AN ECOLOGICAL STUDY OF MACROPODID MARSUPIAL SPECIES ON A RESERVE.

by

D. Algar, B.Agr. Sc. (Hons), M.Agr. Sc.

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SUMMARY

The ecological relationships between four macropodid species on a reserve were examined within the framework of niche theory. Species' ecological niches were defined, using multivariate analyses, on the basis of their spatial distributions and feeding patterns relative to the dimensionality of the community niche. Factors responsible for the separation of species' niches and the degree of separation of each niche were examined.

The ecological relationships between the study species were initially examined under conditions of habitat instability and restricted resource availability created by locally overabundant species' populations. These ecological relationships were then re-examined following manipulation of the community niche by:

a) reduction of species' population levels to reduce overall grazing pressure and,
b) the use of fire to simulate conditions of natural vegetation regeneration.

These management practices were designed to increase resource availability to the species' populations.

Results of this study emphasize the importance of the above management practices for the maintenance of vegetation species' richness and diversity and thus the well-being and survival of the study populations. Following the manipulations there were increases in niche separation between species' spatial distributions and changes in dietary item preferences. Thus, within the broadly defined species' habitat preferences, increased resource availability enabled the populations to be more selective for specific components of the habitat types. The increased availability of certain more palatable plant species enabled animals to be more selective in their diet choice.

Investigation of the species' ecological relationships, using niche theory, provided a sound basis for examination of the suitability and effectiveness of past management practices on the reserve. The results also provide direction for future management policies. The reserve management practices derived from this study are also considered to have wide application to small reserves where macropodid species are present.

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Very few biologists are familiar with and even fewer have worked in the proximity to the flame front of even mild fires. This situation is unlikely to be rectified since it is far too dangerous a research area to allocate to that universal work horse in boring, distasteful or dangerous research - the graduate student (Main, 1981a).

CHAPTER 1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

An examination of macropodid species present on offshore islands of the Western Australian coast indicated that Barrow Island (*ca*. 20,000 ha) retained all the macropods of the adjacent mainland, except the red kangaroo (*Macropus rufus*) (Main and Yadav, 1971). Barrow Island was suggested to be large enough to allow natural causes to operate and retain wide biotic diversity. Thus, the area of Barrow Island indicated the minimum size of adequate reservation to retain a representative assemblage of macropodid species. Smaller reserve sizes would require management in order to maintain biological diversity (*Op. cit*.). Frankel and Soulé (1981) suggested that much larger areas are required to retain populations of large, sparsely distributed species than populations of small, dense ones; such areas would provide a sufficient gene pool for natural evolutionary processes to operate. Discussion of the desirability of a single large reserve or several smaller reserve areas is also reviewed (Frankel and Soulé, 1981).

Main (1979) indicated that the aims of conservation are twofold: firstly, to retain representatives of taxonomically or biogeographically interesting biota and secondly, to retain representatives of evolved communities. These two aims require different but related management procedures and different criteria for selection. Today, due to the restrictions imposed by economic necessity and the area of land available for reservation, it is only rarely possible to select the location and size of reserves in accordance with theory. The conservation of representative communities of ecosystems clearly requires adequate size (Main, 1982). No amount of management can substitute for the area required for natural regeneration of communities to take place. However, species conservation when suitable habitat is available, but of inadequate size in terms of a theoretically ideal area, require considerable biological knowledge and close continuous scientific management for the successful retention of these conserved forms (*Op. cit.*).

In order for any one species to exist within a reserve its needs for food, shelter, water and requirements of minimum population size must be met (Main and Yadav, 1971). However, two or more species cannot coexist if they utilize one or more resources that are essential for their survival, the resources being limited in quantity with respect to the ability of the species to exploit them. Such a situation can eventually lead to the 'competitive exclusion' of certain species (Hardin, 1960). Coexistence may occur if predators reduce species populations below the level at which competition occurs, species populations are reduced by dispersal and/or disturbance or, if one species (the subordinate) has unique refugia (Hutchinson, 1978; Giller, 1984).

A number of studies has shown coexistence of a number of macropodid species where resources are sufficiently diverse to be partitioned (Calaby, 1966; Main and Yadav, 1971; and Kaufmann, 1974). Heterogeneity within the environment will allow resource partitioning between species by enabling them to specialize on different parts, or combinations of parts of the resource spectrum (MacArthur and Levins, 1964). The presence of diverse needs will also tend to stabilize existing habitat diversity (Giller, 1984). Resource partitioning may be accomplished by morphological, physiological or behavioural means. The mechanics of macropod nutritional physiology, of a number of species, have been studied in the laboratory and are well documented (Bartholomew, 1956; Brown, 1969; Brown and Main, 1967; Dawson, 1974; Hume, 1974, 1977; Prince, 1976). Behavioural traits such as spatial distribution and dietary preferences leading to resource partitioning are less well studied. Such studies at the community level deserve closer investigation if the management of wildlife areas is to be ecologically sound.

The Harry Waring Marsupial Reserve, an area of 253.7 ha, was founded to establish and maintain a colony of quokkas *(Setonix brachyurus)* from Rottnest Island. The lease agreement for the reserve stipulated that such a purpose should not jeopardize the native vegetation. Management techniques therefore should in part be orientated towards maintaining the existing vegetation structure and diversity of the area.

The grazing pattern of the quokka, the only herbivore present on Rottnest Island, is one of several factors that has drastically reduced the vegetational diversity of plant communities there. The island has been transformed during this century from an extensive cover of low closed forest and scrub, characterised by *Callitris preissii, Melaleuca lanceolata* and *Acacia* species to a low shrubland dominated by *Acanthocarpus preissii* (Pen and Green, 1983).

In an attempt to maintain the vegetation structure and diversity of the Harry Waring Marsupial Reserve, the area was stocked with, in addition to the quokka, the two naturally locally occurring species: the brush wallaby*(Macropus irma)* and western grey kangaroo *(M. fuliginosus ocydromus)* and the introduced northern euro *(M. robustus erubescens)*. It was proposed to exploit the species' different feeding patterns and habitat preferences so that the resources of the reserve would be partitioned according to the species behavioural and physiological differences. The system of stratified feeding would ensure grazing the range of shrubs, herbs and grasses present to facilitate management of the vegetation for maintenance of the principal quokka population.

This study examines resource partitioning by the macropodid species on the reserve. The study is based on the Hutchinsonian concept of the niche (Hutchinson, 1957). The community niche, here defined by the reserve boundary, is considered as the parent space. Within this space species'realized niches (see below) are located at characteristic distances from one another with varying degrees of overlap. It should be noted that the reserve does not contain a naturally evolved community. The macropopid species do not occur sympatrically in nature but occur within the reserve as part of a management strategy. Prior to European settlement the brush, grey and quokka occurred together in the Perth metropolitan region, however, quokkas were separated by habitat preferences (swamps).

