± 4.7	5	8.1 ± 6.1	7	6.8 ± 2.9	9	11.0 ± 2.0	3
March	3.7 ± 1.2	11	10.5 ± 8.4	9	3.9 ± 1.1	13	11.3 ± 3.2	8
April	6.1 ± 1.5	7			6.0 ± 1.8	6	7.3	1
May	2.5 ± 0.8	8	15.6 ±10.0	2	5.5 ± 2.3	9	1.1	1
June	5.4 ± 2.3	3	10.4 ±10.2	4	7.1 ± 4.3	5	11.0 (9.7,12.2)	2
July								
August	12.1 ± 5.1	6	15.1±15.5	5	13.2 ± 5.5	7	13.9 ± 6.3	4
September								
October	1.20	1	5.0 ±3.2	3	4.0 1.6	4		
November	9.8 ± 1.4	6	12.2 ± 3.6	4	10.5 ± 1.3	9	11.1	1
December	5.3 (6.2,4.5)	2	10.2	2	7.8 ± 4.3	4		
FEMALES								
January	8.6 ± 1.3	5	8.2 ± 1.0	7	8.9 ± 0.8	5	8.0 ± 1.3	7
February	11.2± 2.2	6	7.5 ± 2.0	8	8.8 ± 2.1	9	9.8 ± 2.2	5
March	11.75 ± 1.8	6	12.7 ± 3.9	4	11.8 ± 1.8	6	12.7 ± 3.9	4
April	14.7 ± 4.74	6	17.5 (16.7,18.3)	2	12.2 ± 3.8	3	17.28 ± 5.3	5
May	6.5 ± 1.1	4	22.5 (20.4, 24.7)	2	8.1	1	12.6 ± 4.2	5
June	2.2 ± 0.7	3			2.6 (1.4, 3.6)	2	1.4	
July								
August	13.2 ± 2.7	5	3.4	1	8.6 ± 3.1	3	15.6 ± 4.4	3
September								
October	19.0 ± 3.6	5	31.4 (14.5, 48.4)	2	24.5 ± 7.0	5	17.6 (17.1, 18.1)	2
November	11.5 1.2	7	18.9	1	12.6 ± 1.6	7	11.2	1
December	15.10	1			15.1	1		

* Mean ± standard error (SE) where n > 2. Mean (range) where n = 2

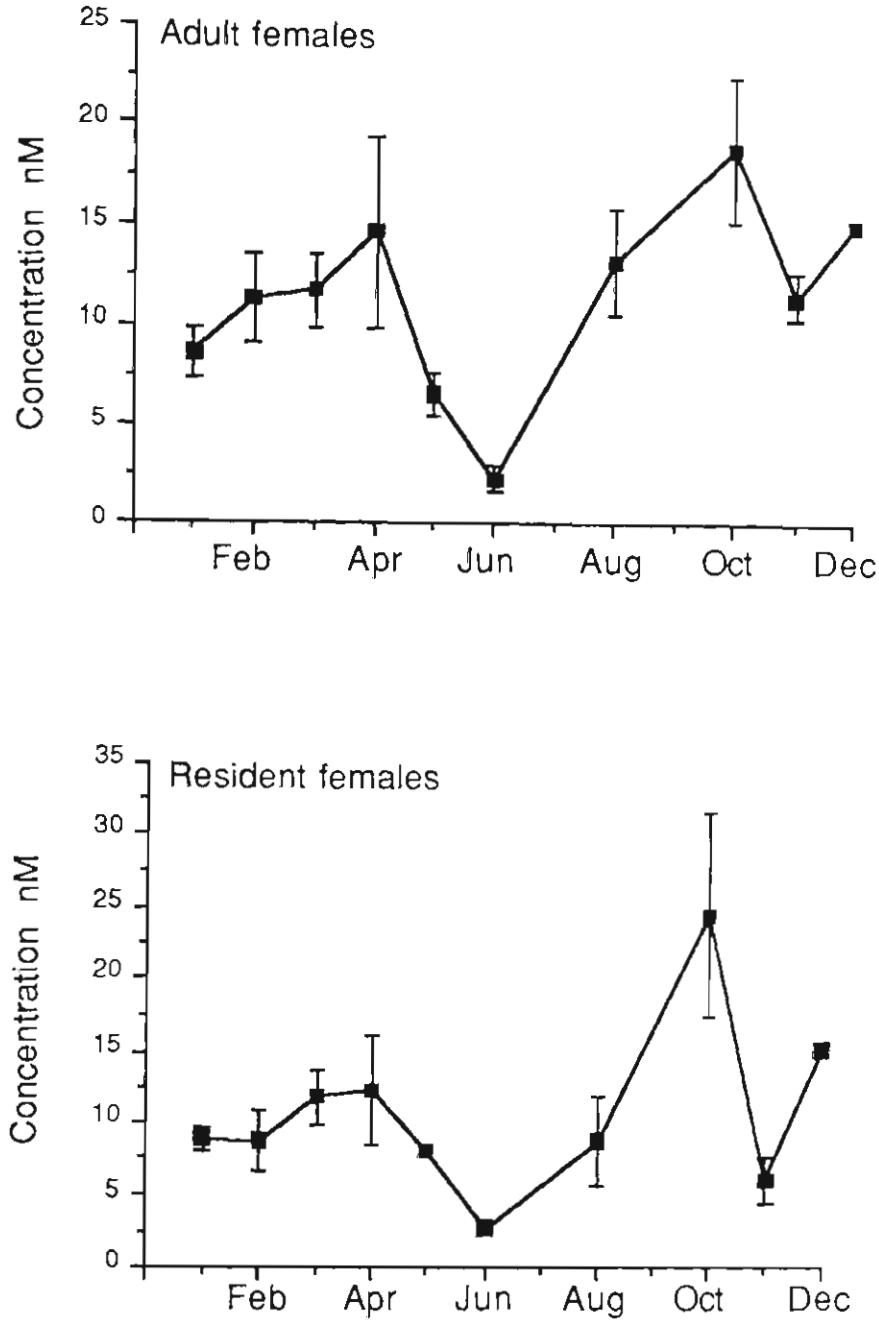


FIGURE 7.3

Mean (± SE) monthly concentrations of free corticosteroids for adult females and resident females. Sample sizes are shown in Table 7.3

common to both, because many adults in the sample were residents. The low, but not significant P value for the adults (λ(p= 0.08), and significant p value for the residents (λ(p = 0.029) suggest that the resident status of the females has contributed to the significant shift in these values. The adult females showed a fairly consistent level of free corticosteroids from January through to April, followed by a sharp decrease through May to June and then a sharp rise to a peak in October (19.0 nM). The decrease in June was significantly different from those levels of April (λF= 9.225) and August (λF= 9.528). The peak in October was accentuated when only the resident adults were analysed and was significantly different from all other months ($F_{(9)}$=16.935, 0.001 < p < 0.05).

The frequency distribution in Figure. 7.4 shows that the levels of free corticosteroids of the different sex and age groups are different relative to each other (Kruskal Wallis test; H_{corr} = 24.63 , p > 0.001). It is this relative difference that may give an indication of the underlying factors affecting the social organisation of the Tasmanian devil, without giving too much emphasis on the degree of stress that is represented.

Figure 7.4 shows that the majority of female adults (73 %) and female juveniles (63 %) were in a " highly stressed" condition using Bryant's (1988) classification. Fewer male juveniles (43.9 %) and adult males were (22.4 %) in a similar state of stress. The mean free corticosteroid levels in the peripheral plasmas of devils was 9.6 ± 0.62 nM (n= 162) suggesting that the "average" devil is in a "highly stressed" condition relative to Eastern quolls which never registered values greater than 8 nM in the field (Bryant,1988), but not dissimilar from *D. hallucatus* (Schmitt et al 1988).

7.3.3 LEVELS OF TESTOSTERONE IN PERIPHERAL PLASMAS OF MALE TASMANIAN DEVILS

Table 7.4 shows the results of assays of testosterone concentrations in peripheral plasmas from 101 male Tasmanian devils. A two-way analysis of variance for unequal sample sizes was performed on the log-transformed data comparing adult and juvenile males and there was no significant difference ($F_{(1,100)}$ = 1.004, p > 0.05). There was also no significant difference between testosterone levels of transient and resident males ($F_{(1,100)}$=0.337, p > 0.05). The age and resident status of male devils is not therefore reflected in relative levels of testosterone.

The seasonal variation in testosterone concentrations of adults and juveniles is shown in Figure 7.5. There was no significant difference between adult and juvenile males when compared between months ($F_{(9,100)}$ = 0.653, p > 0.05). Neither adult

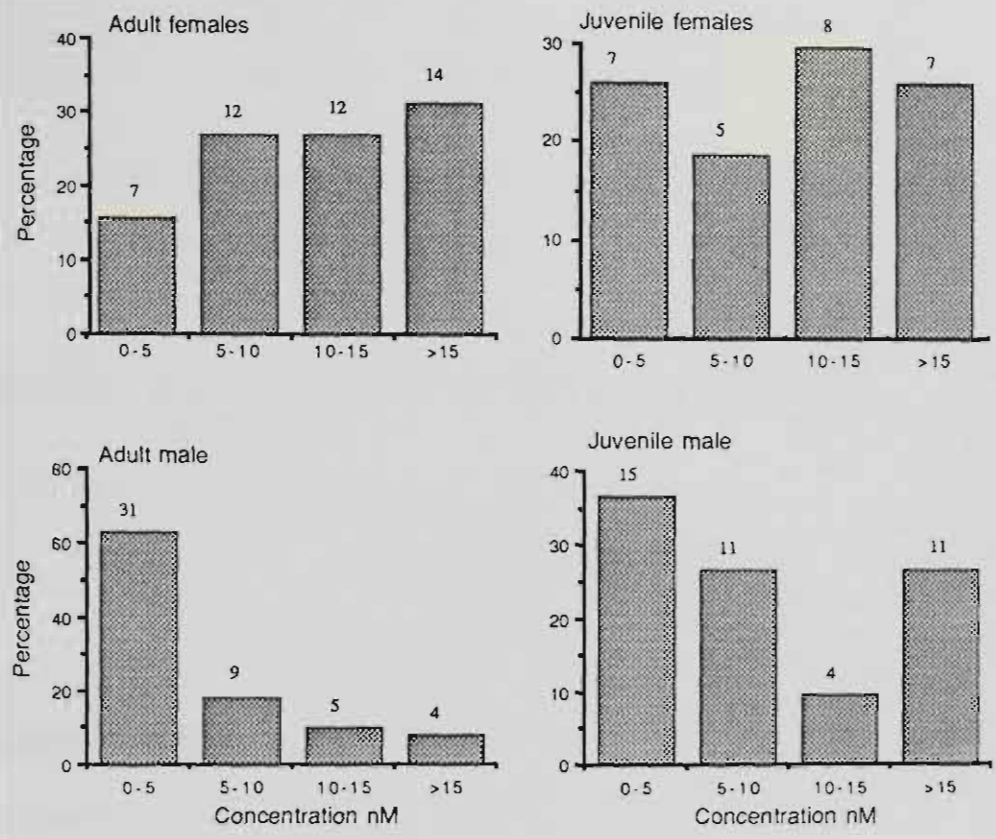


FIGURE 7.4

Frequency of occurrence of free corticosteroid concentrations in groups of 5 nM. Sample sizes are shown for each group.

TABLE 7.4 Mean levels of testosterone (ng/ml) in peripheral plasmas of male Tasmanian devils.

	Mean	SE	Range	n
Adult	0.66	0.08	0.04 - 2.85	53
Juvenile	0.78	0.09	0.07 - 2.50	48
Transient	0.77	0.12	0.10 - 1.88	18
Resident	0.70	0.06	0.04 - 2.85	84

TABLE 7.5 Basal and peak levels of testosterone recorded in dasyurids

Species	Testosterone level ng/ml	
	Basal	Peak
Phascogale calura	2.8	8
Antechinus swainsonii	0.9	3
Antechinus flavipes	2.8	12
Antechinus stuartii	1	8
Dasyurus viverrinus	0.5 - 0.7	5.0 - 7.0
Dasyurus hallucatus	6.5	25
Sarcophilus harrisii	0.7	0.7

Sources of information: McDonald et al. (1981); Bryant (1986); Bradley (1987); A. Bradley (pers comm); this study.

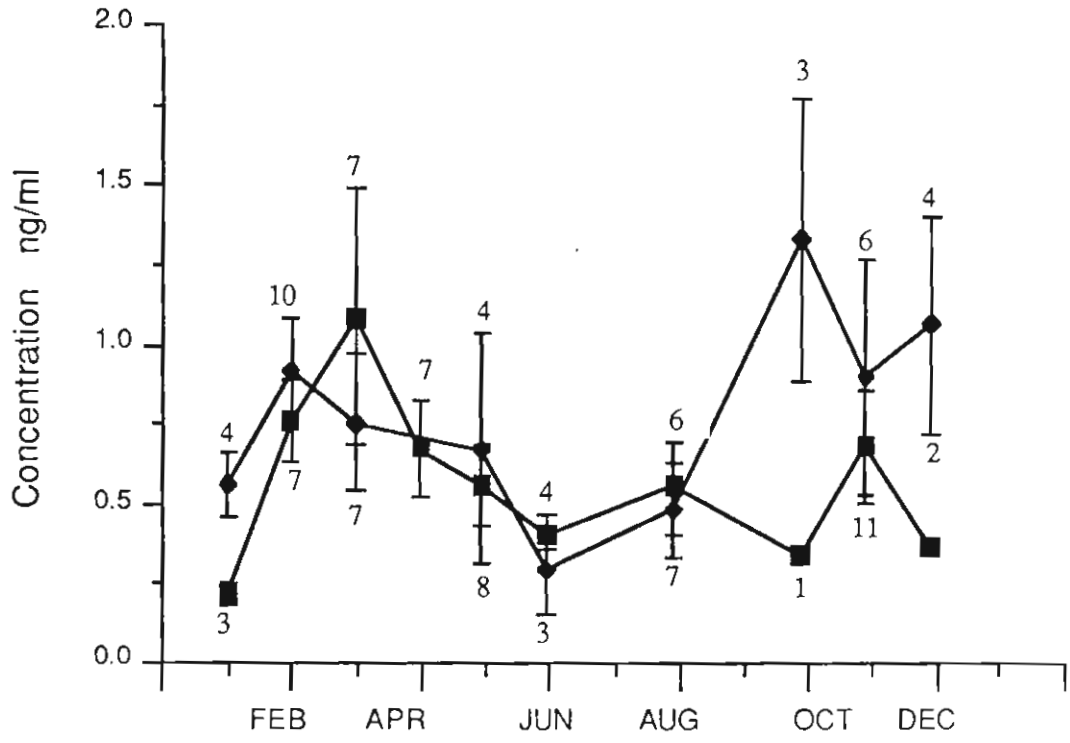


FIGURE 7.5

Mean (±SE) concentrations of testosterone in adult (squares) and juvenile (diamonds) males. Sample sizes are shown above the bars for juveniles and below for adults.

($F_{(5,52)}$=0.898 p > 0.05) nor juvenile males ($F_{(6,47)}$=1.079, p > 0.05) showed a seasonal variation in testosterone levels.

The sample sizes were too small to allow statistical comparisons of seasonal variation in testosterone levels of transients (Table 7.4). However, in March, (the peak of breeding) the levels were compared and showed no significant difference ($F_{(6,14)}$=1.004, p > 0.05). The residents showed no significant seasonal variation in levels of testosterone ($F_{(9,83)}$=1.671, p > 0.05).

The annual variation in adult male testis size (length and width) and mass is shown in Figure 7.6. Testosterone concentrations are also shown for comparison. There was a significant seasonal variation in body mass ($F_{10,120)}$=2.346, p < 0.05) but there was no significant variation in the size of testes either in width ($F_{(10,112)}$=1.045, p >> 0.05) or length ($F_{(10,112)}$=0.284, p >> 0.05).

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7.4 DISCUSSION

These data describing steroid levels demonstrate that the Tasmanian devil shows endocrine changes associated with seasonal variations, age, sex and social circumstances, broadly similar to *D. hallucatus, D. viverrinus* and *S. crassicaudata* (McDonald *et al.* 1981, Bryant 1988, Schmitt *et al.* 1988). However, these species are extremely dissimilar to *A.stuartii, A. swainsonii, A. flavipes* and *P. calura* in terms of large variation in steriod levels associated with breeding (for a review see McDonald *et al.* 1981, Bradley 1987). However, the Tasmanian devil male, unlike all other dasyurids studied to date, shows no peak in testosterone during the breeding season.

There was no correlation between plasma MCBC and testosterone concentration in male devils suggesting that, as for *D. hallucatus, D. viverrinus* and *S. crassicaudata* (McDonald *et al.* 1981, Bryant 1988, Schmitt *et al.* 1988), there is no androgen dependant change in plasma MCBC. In addition, in devils the MCBC levels of both sexes showed a pattern similar to these three dasyurids where the levels always exceeded the total corticosteroid concentration. This is unlike the pattern found in *A.stuartii, A. swainsonii, A. flavipes* and *P. calura* where the opposite occurs in the males during the breeding season (McDonald *et al.* 1981, Bradley 1987). The cortisol binding profile of the devil is thus fundamentally similar to that of *D. hallucatus, D. viverrinus* and *S. crassicaudata*. Devils do not show an androgen dependant increase in free corticosteroids during the breeding season which could cause drastic mortality rates of the males as found in the other dasyurids mentioned above.