Current theory sees the niche as a phenotypic attribute of a local population (Colwell and Fuentes, 1975), equal to the sum of all adaptions of that population (Pianka, 1974). In mathematical terms a species' niche is described as a n-dimensional hypervolume or space (Hutchinson, 1957). The axes of the species multidimensional space relate to all the environmental and biological factors that affect the survival of that species. On each axis are specified limits that denote the region within which a given species can survive and persist. Hutchinson termed a species niche in the absence of interspecific competition 'the species fundamental niche', that is, the niche it could potentially occupy. In the presence of interspecific competition a species may not exist within the full extent of its fundamental niche. This contracted niche space Hutchinson termed 'the realized niche'.

The ecological niche has become identified with the distribution of species activity (resource utilization spectra) along niche dimensions (Vandermeer, 1972). The niche of each species is then defined by a utilization function along a resource gradient. The niche hypervolume may be described in terms of niche width, niche dimensionality and niche overlap (Levins, 1968). Niche width refers to the sum total of the variety of different resources exploited by a species population (Giller, 1984). Rather than niches in a community appearing as discrete, non-interacting units, species tend to share parts of each others fundamental niche (niche overlap). This results in simultaneous demands upon some resource by two or more species populations (*Op. cit.*).

Resource partitioning is generally demonstrated by the separation of species frequency distributions along some resource dimension (Schoener, 1974). Groups of similar species usually partition resources along at least two and often three dimensions (Schoener, 1974) but show high overlap among many more (Levins, 1968). For niche studies to be meaningful, these two or three important dimensions must be correctly identified. Studies of multi-species grazing systems have revealed that functional interactions within these communities are surprisingly subtle and complex (Bell, 1971; Sinclair and Gwynne, 1972; Ferrar and Walker, 1974; Harris, 1973; Jarman and Sinclair, 1979). Nevertheless, it would appear safe to generalize that niche differentiation among coexisting herbivores most commonly involves separation along the dimensions of habitat (space), food and time (Hudson, 1977). Of these, separation along habitat dimensions is perhaps of greatest importance for large primary consumers (Schoener, 1974).

The multidimensional approach involved in niche theory provides a means of conceiving how species relate to one and another in community organization. The hypergeometric interpretation of these relationships enables the use of multivariate statistical techniques as methods of choice in analysing such ecological data (Shugart, 1981). One of the most widely used multivariate techniques is discriminant function analysis. Such an analysis is applicable to the study of: niche width, niche overlap, resource partitioning, habitat selection and community structure (Williams, 1981).

The hypothesis that resource partitioning occurs between macropodid species on the Harry Waring Marsupial Reserve forms the basis of this research programme. The hypothesis advanced in this dissertation is that niche theory, as summarized above, is an adequate basis for management of macropods in a reserve of limited size. The study firstly examines the nature and strength of those factors which serve to separate the macropodid species on the reserve relative to the dimensionality of the overall community niche. Secondly, the niches of the species are described quantitatively using the above factors. The specific aims are:-

1. To quantify the vegetation physiognomy and species' composition within the reserve.
2. To determine the species' spatial distributions and examine the factors responsible for the separation of each spatial niche and the degree of separation of each niche.
3. To determine species' feeding patterns and examine the factors responsible for the separation of the species feeding niches and degree of separation of each niche.

The above objectives are then re-examined following manipulation of the community niche. Manipulation is achieved by using the reserve management practices of fire (to simulate conditions of natural vegetation regeneration) and by reduction of species population levels. Finally, the importance of the results obtained during this study will be discussed with reference to the above hypothesis and current reserve management theories and practices.

CHAPTER 2

THE STUDY SITE

2. THE STUDY SITE

2.1 Reserve Location, Size and Physical Features

The Harry Waring Marsupial Reserve (Reserve No. 29241) is managed by the University of Western Australia and vested in the Minister for Conservation and Land Management. The Reserve is situated approximately 25km south of Perth, Western Australia, at latitude 32^{o} 10', longitude 115^{o} 50'E and occupies an area of 253.7 ha (Clay, 1981).

A 2m high electrified, cyclone netting boundary fence was erected in 1970 and rabbit-proofed in 1982. A network of firebreaks and tracks provide access throughout the reserve (see Figure 2.1). Banganup Lake, an area of 32ha, contains water for approximately six months of the year and small, temporary soaks are present in Melaleuca and Russell Swamps. Water troughs provide permanent water at a number of sites throughout the reserve.

2.2 Climate

The study area is influenced by mild, wet winters and hot, dry summers; described as 'dry mediterranean' (Beard, 1981). Five to six months of the year are considerdd to be dry, that is, precipitation is inadequate to sustain plant growth.

Since 1973, rainfall on the reserve has been monitored daily and temperature data recorded continuously on a Thiess hygrothermograph. Average monthly rainfall and temperature data are presented for the years 1973 to 1980 (see Appendix 1, Figures 1.1 to 1.4). Data during the study period are shown as monthly means (see Appendix 1, Figures 1.5 to 1.8).

The Harry Waring Marsupial Reserve lies within the Jandakot groundwater abstraction area. In order to relate water abstraction to persistence or otherwise of native vegetation, the Western Australian Metropolitan Water Authority have monitored water

Figure 2.1 Map of the study site.