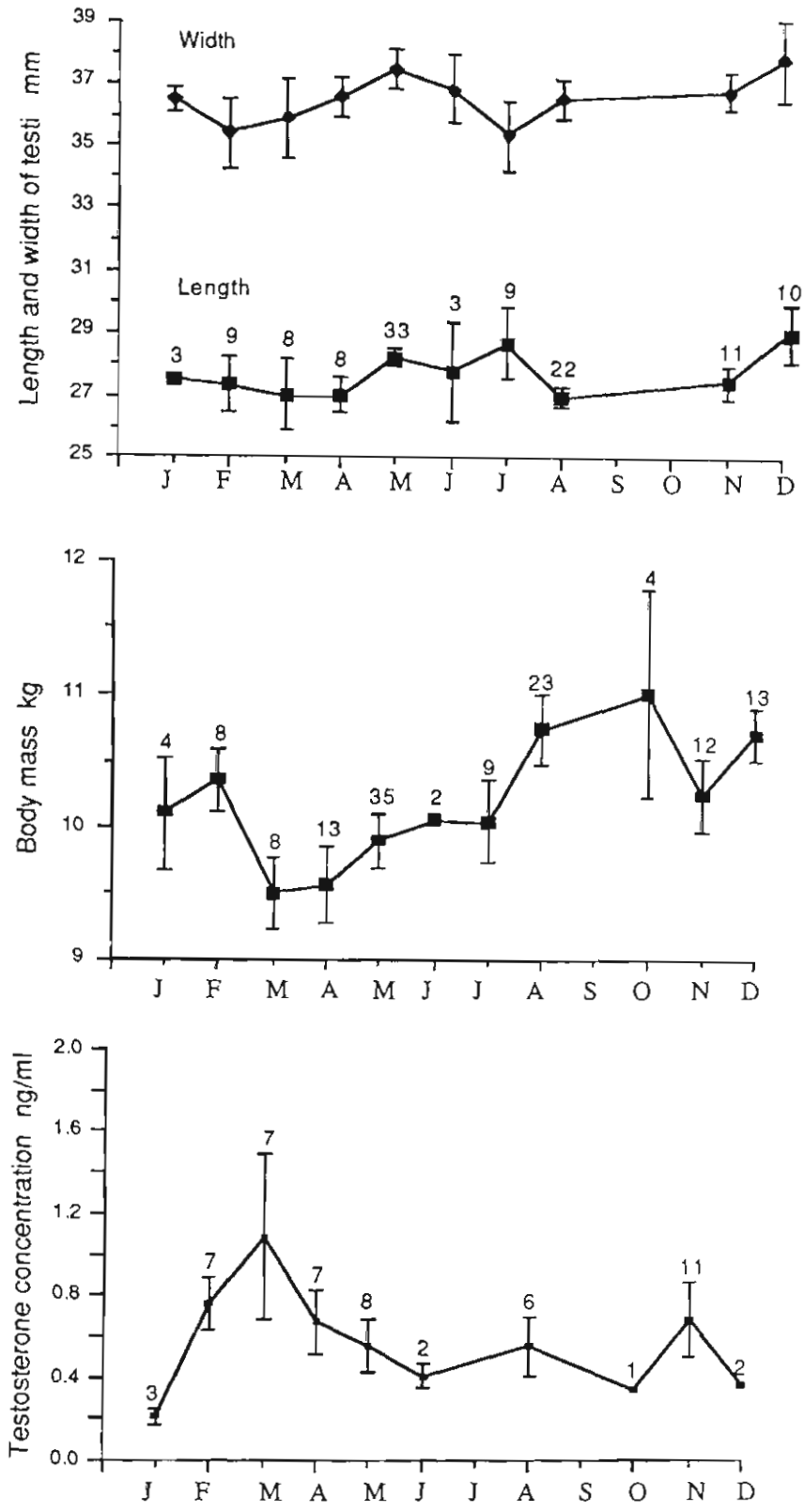


FIGURE 7.6

Mean body mass, scrotal size and testosterone concentration (±SE)for adult male devils. Sample sizes shown above error bars.

In the wild, both *D. hallucatus* and *D. viverrinus* males show an increase in free cortisol concentration when the young are weaned and dispersal commences, and a slight increase associated with the breeding season (Godsell 1983, Bryant 1988, Schmitt *et al.* 1988). These increases are said to be associated with decreased survival in these species (Bryant 1988, Schmitt *et al.* 1988). There was a distinct difference between the free corticosteroid concentrations levels of adult and juvenile male devils. The adults had lower concentrations throughout the year (Fig 7.2). This difference was greatest during the breeding season (from March to June), coinciding with the period of highest population levels. From June to February free corticosteroid of juveniles remained higher but the difference between the two age groups decreased progressively and was not significant.

Adult and juvenile male residents and transient adult males had lower concentrations than male juvenile transients. It appears, therefore, as if high population densities affect stress levels in male devils in a similar way to *D.hallucatus* and *D.viverrinus*.

In many mammals sexual interactions result in a rapid but transient elevation of testosterone concentrations, whilst aggressive interaction results in decreased testosterone levels and increased levels of adrenal corticoids. The results of aggressive interactions tend to be more profound and of longer duration than the affects of sexual interactions, especially among subordinate animals (Moberg 1985, Harding 1981). Brief stress, associated with increased levels of corticosteroids, increases testosterone concentrations, while the prolonged effect of stress is to suppress testosterone secretion (Moberg 1985).

Frank *et al.* (1985), in a study of *C.crocuta* found that the mean androgen levels were less than 2 ng/ml and postulated that the exceptionally low androgen values were a response to social stress brought about by high population densities and the resultant competition for food. A similar pattern may well be occurring with the devil. The depressed concentration of testosterone measured in a total of 101 male devils (Table 7.4) was similar to those found in the high density population of *C.crocutta*. Supporting this proposition is the observation that the juvenile male transients had elevated free corticosteroid during the period of maximum population density indicating that they were under stress.

Bryant (1988) suggests that the high levels of free cortisol in adult *D. viverrinus* males are the result of stress induced by social conflict within the population. Schmitt *et al.* (1988) found no association between population density and stress as indicated by free cortisol levels in *D. hallucatus*. Instead they conclude that

the post-mating elevated levels of free cortisol were the result of socially subordinate behaviour, whereas dominant animals had lower levels of free cortisol. It appears, therefore, that the levels of stress in the males of both these species can be interpreted as the results of social interaction between individuals of the population, brought about by increased population densities or aggression associated with breeding. In many species dominant males have much higher levels of testosterone than do subordinates (Moberg 1985). High levels of testosterone, as the result of aggressive interactions, are thought to control CBG and the consequent increase in free corticosteroids in dasyurids that show a post-mating mortality (Bradley *et al.* 1980; McDonald *et al.* ,1981; Bradley, 1987). Schmitt *et al.* (1988) conclude that the animals with high free corticosteroid and low testosterone levels were subordinate and more likely to survive than those that had low free corticosteroid and high testosterone levels and which were probably dominant. Bryant (1988) found that juvenile Eastern quolls had high levels of testosterone during dispersal whilst the adults had low testosterone and high cortisol levels. She concludes that, as found for *D.hallucatus*, a similar behaviour linked endocrinological mechanism is operating, where social interactions rapidly modulate testosterone profiles resulting in stress (as measured by free corticosteroids) which thereby affects the survival of males.

The basal and peak testosterone concentrations measured in the peripheral plasmas of these dasyurids are shown in Table 7.5. All of these species show a peak in testosterone just prior to or during the breeding season, that is significantly higher than basal levels. The concentration of testosterone found in the male devil was consistently low with regard to the other dasyurids, regardless of the age of the devils, social status or time of year. There was no peak in testosterone concentrations, testi size or mass around the breeding season (Fig. 7.6) as has been shown for *D.viverrinus* and *D. hallucatus* (Bryant 1988, Schmitt *et al.* 1988). The lack of a concomitant increase in testi size supports the finding that there was no peak in testosterone concentrations.

Although the life history pattern of the Tasmanian devil is similar to both *D.hallucatus* and *D.viverrinus*, except extended with respect to the duration of lactation, it appears that there is a fundamental difference in the form of social interactions which occur during breeding, producing a testosterone profile very different from that of the other species. One explanation could be that the expected increase in testosterone does not appear in the peripheral plasma of devils but is held within the testes (Bradley pers comm). Alternatively, perhaps the devils do not experience stress induced by social interactions during sexual encounters with conspecifics. Which of these is correct remains unclear, but the observation of one male denned for 8 days whilst copulating (and as reported by Roberts 1915, Fleay

1935) indicates that devils may reduce social interactions at this time by occupying a burrow which is defensible from other males competing for the female.