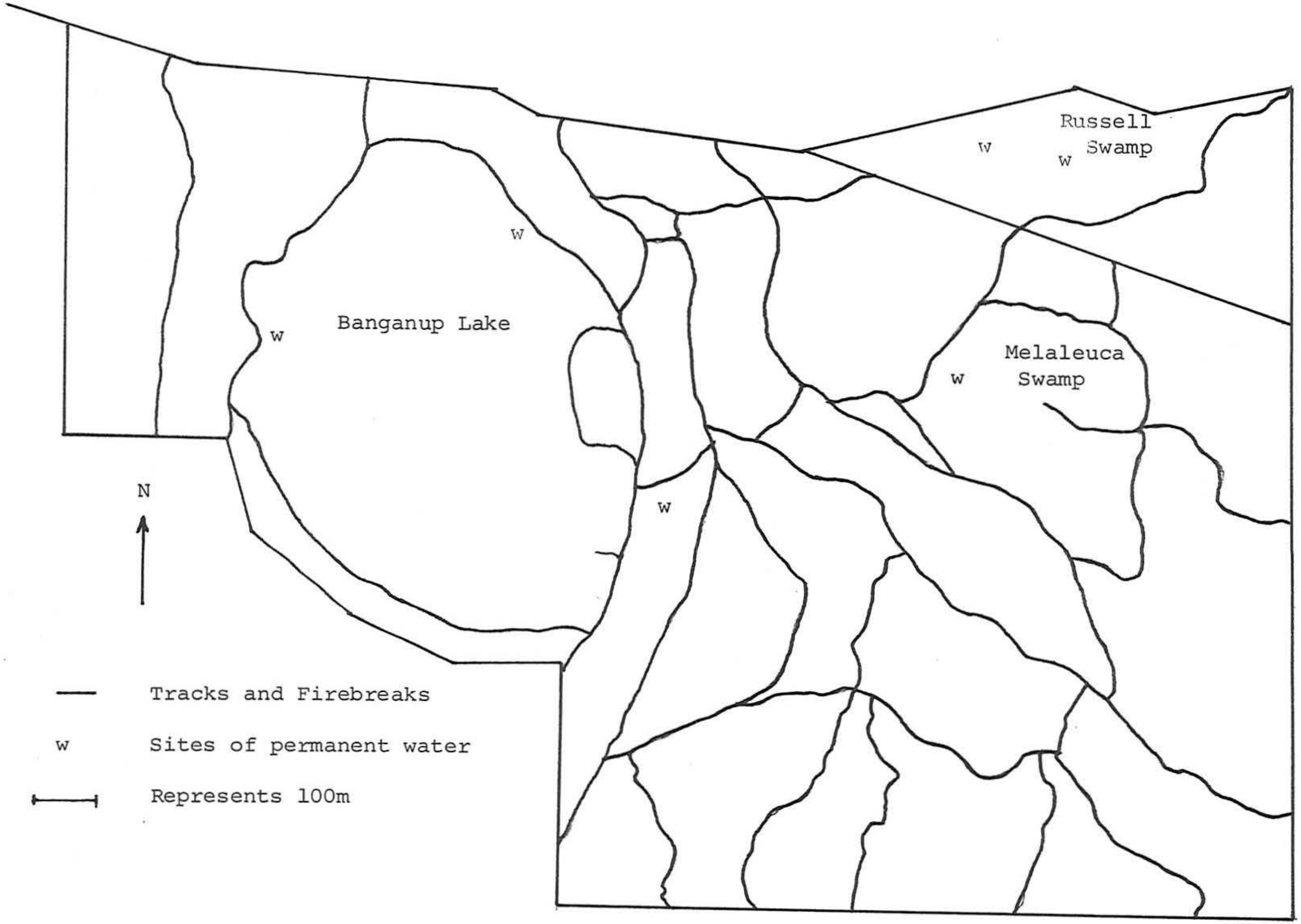


table depth within the reserve over a number of years. These data are presented (see Appendix 1, Table 1.1).

2.3 Soils

The reserve lies predominately within the Bassendean Dune system, with a small intrusion of the Spearwood Dune System, in a gently undulating Pleistocene landscape in the Swan Coastal Plain (McArthur and Bettenay, 1960). The western fringe of the Bassendean Dune System consists of deep, grey sands that is, the iron podzols of the Jandakot series. The soils are highly leached and poor in plant nutrients (Bettenay, McArthur and Hingston, 1960). The Karrakatta soil association represents the easternmost section of the Spearwood Dune System. The soils are leached, yellow and brown sands overlying limestone at depth (*Op. cit.*).

2.4 Vegetation

Using a classification system based upon the physiognomy of the ecologically dominant stratum to determine plant formations, Beard(1981) describes the vegetation of the area as being a low woodland with scattered trees. The overall cover is a *Banksia* low woodland dominated by *B. attenuata, B. menziesii, B. ilicifolia* and the occasional *Eucalyptus marginata, Casuarina fraseriana* and *Nuytsia floribunda.*

There are two shrub layers. The common tall shrubs are; *Jacksonia furcellata, J. sternbergiana, Acacia spp., Macrozamia riedlei* and *Xanthorrhoea preissii.* The low shrub layer is represented by numerous families including Proteaceae, Liliaceae, Fabaceae and Epacridaceae. Two of the more common shrubs are *Hibbertia hypericoides and Stirlingia latifolia.*

Low lying areas in the topography are often swamps with low woodland and forest of *Melaleuca rhaphiophylla,* alone or in combination, with *Eucalyptus rudis* and *Banksia littoralis*. At the margins of the swamps shrubs such as *Hypocalyma angustifolium*, *Astartea fascicularis* and various *Melaleuca spp.* are common. Sedges including *Cladium spp.* are also numerous in these areas. The swamps are dominated by a continuous cover of *Baumea articulata*.

2.5 The Study Species

The four macropodid species present on the reserve are the Brush Wallaby *(Macropus irma)*, Western Grey Kangaroo *(M. fuliginosus ocydromus)*, Euro *(M. robustus erubescens)* and Quokka *(Setonix brachyurus)*. Other marsupial species occuring on the reserve include the Short-nosed Bandicoot *(Isoodon obesulus)* and Brush-tailed Possum *(Trichosurus vulpecula)*. A number of exotic mammal species are also present on the reserve:House Mouse *(Mus musculus)*, Black Rat *(Rattus rattus)*, Rabbit *(Oryctolagus cuniculus)* and the occasional domestic Cat *(Felis catus)* and Fox *(Vulpes vulpes)*.

The brush wallaby was present in the area when the reserve was fenced. The grey kangaroo was also present however, a number of animals have also been introduced. The quokka and euro were introduced into the reserve. The number of animals introduced and year of introduction onto the reserve are presented in Table 2.1. Quokkas from Rottnest Island were relocated annually onto the reserve prior to 1981 because of low establishment success. Records of euros introduced are incomplete however, it is believed these animals were the offspring of animals captured in the Pilbara.