The adult females had elevated free corticosteroids during the breeding season and in early summer. The early phase of the breeding season, corresponds to the period of high population density and these pressures are manifested in the stress levels. The subsequent decrease in stress levels after the breeding season but still during the period of high population density suggests that, for adult females, there is greater stress associated with breeding activities than with high population densities. The increase in stress levels in the females from August to October corresponds with the period where the adult females are attending dependant young in dens. Foraging trips at this time are probably dictated by the need for regular feeds by the pups prior to late lactation The females then become less regular in their attendance patterns (Chapter 6).

Therefore it appears that males experience less stress than females and that stress in males is primarily influenced by the population density. Females, however, incur stress primarily via sexual interactions at the beginning of the breeding season and the regular attendance requirements of the denned pups during late lactation. The lowest levels of free corticosteroid measured in females were similar to the average level found in males. These values fell in the range of moderate to high stress levels and therefore suggest that the devil population is constantly under stress.

7.5 SUMMARY

1. There was no correlation between plasma MCBC and testosterone concentration in male devils suggesting that there is no androgen dependant change in plasma MCBC.

2. The maximum corticosteroid binding capacity was in excess of the peripheral plasma corticosteroid concentrations in all months for both sexes.

3. Adult males showed a lower degree of stress than juvenile males, which in turn were lower than all females.

4. There were two peaks in stress levels measured in adult females, one at the beginning of the breeding season and the other during mid-lactation. Sexual activity and obligation to denned young are suggested as explanations for these observed trends.

5. Stress levels and testosterone concentrations in adult males remained constant throughout the year. it is suggested that this is a response to constant stress as the result of social interactions within a dense population.

6. Unlike all the other dasyurids for which data are available, the adult male devil does not show a peak in testosterone associated with breeding.

CHAPTER 8

GENERAL DISCUSSION

The central aim of this thesis has been to describe the social organisation and behaviour of the Tasmanian devil, *Sarcophilus harrisii* , the largest of extant Dasyuridae, the carnivorous marsupials. The secondary aim of this thesis was to describe the dynamics of the devil population and movements and to relate these to changes in extrinsic factors, in particular prey availability. To fulfil these aims, an investigation was carried out into the demography, social behaviour, home range and fluctuations in the population as measured via stress related steroids.

8.1 THE SOCIAL ORGANISATION OF THE TASMANIAN DEVIL

The demographic parameters described in Chapter 4 of this study compare favourably with those used by Russell (1982a, from data in Guiler 1970 b) in a synthesis of patterns of parental care and parental investment in marsupials (Table 8.1). However, significant differences are also evident. The litter size recorded at Mt. William, for example, is smaller than that used by Russell (1982a) and variations in litter size with age or social status can have important implications in analyses of life history strategies. The present study also showed that litter size decreased with the age of the mother. Further, transient females usually carried fewer pouch young than did resident females and discontinuous residents had lower fertility levels than continuous residents. The length of pouch life differed considerably with 105 days from birth used by Russell (1982a) and 130 days found in the present study. Similarly, the date of weaning, 240 versus 280 days after birth, was greater in this study. Guiler (1970 b) stated that mating occurred in mid-March and so I infer that birth occurred in early April as the gestation period is 21 days (L. Hughes pers comm). Comparison of these data therefore suggests that the nature of parental care and investment in the devil may be flexible to some degree. Guiler's study was carried out at Cape Portland, approximately 40 km from Mt.William, so climatic factors did not contribute to the differences observed. The reason for these differences remains an enigma and warrants further investigation. In the present study, it was found that permanent pouch emergence occurred 130 days after birth and young left the den alone, 227 days after birth. The timing of these events in the life history of the devil were previously unknown.

Russell (1982a, 1984) classified the reproductive pattern of devils as seasonal polyoestrous. Devils are reported as being polyoestrous with most births recorded in April, the peak birthing period, but out of phase breeding has been recorded for May, July, August (Fleay 1935, Green 1967, Guiler 1970b). Spermatogenesis in males has

TABLE 8.1 Variables used by Russell (1984) and from the present study to describe the pattern of development of young and parental care in the Tasmanian devil.

Major variables	Units**	Russell	Present study
Reproductive pattern		SP*	SFP#
Litter size	n	3(1-4)	2.3 (1-4)
Weight of mother	kg	6.7	6.7
Weight of young at birth	kg	0.18-0.29	-
Young first off teat	DAB	90-100	-
Hair growth	DAB	50-90	-
Eyes open	DAB	90	>130
Young first out of pouch (FPE)	DAB	105	-
Young left in nest alone (LIN)	DAB	105	130
Young leaves nest alone (LNA)	DAB	-	227
Permanent pouch exit (PPE)	DAB	-	130
Weaning	DAB	240	280
Sexual maturity	months	24	24

SP* Seasonal, polyoestrous
SFP# Seasonal, facultatively monoestrous
** DAB = days after birth

been recorded in August (Hughes 1982) and spermatogonial mitosis in June (Sharman 1959). In the present study I found no evidence of out of phase breeding and the birth pulse was synchronised, both within and between years, within a period of 3 weeks in early April.

Lee & Cockburn (1985) revised a system of Lee *et al.* (1982) and classified the life history patterns of dasyurids into six strategies. This classification was based on the duration and timing of male reproductive effort, the seasonality of breeding and the age at maturity. They pointed out that the devils position in this classification was unclear, because whilst having a synchronised breeding season, being facultatively monoestrous and sexually mature in the second year, devils have a far longer lactation period and live far longer than the other members of the group. The lactation period of devils at Mt.William was one month longer than that used by Lee & Cockburn (1985), and so increases the divergence of the devil from other dasyurids in the criteria used in the classification of Lee & Cockburn (1985). The results of the present study however, support their definition of the devil as being facultatively monoestrous, rather than seasonally polyoestrous as used by Russell (1982).

In a detailed synthesis of the social organisation of marsupials, Russell (1984), concluded that the majority of dasyurids are solitary an promiscuous, living in overlapping home ranges. The parameters used in this synthesis are shown in Table 8.2 and compared with those found in the present study. The mating system as used by Russell (1984) categorises the devil as promiscuous with extreme sexual dimorphism. The observations in the present study of a 'consort' period where the male holds the female in a den for up to 8 days suggests that devils are better classified as having a "K" mating system (Russell 1984), in which otherwise promiscuous adults remain together for a short time during the mating period . The pattern of parental care as used by Russell (1984) is essentially the same as found in this study, except that dependent young were never recorded traveling with and on the mother once they had left the pouch. The major difference in Table 8.2 relates to the dispersal of young. The placement of devils in category "S" (extended association between mother and female young until sexual maturity, Russell 1984) does not comply with the results found here where, although females are more tenacious to their natal area than are males, the young of both sexes disperse soon after weaning. These observations are more similar to the description of dispersal of young provided by Russell (1984) later in the review (page 125). The remaining facets of social organisation of the devil described by Russell (1984) and shown in Table 8.2 are similar to those found in the Mt. William population.

TABLE 8.2 Summary of the variables used to describe the pattern of social organisation in the Tasmanian devil by Russell (1984) and the present study.

Variables	Russell (1984)	Present study
Social unit	Individual-Young disperse at weaning	Individual-Young disperse at weaning
Dispersion	Little or none of home range exclusive	Little or none of home range exclusive
Mating system	Promiscuous. Extreme sexual dimorphism	Promiscuous. Extreme sexual dimorphism Association of pair for a few days
Parental care	Reduced pouch, large litter, use of maternity den	Reduced pouch, large litter, use of maternity den Young did not travel on mother after PPE*
Dispersal of young	Young disperse after weaning	Young disperse after weaning Female biased natal philopatry
Reproductive pattern	Seasoal monoestrous, litter size >1, sexual maturity in next season after birth	Seasoal monoestrous, litter size >1, sexual maturity in second season after birth

* PPE refers to permanent pouch emergence

Eisenberg (1981) has classified the devils mating system as being polygamous with a dominance hierarchy existing amongst males and semi-exclusive home ranges for both sexes. The behavioural information in the present study supports the existence of a polygamous mating system. However contrary to Eisenberg (1981) it suggests that, at least around food, there is no hierarchal formation and home ranges are totally overlapping. Again, Eisenberg's description of the rearing pattern and foraging strategy of the devil is different to the observations from Mt.William since he proposes the existence of semi-exclusive home ranges. However, the rearing pattern of devils in the broad sense as described by Eisenberg and as documented in this study are similar with females rearing their young independently. The refuge system used by devils at Mt.William, where they occupy separate dens, is also in accordance with that used by Eisenberg (1981) in his review of the evolution of mammalian social organisation.