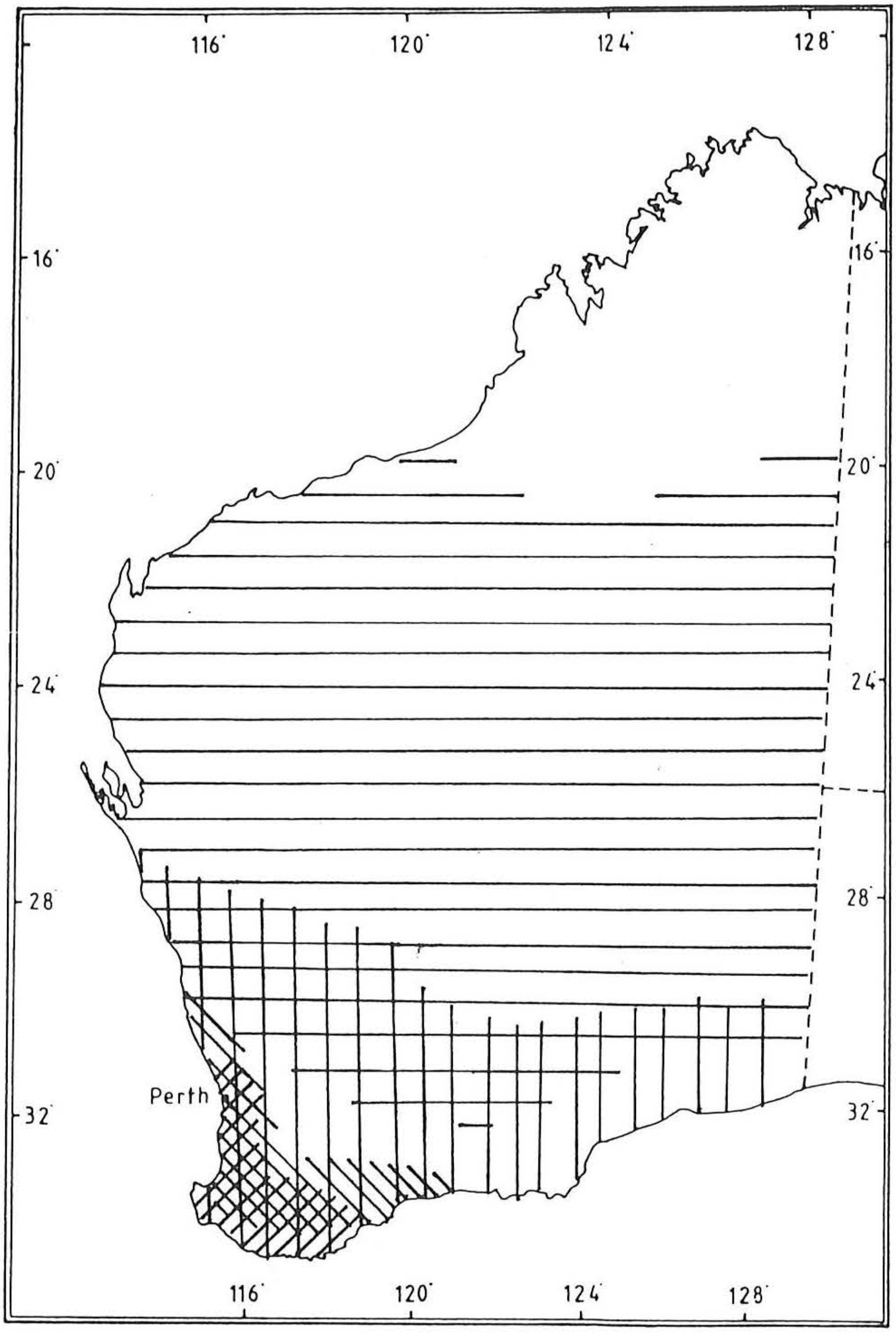
General descriptions of the four species studied are given in Strahan (1983). The distributions of these species are presented in Figure 2.2.

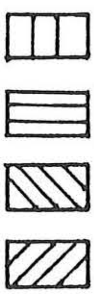
Of the four species most attention in the scientific literature has been focused on the quokka. Well documented studies include; general nutrition (Moir, Summers and Waring,

	YEAR													
SPECIES	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	TOTAL
QUOKKA		22	45	27	58	69	47	125	58	54	99		62	666
EURO	11													11
GREY	9	1									1			11

Table 2.1 Yearly totals of animals introduced into the reserve.

Figure 2.2 Study species' general distributions in Western Australia (from Strahan, 1983).





(*Macropus fuliginosus ocydromus*)

(*M. robustus erubescens*)

(*M. irma*)

(*Setonix brachyurus*)

1956; Calaby, 1958; Barker, 1961; Brown, 1964, 1968), field diet (Storr, 1964), physiological responses and mechanisms of response to stress (Bartholomew, 1956: Bradshaw *et al.*, 1975; McDonald and Bradshaw, 1977) and behavioural response in avoidance of stress (Kitchener, 1972).

Aspects of nutrition and related physiology of the euro have been studied by a number of authors (Ealey, 1962; Brown, 1964, 1968, 1969; Ealey *et al.*,1965; Brown and Main, 1967; Ealey and Main, 1967; Storr, 1968; Prince, 1976). Observations on certain other ecological features are given in Ealey (1967) and reviewed by Newsome (1975).

Prince (1976) also examined nutritional aspects and related physiology of the western grey kangaroo. However, little else has been published on this species.

The brush wallaby has not been the subject of any detailed study.

Photographs of the four study species are presented (see Photos. 2.1 to 2.4).

CHAPTER 3

EXPERIMENTAL MANIPULATIONS

3. EXPERIMENTAL MANIPULATIONS

3.1 Introduction

Whether one decides to create or retain desired states within Wildlife Reserves and National Parks by manipulative management or, let ecological processes choose their own course, the decision is a value judgement of the authorities concerned (Caughley, 1981). If an area is to be managed, the objectives must be clearly defined and expressly stated (Main, 1968).

The Harry Waring Marsupial Reserve was founded to establish and maintain a breeding colony of quokkas whilst maintaining the existing vegetation structure and diversity. Within this reserve, of limited size, the authorities concerned decided it was necessary to adopt a programme of active management. The reserve was stocked with certain macropod species to stratify grazing patterns. Water supplies were introduced and the reserve was fenced. Efforts were also made to control predators and wildfire within the area. It was hoped that such policies would lead to some stable equilibrium, whilst achieving the objectives of the reserve.

At the start of this research programme it was noticeable that the above policies had not achieved their stated aims. Erection of the boundary fence had prevented dispersal as a regulator of population density. Control of predators had also enabled populations of certain species to increase. Populations of western grey kangaroos, brush wallabies and rabbits, species present within the area prior to fencing, had become locally overabundant. As a result of sustained population increases, excessive overgrazing had occurred (Main, pers.comm.)[1] and plant species richness and diversity had decreased (Bell, pers. comm.)[2]. Wildfires during 1977 and 1978 had exacerbated

1. Prof. A.R. Main, Dept. Zoology, Univ. of Western Australia.
2. Dr. D.T.Bell, Dept. Botany, Univ. of Western Australia.

the problem of overgrazing.

The above factors presented the opportunity to;

i) examine the community niche in terms of the macropod species' realized niches. Locally overabundant species' populations had created a system of habitat instability and restricted resource availability.

ii) re-examine the species'realized niches following manipulations of the community niche designed to increase the resources available to the species' populations. That is:

a) Reduction of species' population levels to reduce overall grazing pressure.

b) The use of fire to simulate conditions of natural vegetation regeneration.

The remainder of this chapter is devoted to a general discussion of the manipulations used and the methods of implementation. The results of these manipulations are presented and discussed in the relevant chapters.

3.1.1 Reduction of species'population levels

Reserves of limited size pose a number of problems, especially if it is desirable that they contain populations of large herbivores, yet retain existing vegetation structure and diversity. Ecological equilibrium (Caughley, 1979), and depletion of genetic variability (Frankel and Soulé, 1981) are examples of problems that are magnified in such areas.

The plant - herbivore system is interactive. The position of the equilibrium is determined by both the dynamics of the plants and the herbivores that feed on them (Caughley, 1979). A stable equilibrium, by definition, has some bounds or thresholds. However, if variability within the system enables it to exceed this threshold then the system will not return to its original state (Walker, 1981). There are also mechanisms whereby ecosystems can exhibit more than one alternative stable state (Noy - Meir, 1975, 1981; Hilborn and Sinclair, 1979; Walker, 1981). Thus, there is the possibility that a disturbance will transfer a system across the "breakpoint" dividing one stable configuration from an alternative, so that recovery will be to a totally new state (May, 1981).

An increase in animal density locally may create browsing and grazing in excess of the vegetation's rate of renewal and thus reduce food availability. If the system is left unchecked the herbivore density will peak and eventually crash. The system will tend to some new equilibrium and the plant and/or herbivore community will be modified in composition (Caughley, 1970, 1979; Klein, 1970).

Reducing the population levels of locally overabundant species in Wildlife Reserves and National Parks is a contentious issue. Discussion of overabundance, its ecological implications and the merits or otherwise of species' population reduction have been reviewed by a number of authors (Jewell and Holt, 1981). Manipulation of species' population levels does permit examination of the species' responses to increased resource availability. The information gained enables future reserve management policies to be placed on a sound scientific basis.

3.1.2 Fire to simulate natural vegetation regeneration

Fires are a natural part of the environment influencing sclerophyll communities in mediterranean climates of the world (Gardner, 1957; Mooney and Dunn, 1970; Gill, 1975, 1981a; Bell *et al.*, 1984). These regions, termed mediterranean fire bioclimates by Naveh (1974), are extremely fire - prone. The regions receive a hot rainless summer period and autumn days of strong winds and low humidity when vegetation and litter layers achieve minimum levels of moisture (Naveh, 1973; Biswell, 1974; cited in Bell *et al.*, 1984).

Fires caused by lightning have been associated with sclerophyll shrub communities for at least the past 100,000 years (Komarek, 1967a). Lightning is common in two situations:

i) with synoptic conditions associated with intense cold fronts

ii) where unstable air masses are heated over hot land.

The latter is common as summer progresses and is responsible for wildfires (Main, 1981). In Australia, changes from a humid tropical environment to a much drier climate during the late Tertiary (Main, 1976) resulted in drought and associated fires becoming a progressively more common feature (Singh *et al.*, 1981). Churchill (1968) concludes from palaeontological evidence that lightning induced fires have occurred frequently in southwestern Australia for at least the past 5,000 years.

The history of man's use of fire to manipulate his environment is well documented (Komarek, 1967b). Aboriginal man moved into southwestern Australia at least 25,000 years ago (Merrilees *et al.*, 1973). It is thought that fire was used to flush out game and to attract animals to regrowth in newly burned areas (Stocker, 1966).

Today in Western Australia forest fires are a mixture of rotational control burns, used as a management tool, and periodic wildfires started by man or lightning. Controlled burns have been conducted in the spring on a five to seven year cycle (Christensen and Kimber, 1975). Controlled burning is used to reduce leaf litter and dry scrub, without affecting the tree canopies, in order to reduce the severity of wildfires (*Op. cit.*). However, recently a number of controlled experimental autumn burns have been conducted, to gain an understanding of their importance to plant and animal communities (Christensen, pers.comm.).[1]

Whelan (1977) suggested that the features of sclerophyllous

1. Dr. P.E.S. Christensen, Dept. Conservation and Land Management.

species which make them resistant to fire may not have evolved purely in response to fire. It is more likely that the increased aridity, decreased soil fertility (determined primarily by phosphate level, see Beadle, 1966) and the increased frequency of fire have combined since the late Miocene to produce a vegetation remarkably tolerant to fire. The methods by which plants survive and reproduce in a fire environment have been comprehensively reviewed (Gill, 1975, 1981a, 1981b; Gill and Groves, 1981; Bell *et al.*, 1984). Gill and Groves (1981) suggest plant species are adapted to particular fire regimes, incorporating fire intensity, frequency and season, rather than occurrence of fire itself.

A number of studies has been conducted examining the effects of fire on fauna species (Christensen and Kimber, 1975; Newsome *et al.*, 1975; Christensen, 1977; Whelan, 1977; Kikkawa *et al.*, 1979; Main, 1981a; Fox, 1982). Results indicate survival and utilization of an area following fire and/or re-invasion is similarly affected by the fire regime and the phase of pyric succession following fire.

In southwestern Australia, kangaroo populations often increase in burnt areas (Christensen and Kimber, 1975). Macropods are commonly observed feeding on regenerating vegetation following fire (Whelan, 1977; Catling and Newsome, 1981). It is also possible that the nutrient status of food sources changes following fire. In parts of southern Australia trace elements, such as zinc and copper, are released after fire and these too will be incorporated in new plant growth (Specht *et al.*, 1958, cited in Kikkawa *et al.*, 1979). Individuals of territorial macropod species are known to remain within their home ranges, both during and subsequent to fire (Christensen, 1977; Whelan, 1977).

Whelan (1977) suggested that the two responses of macropods after fire (i) feeding behaviour of free-ranging macropods

(ii) responses of territorial macropods

be separated because the relative effects of these responses on the regenerating vegetation are likely to differ with the intensity and area of the fire.

A number of wildfires has occurred on the Harry Waring Marsupial Reserve since 1970 (see Figure 3.1). Following these fires; western grey kangaroos, euros and brush wallabies have concentrated their feeding on the burnt areas (Clay, pers. comm.)[1]. Of particular interest is the importance of the leguminous species to macropod populations. Native legumes are an important source of nitrogen for macropods (Main, 1968, 1970; Shea *et al.*, 1979). Genera, such as *Jacksonia and Acacia* that grow in thickets are important as shelter areas (Clarke, 1975).

In the northern jarrah forest, native legume species rarely regenerate following low intensity spring burns. When areas with a legume dominated understorey are burnt at low fire intensity, the legume species are killed and proteaceous species become the dominant components of the shrub and understorey layer (Peet, 1971). In the absence of fire, legume stands decline after approximately 15 years and no regeneration occurs. However, germination of the legume seed store in the ground occurs following high intensity burns (Shea *et al.*, 1979).