In light of the interpretations of Russell (1984) and Eisenberg (1981), and based on the findings of the present study, the devil can now be confidently classified as a solitary, promiscuous or polygamous species in which the female raises her young on her own, they occupy home ranges which are totally overlapping and exclusive and some juveniles remain in the natal area. Reviews concerning the theory of social evolution and life history strategies have in the past been restricted by the gaps in the knowledge of even the well known species, as pointed out by Russell (1984). More particularly for the dasyurids detailed information was restricted to the small and short-lived species. The detailed information on the social organisation and life history of the devil documented in this study has redressed this situation and will contribute to future studies on the theory of the evolution of social organisation by comparative review across and between taxa. It has been suggested, for example, that asociality in felids is a function of the size of prey and that sociality could develop in this group in association with larger prey (Caro 1989). At Mt. William the prey available to devils is comprised of the largest terrestrial mammal species present in Tasmania and these also occur very high densities. Following this and the ideas of Caro (1989) it is not suprising that devils are solitary animals. However, the sociality exhibited around the carcasses may change between prey rich areas such as the dry sclerophyl forests of Mt. William and other areas such as the rainforests of the west coast. This variation in interaction over food and how it varies in relation to changing prey could form an interesting comparison with the felid situation.

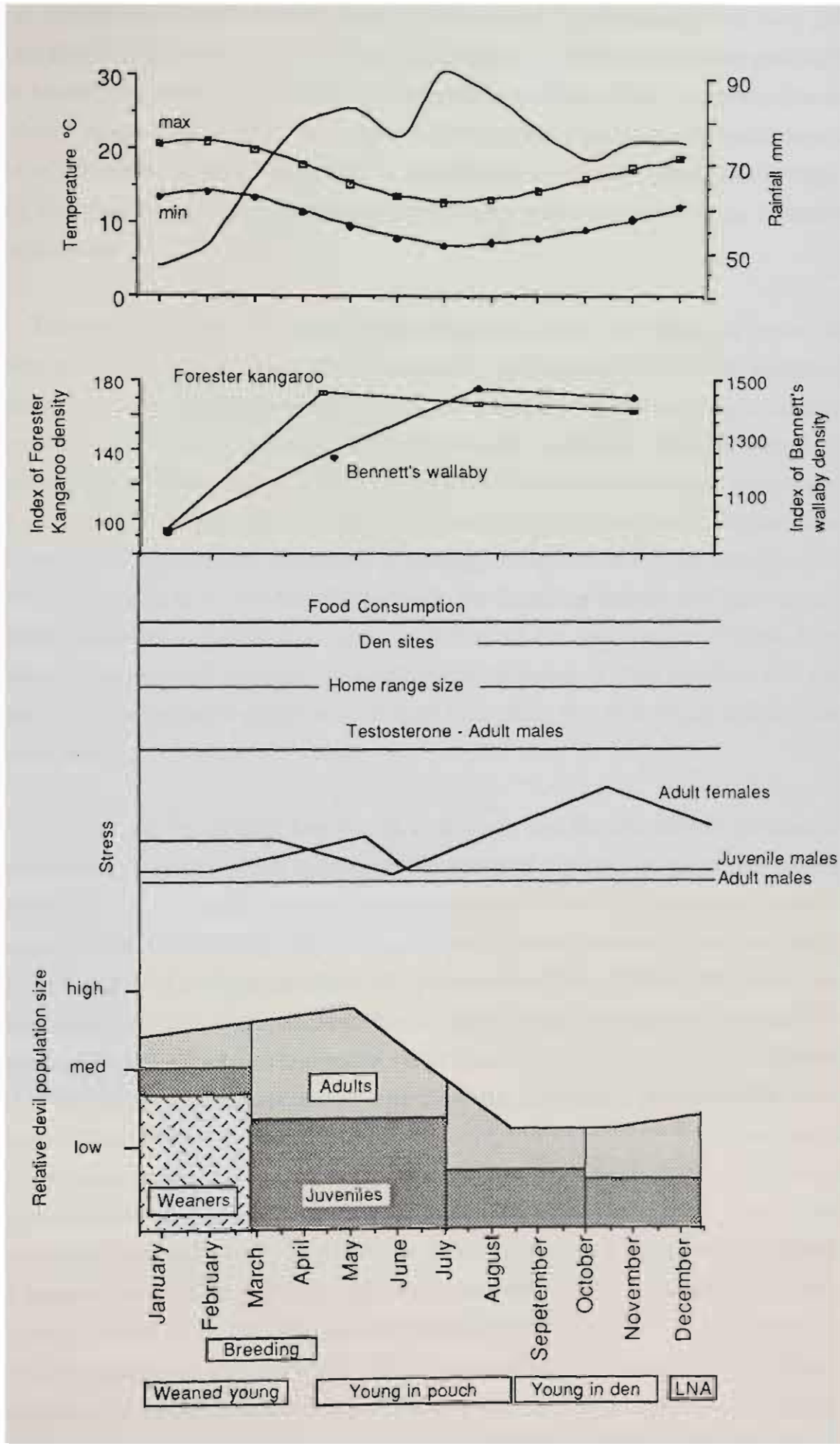
8.2 SOCIAL INTERACTIONS AS INDICATED BY STRESS

The stress levels measured in the Mt. William devil population have been shown to vary according to sex and age (Chapter 7). The major variations are shown schematically in Figure 8.1. The adult males showed a lower degree of stress than the

juvenile males which in turn were lower than all females. There were two peaks in the stress levels measured in adult females, one at the beginning of the breeding season and the other during the middle of the lactation period when females were attending young in dens at regular intervals. Behavioural differences reflected in these stress levels may result from differences in the requirements of the sexes: mates for males and dens for females as is found in many other mammals(Emlen & Oring 1977, Clutton-Brock & Harvey 1978). In the present study it was shown that the females rely on primary dens to raise their young (Chapter 6). These dens are restricted in their distribution and hence it follows that so are the females. However, the females still

FIGURE 8.1

Schematic representation of devil population size and composition (Chapter 3), fluctuations in hormone levels (Chapter 7), food consumption rates (Chapter 5), home range and tenacity to den sites (Chapter 6). Indicies of annual fluctuations in macropod populations (from Hocking & Pemberton, unpublished data) and temperature and rainfall records are also presented. When the graph is represented by a straight line there was no significant seasonal variation. Where absolute values are not given they can be found in the relevant Chapter.


Temperature °C
30
20
10
0
max
min
90
70
50
Rainfall mm
Index of Forester Kangaroo density
180
140
100
Forester kangaroo
Bennett's wallaby
1500
1300
1100
Index of Bennett's wallaby density
Food Consumption
Den sites
Home range size
Testosterone - Adult males
Stress
Adult females
Juvenile males
Adult males
Relative devil population size
high
med
low
Adults
Juveniles
Weaners
January
February
March
April
May
June
July
August
Sepetember
October
November
December
Breeding
Weaned young
Young in pouch
Young in den
LNA

need to forage. The distribution of food is constant and food consumption rates are constant (Fig 8.1) for both males and females (Chapter 5). Therefore females probably forage harder than males, which have no obligation to return to the maternity den to feed their young. This increase in foraging effort could explain the different stress cycles of the sexes, at least during mid to late lactation when the young are denned. During this time female stress levels rise significantly while the stress levels in males remain constant.

During copulation and early in the breeding season the levels of stress in females increases while males show relatively low levels. This is in apparent contradiction to the trend in sexually dimorphic polygamous species which usually show intra-sexual male competition for females (Lee & Cockburn 1985) and therefore behaviour induced stress in the males (Harding 1981). Two observations in the present study of a male denning with a female in a burrow during copulation indicate that males may avoid intra-sexual aggression by holding the female in a defensible site. The duration of the stress of the females through the breeding season and subsequent decrease thereafter suggests that stress is linked to the breeding activities. It is postulated that repeated attempts by many males to copulate with females, and the duration of the copulation event when it does take place (up to 8 days), induces the observed stress.

Adult male devils may live for up to 6 years and do not exhibit the drastic stress-induced mortality which is observed in many of the smaller dasyurids (for a summary see Lee & Cockburn 1985). Stress levels of adult males remained constant throughout the year. Similarly, testosterone concentrations remained constant. Stress levels were higher than those measured in *D.viverrinus* (Bryant 1988) and lower than those measured for *D.hallucatus* (Scmidt *et al.* 1988). Stress in these two species was related to population densities and social status respectively and both species showed peaks in testosterone levels associated with breeding. It appears, therefore, that there are fundamental differences in the causal relationships of stress in the adult male devil when compared with these two closely related species. Prolonged stress as the result of aggressive interactions results in depressed testosterone levels (Harding 1981). The stress profile observed in adult male devils is interpreted as a response to constant stress imposed by the high population density, resulting in many agonistic encounters, particularly around food. The population density at Mt.William (2.2 - 8.7 devils /km^2) could not be compared with the other studies, as these were assessed only via indices of abundance. If social stress affects devils in the way postulated here, then it follows that devils in a lower density, less competitive population would be expected to have higher levels of testosterone than the males at Mt.William.