From the above discussion, evidence suggests that fire is an important natural environmental tool in the management of reserves designed to protect representative elements of both flora and fauna. As such, detailed knowledge is required of;

i) the effects of fire on vegetation , and

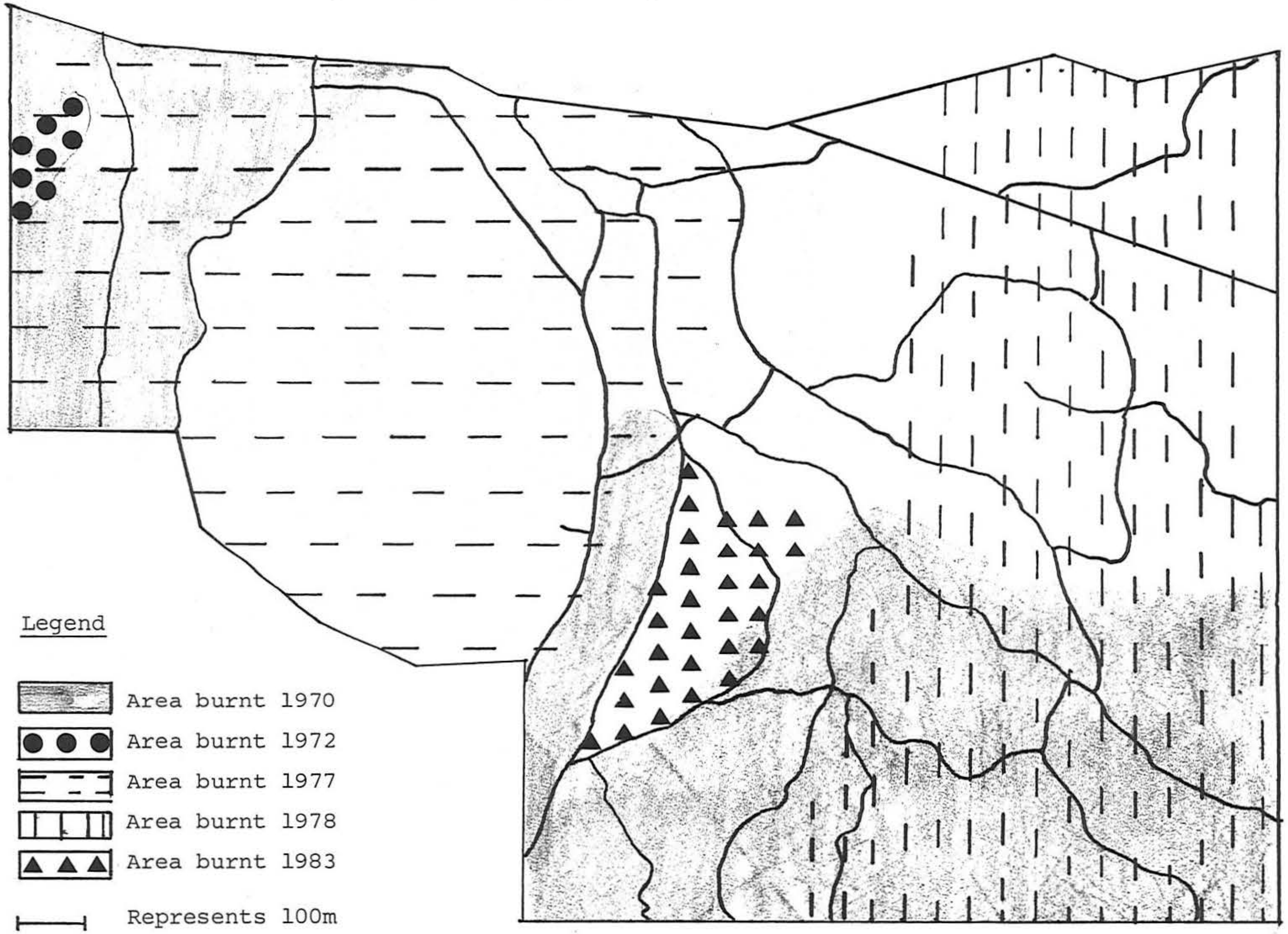
ii) grazing impact following fire, to permit formulation of suitable management policies for reserves.

3.2 Method

Replication and control are desirable in manipulation

1. Clay, B.T., Warden, Harry Waring Marsupial Reserve.

Figure 3.1 Burn history of the Reserve.



experiments, however, such considerations were not feasible in this study. The reserve was too small in size and the distribution of the various plant associations prevented fencing the area into sites of adequate size and similarity for the purposes of replication and control. Possible changes in plant species composition, abundance and frequency due to manipulation effects, would not be expected to occur immediately but over some extended time period. The response of the study species, in terms of species - habitat relationships and feeding patterns, to these changes would reflect a similar time period because of the interactive nature of the plant - herbivore system. As such, the manipulation effects are inferred from observed changes over time and it is assumed that these changes would not have occurred without manipulation.

3.2.1 Reduction of species' population levels

Overpopulation, creating habitat instability on the Harry Waring Marsupial Reserve, indicated that the primary objectives of the reserve were not feasible under the existing management policies without reducing the population levels of certain species. Data were not available on densities of the study species present prior to fencing, nor during the years following fencing the reserve. Also, information on densities of these species in comparable habitats was not present in the scientific literature. As such, authorities familiar with the study area: (Dr. R.I.T. Prince, Dept. Conservation and Land Management, W.A.) and (Dr. G.W. Arnold, C.S.I.R.O. Div. of Land Resources Management, W.A.) were consulted. It was suggested that, within the constraints of the reserve objectives, a maximum of 10 animals/species/km^2 was an "acceptable" density for the western grey kangaroo, brush wallaby and introduced euro. Problems associated with establishing and maintaining a quokka colony precluded the species from population control measures.

A policy decision was formulated by the reserve management committee to restrain the study species' population levels annually at the above defined levels. Animals were to be culled across sex and age classes throughout the reserve to maintain as much genetic variability as possible.

Animals were culled during late autumn each year. The number of animals to be removed from each species' population was based on population surveys and capture records. Population "crashes" in the euro and brush wallaby populations after autumn 1982 precluded these species from further culling programmes. The method of survey and species' population estimates, including sex and age structure, are presented elsewhere (see Chapter 5).

Animals were shot using a 0.22 (hornet) calibre rifle. Each animal was weighed, pes and short-leg measurements recorded, pregnancy status noted and a faecal sample obtained for diet determination. Methods of measurement and sample preparations are discussed in the relevant chapters. The species, number, sex and age class of animals culled are presented (see Table 3.1).

To reduce total grazing pressure within the reserve it was also desirable to reduce the rabbit population level. Preliminary surveys of the rabbit population within the reserve during 1981 suggested numbers in excess of 1,000 animals. To satisfy this objective a number of methods, used in conjunction, were implemented in 1982:-

1). A rabbit-proof skirt was attached to the boundary fence to prevent movement into the reserve from adjacent areas.

2). Broad-scale 1080 bait was laid annually each summer.

3). Phostoxin poison was placed in burrows in use during the

Table 3.1 Species' culling records (No. of animals removed).

YEAR	SPECIES	ADULT		SUB-ADULT		JOEY AT FOOT		JOEY IN POUCH		TOTAL
		Male	Female	Male	Female	Male	Female	Male	Female	
1982	Brush	8	3	1	0	0	0	1	0	13
1982	Grey	1	7	3	5	2	2	3	3	26
1983	Grey	3	4	2	1	0	0	1	2	13
1984	Grey	4	6	2	1	2	2	5	1	23

winter.

4. A programme of regular rabbit shooting was implemented.

In addition to the above, widespread winter and summer myxomatosis epizootics regularly occurred within the reserve. Occasional surveys during the course of the study programme suggested these methods were successful in reducing the total rabbit population. By late 1983, estimates suggested the rabbit population had declined to less than 100 animals.

3.2.2 Fire to simulate natural vegetation regeneration

An area of approximately 10 ha (see Figure 3.1) was selected for a hot, late autumn burn to stimulate shrub growth, particularly leguminous species. The site had not been burned for at least 14 years. The burn was originally planned for 1982, however, early unseasonal rain caused postponement of the programme until the following year.

Eight vegetation study plots ($400m^2$), used in the initial vegetation survey (see Chapter 4) were selected within the proposed fire zone as burn study sites. A further eight plots were selected, within the same vegetation association adjacent to this zone to represent the non-burnt sites. Understorey species composition, abundance and frequency within the study plots were surveyed in the spring prior to the fire and for the two years following the fire. The method of survey was as used in the examination of vegetation within the reserve each year, and is discussed in detail in Chapter 4.

On the day prior to the fire, five randomly-selected sites adjacent to each fire plot were sampled for fuel load, fuel and soil moisture contents. Fuel load and moisture content were determined by removing all vegetation and litter in $1m^2$ plots. The material was weighed and then oven-dried at 80^oC to constant weight. The mean fuel load within the fire zone was 7.08 ± 0.58 tonnes/ha ($\bar{x}$ ± s.e.) and the fuel moisture content was 21.50 ± 1.10% ($\bar{x}$ ± s.e.). Soil samples were removed to a depth of 5.0 cm, weighed and oven-dried at 80° C to constant weight. The mean soil moisture content was 0.85 ± 0.08% ($\bar{x}$ ± s.e.). The last isolated rain of 2.0mm occurred five days prior to the burn.

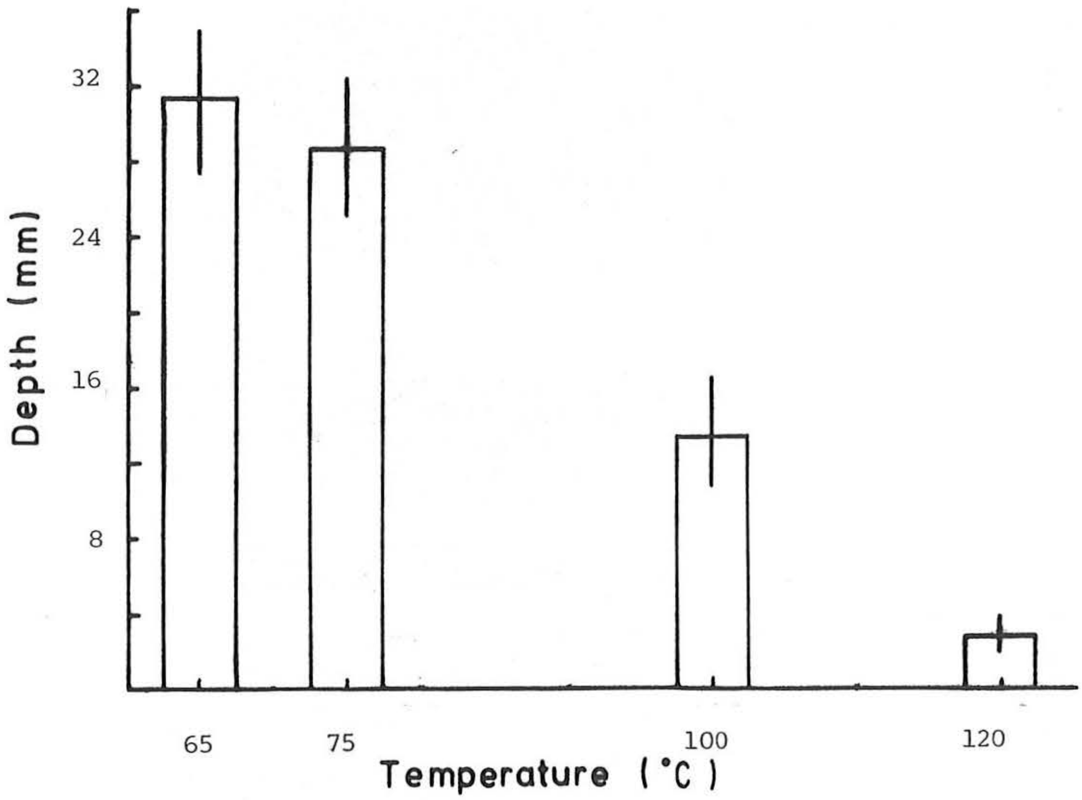
Asbestos plates (20cm x 15cm) marked with heat-sensitive crayons (Thermochrom, Faber-castell Ind.) of melting points; 65°C, 75°C, 100°C, 120°C and 150°C were installed perpendicular to the soil surface at five locations in each of the eight burn plots to determine soil temperatures during the fire. The soil temperature - depth profile is presented (see Figure 3.2).

At the time of the burn, the temperature was 28.7°C and the relative humidity was 45%. Wind strength was measured using a Sensitive Anemometer (C.F. Casella and Co. Ltd.) and recorded from the south-east at 3 to 5 km/hr. During the course of laying a firebreak the wind changed to a south-westerly at 5 to 8 km/hr, transforming a control burn to a wildfire. The burn was eventually controlled, however, the path of the fire precluded the use of three of the proposed burn study plots. Three additional burn plots were subsequently selected, adjacent to existing plots, within the fire zone. As such, data were not available on species composition, abundance and frequency prior to the fire for these plots.

Fire intensity derived by Byram (1959) is used as an index to describe fire behaviour. Numerically, the intensity is equal to the product of nett heat of combustion of fuels, quantity of fuel consumed in the active combustion (not including large fuel particles such as logs) and a rate of linear spread.

i.e. $I = HWR$

Figure 3.2   Fire soil temperature - depth profile.



where I = fire intensity (KJ m/s)

H = fuel heat yield which is 18,600 KJ/kg of fuel for most forest fuels (Burrows, 1984)

W = fuel weight kg/m^2

R = linear rate of advance m/s

The fire intensity of the burn was calculated at approximately 1,220 KJ m/s. Such a fire intensity describes a hot to moderate burn of high intensity (Burrows, 1984).

Following the fire, four of the burn study plots were fenced to examine the grazing impact following fire. A further four study plots were fenced in the non-burnt area to assess grazing outside the fire zone. The fence was constructed of rabbit netting with a skirt 30cm below ground. Two strands of 12 gauge wire were used to raise the height of the fence to 1.5m. Periodic examination of the exclosures suggested they were successful in restricting animal access.