8.3 FACTORS AFFECTING POPULATION SIZE AND MOVEMENT

The information on the social organisation of the devil as determined and assessed in this study can also be used in an effort to identify the factors which influence the population density and movements. The various facets of the social organisation of the devil and the factors that may affect it are summarised in Figure 8.1. There are a suite of parameters associated with the social organisation of the devil including population size and the age composition, dispersal of different age groups, and stress in adult females, all of which show fluctuations over the year. There are also a suite of constant parameters including food consumption rates, home range size, tenacity to den sites and stress in the adult males. I hypothesise that the major extrinsic factor that affects the social organisation of the devil is the distribution and abundance of food.

The highest devil population densities occur from late summer until autumn. This is largely the result of the recruitment of weaned young and ultimately juveniles into the population after weaning in January. Until mid-winter the population is largely composed of a fairly equal complement of resident adult and juveniles of both sexes, after which numbers decline as a result of dispersal and mortality. The numbers of Bennett's wallaby *M. rufogriseus* and Forester kangaroos *M. giganteus* in the study area is lowest at the end of summer, which is hot and dry relative to the rest of the year (Fig 8.1). In contrast, the period of maximal growth of the pastures (August to September, R. Caldwell pers comm, G. Hocking unpublished data) corresponds with maximum macropod populations and the appearance of young at foot. It follows that mortality of kangaroos and other herbivores is highest during late summer when their food is scarce. At Mt. William these animals therefore represent the greatest biomass of potential food for devils, which have an opportunistic broad spectrum diet (Guiler 1970a). This period of predicted high food availability corresponds with the observed time of weaning in devils. It is likely that the weaned young are inexperienced in foraging techniques, as they do not have any prolonged association with their mothers subsequent to weaning and hence would not gain foraging experience prior to independence. The length of lactation in dasyurids, as for all mammals, is related to body size (Russell 1982). Hence, the timing of the birth pulse is intricately linked to the timing of weaning, so that the young become independent at the time of maximum prey availability. This situation is also found in many other dasyurids (Godsell 1983, Lee & Cockburn 1985).

Late lactation is a period of high energy cost to the mothers, as shown for example, in the Eastern quoll *D.viverrinus* (Green & Eberhard 1979) and further discussed by Lee & Cockburn (1985). Given that late lactation and weaning are closely linked events, the latter phase of lactation would also coincide with the period of

predicted maximal prey availability. These late lactating females would therefore gain a similar dietary advantage to the weaned young.

The biomass of food necessary to support the devil population at Mt. William at different times of the year are shown in Table 8.3. There was no variation in individual food consumption rates through the year, and it is estimated that the total population consumed 71.6 tonnes of food per year. The amount of prey available and the assumptions used to make these calculations are shown in Table 8.4. The Forester kangaroo population was stable for the duration of this study (Hocking & Pemberton unpublished data) and hence recruitment each year (birth pulse in August) equaled mortality. Counts in the Park showed that 77 % of females Forester kangaroos carried pouch young, and assuming zero mortality before young left the pouch, 390 young entered the population each year. This is a reasonable assumption as kangaroos are capable of weaning 100 % of young when climate and pastures are favourable (for a discussion on this topic see Lee & Cockburn 1985). From the calculations in Table 8.4 devils consumed 9.9 tonnes of Forester kangaroos each year. This translates to 330 kangaroos, a number similar to the estimated mortality rate i.e. 390 animals. Despite simplifications in the assumptions inherent in the calculations, it appears that the numbers of marsupials that are predicted dying each year closely matches that which the devils are estimated to have consumed. The available data therefore suggests that the availability of food influences the population density of devils.

In a review on mating tactics and spacing patterns of solitary carnivores Sandell (1989) concluded that there was evidence to support the hypothesis that home range size of females was controlled by food whilst home range size of males was controlled by access to females during the breeding season and food at other times. This form of control on home range size may occur on devils at Mt. William, where it appears that during copulation males may remain denned for a number of days on succesive occassions with different females. This behaviour may then restrict their home range during this part of the breeding season. The copulation period however lasts for only three weeks each year and so home range size would probably be determined by access to food for most of the year. A close relationship has been shown to exist between social organisation, diet and distribution of food in many vertebrates (Mills 1982, Kruuk 1978a, Bradbury & Vehrencamp 1976), including the Eastern quoll (Godsell 1983). Mills (1982) found that the home range size of brown hyaenas *H.brunnea* was controlled by the distance between food sites, size of these sites and the number of sites needed. Group size of the brown hyaena was, however, influenced by the average richness of the food site. In this way the dispersion of food controlled home range size and

independently the richness of the food patch controlled group size as predicted by the model of Bradbury & Vehrencamp (1976) and the Resource Dispersion Hypothesis, RDH (Macdonald 1983, Kruuk & Macdonald 1985, Carr & Macdonald 1986). Aspects of the social organisation of the devil, namely population density and size of home range can be explained in terms of the Resource Dispersion Hypothesis.

Gittleman (1989) categorised Carnivora groups into four major types. One of these, the population group, was defined as individuals sharing a common home range. Devils at Mt. William are considered to fit into their group as the home ranges were totally overlapping.

TABLE 8.3 Calculation of the mass of food consumed by the devil population through the year.

Month	Sex	Age class	Number of devils **	Mean mass kg	Total mass kg	Food consumption* kg/day	Food consumption* kg/3 months
Jan to Mar	Male	Weaners	153	3.9	596.7	71.6	6533.4
		Juvenile	17	6.9	117.3	14.1	1286.7
		Adult	30	10.3	309	37.1	3385.4
	Female	Weaners	133	3.5	465.5	55.9	5100.9
		Juvenile	21	6.5	136.5	16.4	1496.5
		Adult	57	7.3	416.1	49.9	4553.4
Apr to Jun	Male	Weaners	0	-	-	-	-
		Juvenile	138	6.3	869.4	104.3	9517.4
		Adult	74	9.9	732.6	87.9	8020.9
	Female	Weaners	0	-	-	-	-
		Juvenile	128	5	640	76.8	7008.0
		Adult	114	7.1	809.4	97.1	8860.4
Jul to Sept	Male	Weaners	0	-	-	-	-
		Juvenile	34	7.3	248	29.8	2719.2
		Adult	16	10.7	171	20.5	1870.6
	Female	Weaners	0	-	-	-	-
		Juvenile	32	5.5	176	21.1	1925.4
		Adult	18	7.5	134	16.1	1469.1
Oct to Dec	Male	Weaners	6	2	12	1.44	131.4
		Juvenile	25	8.2	205	24.6	2244.8
		Adult	19	10.5	199.5	23.9	2180.9
	Female	Weaners	2	2.2	4.4	0.5	45.6
		Juvenile	24	5.4	129.6	15.5	1414.4
		Adult	25	6.8	170	20.4	1861.5
TOTAL							71625.9

* Rate of food consumption based on requirement of 12 % body mass as determined from isotope turnover techniques (Section 5.4.4)

** Number of devils represents maximum numbers: n = 400 Jan to Jun; n = 100 Jul to Dec. Number in age class proportional representation from trapping record (Chapters 3 and 4)

TABLE 8.4 Calculation of the biomass and number of macropods consumed by devils at Mt. William each year

Species	Mean body mass kg	Density per square km n	Density per 46 square km kg	Density per 46 square km %	Predicted food consumed by devils* tonnes	Predicted food consumed by devils* animals n
M.rufogreseus	17	105	82110	76.3	54.9	3229
M.giganteus	30	10.7	14766	13.7	9.9	330
T.billardieri	5.5	30	7590	7.1	5.1	927
V.ursinus	20	3.4	3128	2.9	2.1	105
TOTAL		149.1			72	4591

Biomass consumed based on total annual food requirement of 72 tonnes (see Table 8.3)
Body mass of macropods based on Strahan (1983) and personal observations.

Assumptions inherent in calculations are:

1. All food consumed by the devils comprised the four macropod species listed in proportions equal to the densities in which they occur.

2. Equal mortality rates of prey species.

3. Food consumption rates based on population of n = 400 (Jan - Jun) and n = 100 (Jul - Dec)

The resident devils occupy overlapping home ranges, the dimensions of which are controlled by the distribution both of dens and food. Tenacity to the den sites, particularly the primary den, restricts the straight line distance, the traveling component, that the devil can move each night. The distribution of the potential sources of food dictates the width of the home range, the searching-foraging component. The radio tracking data in this study showed that most home ranges were centred directly over the habitat containing the highest densities of macropods.

Within the home ranges location of food is facilitated by auditory cues from conspecifics (Chapter 5) and the use of three foraging strategies: Exponential, Linear and Stepped. It is suggested that the latter two strategies are primarily employed during the searching-foraging component. The Stepped strategy probably relies on other members of the population group finding food by spending considerable periods of a foraging trip stationary whilst the Linear strategy involves rapid and constant movement around the home range, generally in a circular pattern. Devils travel an average of 8 km per night on these foraging trips, allowing them to traverse much of their 13 km^2 home range each night.

It has been shown that the food consumption rates of the population closely match the food available from macropod mortality. In terms of the RDH, macropods as a food source are essentially rich patches, due to their restricted and predictable concentration in the pasture-scrub habitat. The macropods are also highly gregarious animals, further concentrating the source of food. On the individual level, a dead Bennett's wallaby represents a rich patch of food, as it can feed up to 5 devils. A dead Forester kangaroo could conceivably feed double this number.

In this way then the size of home ranges of devils at Mt.William are controlled by the dispersion of food and the population group size by the richness of patches as would be predicted by the RDH. I predict therefore, that in an area with similar richness of patch, but greater dispersion of food, the home ranges of devils would increase and the group size would remain constant. Conversely, in a situation where the food availability is the same in terms of dispersion, but the patches are not as rich, the home ranges would remain the same but the population group size would decrease. The variety of habitats in which devils occur make these predictions possible to test.

This study has provided new information concerning many aspects of the social biology of the Tasmanian Devil. It has also identified areas of future research which would extend our understanding of this solitary and highly complex species. Further studies of the devil should ideally be undertaken in a number of different areas and habitats in order to assess the flexibility and adaptability of the devil society. The predictions and hypotheses which have been proposed in this study will, I hope, provide impetus and stimulation for further work into this fascinating species.

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APPENDIX 1

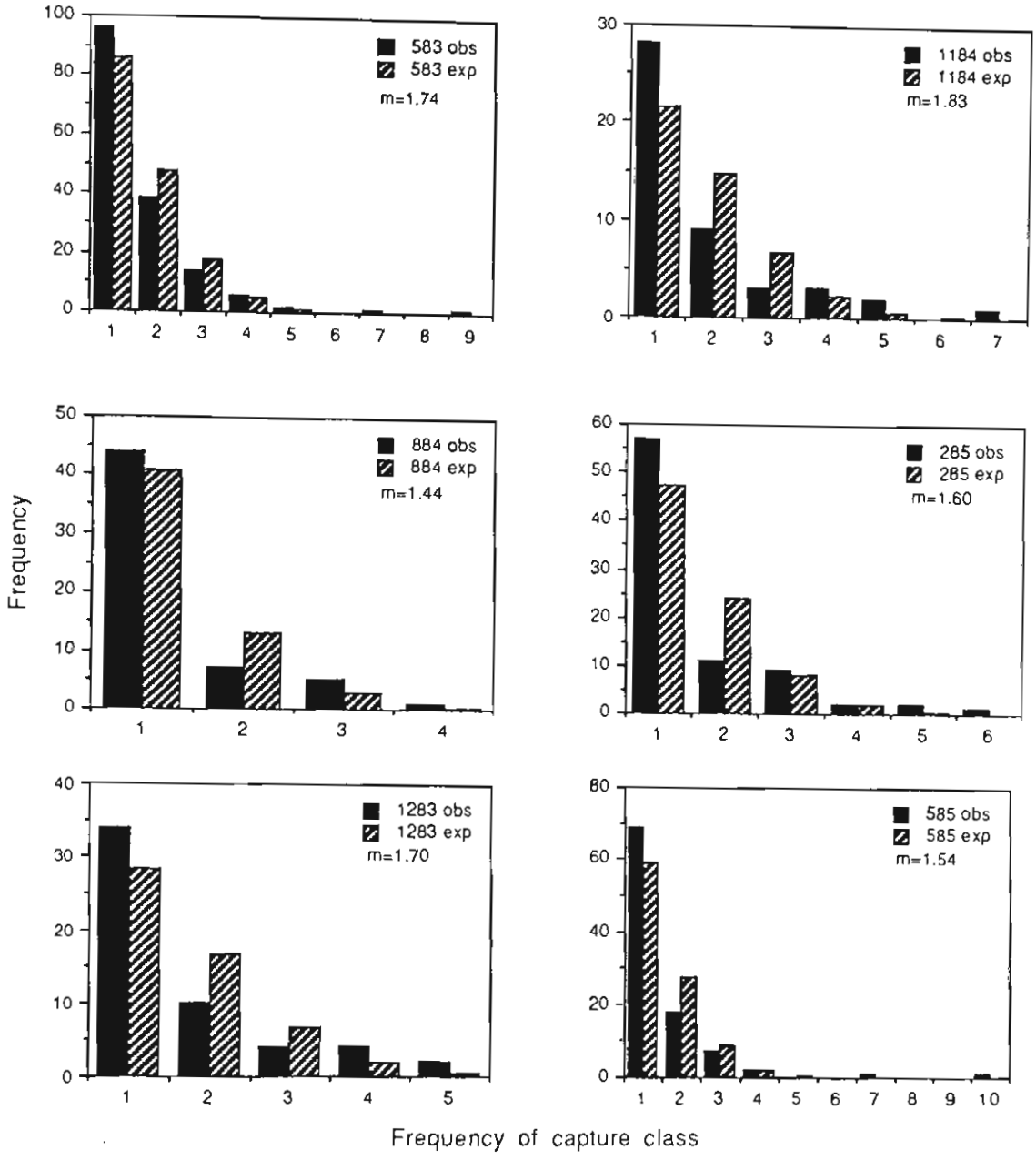
Data used to plot growth curves of known age devils which lacked a M4 at initial capture
Data summarised in Figures2.4 and 2.5

Age months	n	Back leg length mm		Pes length mm		Head length mm		Head width mm	
		mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.
FEMALES									
8	1	110.8		62.2		112.2		74.4	
9	1	117.8		67.9		116.7		80.1	
10	5	118	0.7	66.6	0.3	120.8	0.7	83	1.1
11	33	123.7	0.7	68.9	0.4	127.9	0.9	88.5	0.6
12	9	131.1	1.5	71.1	0.6	132.3	0.8	92.4	0.7
13	7	132.6	1.8	71	0.8	133	2.2	93.1	1.4
14	4	130	3.6	71.3	1.3	134.3	3	94.5	2.3
17	2	141.8	3	73.6	0.5	144.9	1.5	103.6	1.8
19	4	140.3	2.5	73.3	0.5	144.5	0.9	103	1.8
20	3	141	0.6	74.7	0.6	149.5	0.5	104.3	0.3
23	1	142.1		77.8		147.3		106.5	
24	1							103	
25	1	143.5		75.3		150.3		106.5	
26	1	143.6		75.4		146.9		107.5	
27	1	145.2		73.5		145.1		108.8	
29	3	143.7	2	75	1.5	149	0	107	0.6
MALES									
9	3	112.4	4.9	66.1	0.7	118.8	1.3	80.4	0.7
10	8	122.7	1.3	69.3	0.6	124.8	1.3	86.3	0.7
11	40	128.0	0.8	71.6	0.4	131.6	0.4	91.3	0.7
12	14	132.4	1.4	73.7	0.8	135.0	1.3	94.4	1.0
13	5	138.4	1.4	74.6	0.5	141.4	1.0	97.9	1.9
14	2	141.7	4.2	72.6	0.3	145.5	5.7	102.5	4.2
15	1	144.7		74.9		146.3		103.5	
16	1	147.6		79.4		157.2		109.3	
17	7	146.9	0.9	78.7	0.8	149.6	1.9	109.4	1.4
19	3	151.8	2.7	78.9	1.1	154.5	4.2	117.6	2.7
20	1	151.4		78.1		153.5		119.4	
23	2	153.5	1.4	81.5	1.9	163.9	0.3	120.7	0.5
24	1	158.7		81.2		159.9	2.4	120.6	1.2
25	2	152.1	2.0	82.7	0.4	163.6	0.5	121.1	2.2
27	1	157.2		82.7		159.8		119.1	
31	1	130.1		76.8		157.5		122.3	

APPENDIX 2

Data used to plot growth curves of known age devils.
Data summarised in Figures 2.6 and 2.7

Age months	n	Back leg length mm		Pes length mm		Head length mm		Head width mm	
		mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.
FEMALES									
8	1	110.8		62.2		112.2		74.4	
9	1	117.8		67.9		116.7		80.1	
10	9	119.1	1.1	67.1	0.4	121.3	0.7	83.7	1.1
11	44	124.6	0.7	69.0	0.3	129.1	0.9	89.4	0.5
12	10	130.5	1.4	71.1	0.5	132.1	0.7	92.6	0.6
13	11	131.8	1.2	71.1	0.6	133.3	1.4	94.0	1.0
14	39	129.0	2.6	71.4	0.3	139.1	0.9	95.7	0.4
15	1	127.2		70.8		133.7		90.4	
16	3	130.1	0.7	71.0	0.9	139.7	5.4	96.0	0.6
17	12	134.2	1.7	72.3	0.7	140.3	1.5	99.3	1.2
19	5	141.6	2.5	73.5	0.4	144.7	0.6	103.5	0.9
20	6	139.1	1.0	73.7	0.6	145.1	2.0	102.6	1.3
21	3	136.9	0.5	71.6	0.5	145.8	0.5	103.9	0.5
23	3	138.4		74.8	2.0	147.4	2.7	105.0	0.8
25	2	142.7	0.9	76.2	0.9	152.4	2.1	105.5	0.5
26	1	143.7		75.4		146.9		107.5	
27	1	145.2		73.5		145.1		108.8	
29	3	145.4	1.2	75.8	1.9	149.1	0.2	106.6	0.5
32	3	139.3	2.2	73.3	1.8	151.3	1.2	106.3	0.3
34	1	139.1		72.6		149.5		109.1	
36	1	140.2		71.2		150.5		105.8	
41	1	144.0		75.4		154.6		111.0	
46	1					152.2		108.2	
MALES									
9	3	110.5	4.9	65.1	1.5	119.0	1.5	78.9	2.0
10	9	123.5	1.4	69.6	0.6	125.3	1.3	86.7	0.7
11	49	128.9	0.8	72.0	0.4	132.5	1.0	91.8	0.7
12	16	132.5	1.3	73.6	0.8	135.2	1.1	94.7	1.0
13	16	141.0	0.9	76.4	0.6	143.4	1.1	101.3	1.0
14	63	137.3	1.0	75.6	0.5	145.4	0.9	101.8	0.5
15	3	145.4	0.4	77.4	1.4	149.3	1.5	107.3	1.9
17	33	144.9	0.9	77.2	0.5	156.7	0.7	107.0	0.6
19	6	149.9	0.9	79.1	0.6	153.6	2.6	114.4	2.7
20	4	148.1	3.7	77.7	1.9	154.6	2.9	109.5	2.7
21	7	149.5	1.5	77.7	1.1	157.7	1.1	112.9	2.0
22	2	152.2	1.6	79.6	1.2	163.9	2.5	118.5	3.5
23	4	153.5	0.6	79.3	1.7	160.0	2.3	117.1	2.4
24	3	158.7	0.0	81.2	0.0	160.4	1.5	120.6	0.7
25	4	151.2	1.2	80.2	1.4	161.5	1.4	119.3	1.5
27	2	155.0	2.2	80.9	1.8	161.6	1.8	119.4	0.3
28	5	151.2	1.7	77.6	1.3	161.6	1.8	119.4	0.7
29	6	151.7	1.8	79.4	1.5	164.2	1.5	122.0	1.0
31	3	147.1	8.5	77.6	0.4	160.6	2.3	121.3	1.4
32	4	151.2	3.4	77.5	1.5	162.1	2.8	121.9	0.4
34	2	147.8	6.7	77.2	3.1	159.5	5.0	120.6	0.5
35	2	147.3	3.2	76.0	2.5	158.9	4.6	121.6	2.0
36	2	154.8	5.3	82.1	2.2	165.9	4.2	124.4	2.0
37	2	152.9	3.3	79.6	1.0	163.3	0.6	121.1	1.2
38	1	161.4		85.3		171.3	0.0	124.7	
44	1	152.0		78.0		165.5	0.0	122.1	
48	1	155.3		81.3		165.3	2.9	125.0	



APPENDIX 3

Frequency distribution of the number of captures per frequency class. The observed values are the actual number of animals captured in the frequency class and the expected is the frequency distribution calculated from the poisson series, m = the mean number of captures.

APPENDIX 4

Kolmogorov-Smirnov two-sample test for differences in the distribution of the capture frequencies of male, female and diffirent age classes in the monthly samples.

	Sample	D max.	D∞	Significance
Monthly samples	May-1983	0.039	0.214	N.S.
	Aug-1983	0.208	0.447	N.S.
	Dec-1983	0.585	0.373	N.S.
	Feb-1984	0.061	0.346	N.S.
	May-1984	0.231	0.507	N.S.
	Aug-1984	0.037	0.358	N.S.
	Nov-1984	0.135	0.410	N.S.
	Feb-1985	0.122	0.300	N.S.
	May-1985	0.178	0.277	N.S.
	Aug-1985	0.114	0.360	N.S.
	Total	0.017	0.104	N.S.
Sex-age classes May-83	Male-1 vs. Male-2	0.164	1.358	N.S.
	Female-1 vs. Female-2	0.083	0.304	N.S.
	Male-1 vs. Female-1	0.140	0.271	N.S.
	Male-1 vs. Female-2	0.140	0.289	N.S.
	Male-2 vs. Female-2	0.163	0.342	N.S.
	Male-2 vs. Female-1	0.246	0.327	N.S.

D max, D∞ are the maximum difference and the critical difference, see Sokal and Rolf (1981; pp. 440-445).
N.S. not significant.

APPENDIX 5

TESTING FOR A DECREASE IN FERTILITY WITH AGE

Method 1 using sequential captures of known individuals

A Kendalls t (tau) statistic was recorded for each of the 17 individuals, and added together as a combined test statistic. The variance of which is the sum of the individuals variances and whose approximate normality is enhanced by the central limit effect of summing many independent random variables (Dr. B. Brown pers comm.).

Results :

Number of pouch young			t	variance (∂)
3	2		-1	$\partial_2^2 = 1$
3 4		4	2	$\partial_3^2 - \partial_2^2 = 8/3$
1	4		1	$\partial_2^2 = 1$
2	2		0	0
3	3	3	0	0
4	4	3	-2	$\partial_3^2 - \partial_2^2 = 8/3$
3	0		-1	$\partial_2^2 = 1$
4	3	2	-3	$\partial_3^2 = 11/3$
4	1		-1	$\partial_2^2 = 1$
2	2	0	-2	$\partial_3^2 - 1\partial_2^2 = 8/3$
1	3		1	$\partial_2^2 = 1$
2	1		-1	1
4	4		0	0
0	3		1	1
1	1		0	0
4	3		-1	1
4	3		-1	1
			-8	20.6667

Declining fertility would promote negative t values so evidence suggesting such a decline is measured by a small value of the significance level;

$$P(t \leq -8) = P(t \leq -7) \text{ (continuity correction)}$$

$$\approx \phi \left(\frac{-7}{\sqrt{20.6067}} \right) \quad \text{(} \phi \text{ is the standard normal distribution function)}$$

$$= 0.0618$$

Method 2 using animals ranked according to age

The number of concordant pairs was calculated giving t = 508.
Both rankings contain ties so the variance modification is calculated with the following formulae;

Let one of the rankings contain ties in groups, sizes $m_1,.....,m_l$ while the other ranking has ties in groups of sizes $k_1,....., k_n$. Let

$n_2 = n(n-1),$ $n_3 = n(n-1) (n-2),$

$$\text{var}(t) = \frac{1}{9n_3}\{ n_3 - M_3 \}\{ n_3 - K_3 \} + \frac{1}{2n_2}\{ n_2 - M_2 \}\{ n_2 - K_2 \}$$

$$= 113\,828.55$$

$$= (337.385)^2$$

The significance level is

$$P(t \geq 508) = P(t \geq 507) = 1 - \phi(1.494)$$

$$= 0.0676$$

APPENDIX 6

Intersex comparison of the frequency of occurrence of animals by season and residence status#.

Resident status	Season	Male	Female	G(1)	Significance
Transient juveniles					
	Autumn	63	59	0.131	N.S.
	Winter	23	31	1.185	N.S.
	Spring	6	5	0.091	N.S.
	Summer	5	4	0.111	N.S.
Transient adults					
	Autumn	19	23	0.382	N.S.
	Winter	3	2		
	Spring	0	3		
	Summer	3	15	8.895	*
Resident juveniles					
	Autumn	27	19	1.391	N.S.
	Winter	24	18	0.857	N.S.
	Spring	16	9	1.986	N.S.
	Summer	21	4	12.674	*
Resident adults					
	Autumn	38	44	0.439	N.S.
	Winter	31	28	0.153	N.S.
	Spring	16	23	1.263	N.S.
	Summer	18	29	2.598	N.S.

No comparisons are made were the sample size is to small
* $p < 0.01$
N.S not significant.