CHAPTER 4

VEGETATION STUDY

4. VEGETATION STUDY

4.1 Introduction

In this chapter quantification of vegetation physiognomy and species' composition, abundance and frequency are presented. These attributes form the basis for examination of macropod species habitat relationships, feeding patterns and resource partitioning, discussed in detail, in later chapters. The impact of reduced grazing pressure and grazing pressure following fire on plant species' composition, abundance and frequency is also presented.

4.2 Method

4.2.1 Vegetation Survey

4.2.1.1 Vegetation plot size, number and location

A reconnaissance study of the reserve was conducted to determine major vegetation associations, their size and general species presence. The reconnaissance study was also used to suggest what community sampling procedures might be appropriate. Several associations were found to occupy areas of less than 0.5 ha. As these were of doubtful significance in influencing macropod distributions they were excluded from the study.

The permanent quadrat method (Oosting, 1956; Daubermire, 1968), was used to sample the vegetation. The number and size of plots, for adequate sampling within the community, were considered prior to detailed surveying. Previous studies on the reserve, using species' number: area curves, found square plots of $400m^2$ adequate for the examination of overstorey species (Bell, pers. comm.)[1]. Understorey species were examined in a number of $1m^2$ quadrats nested within each $400m^2$ plot. Preliminary sampling, in several vegetation associations, recorded 96.1 ± 3.2% ($\bar{x} \pm$ s.d.) of all understorey species in the first ten randomly-located $1m^2$ quadrats.

1. Dr. D.T. Bell, Botany Dept., University of Western Australia.

The number and location of $400m^2$ study plots required for adequate sampling was based on several criteria. Examination of herbivere/habitat relationships required samples to be taken on a uniform basis across the reserve, along macropod census routes, and the sample size be large, especially in relation to the number of variables involved. (Green, 1979).

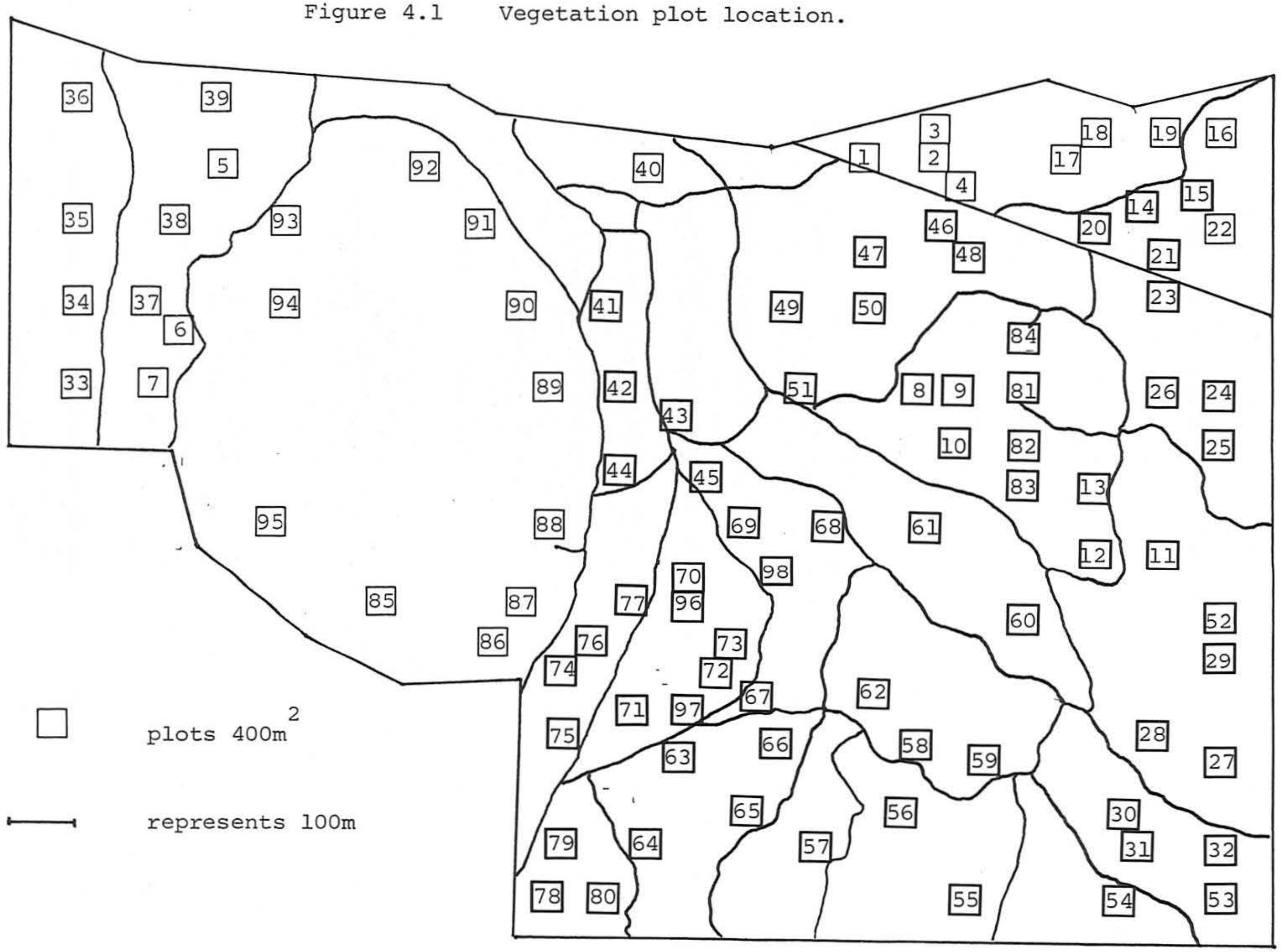
A total of 98 study plots were located across the reserve using a stratified sampling method (Brown, 1954; Greig-Smith, 1964; Gauch, 1982). The reserve was subdivided into one hectare compartments and randomly sited plots were located in 98 of these cells. The location of these plots is shown (see Figure 4.1). No plots were located within Banggenup Lake, as the entire area was covered in a dense thicket of *Baumea articulata* and contained water for up to six months of the year. Plots were sited distant from tracks, firebreaks and disturbed areas to avoid the possibility of edge effects. The number of plots and their locations also provided sufficient replicates, within the broadly defined vegetation associations, for all habitat variables to be within 10% of the population mean at 0.1 confidence limits. Sample size formulas to meet this criterion are given in Steel and Torrie (1960), De Vos and Mosby (1969).

4.2.1.2 Overstorey stratum

Trees were distinguished from shrubs in possessing a distinct main trunk, unbranched in their lower part, and being greater than 3m high. The $400m^2$ plots were permantly pegged in the middle and corners. During the surveys, the perimeter was defined by a flexible tape.

The overstorey stratum was initially surveyed during spring, 1981. It was thought that species composition and physiognomy

Figure 4.1 Vegetation plot location.



would change little during the study and thus it was unnecessary to survey the overstorey stratum more than once. During the survey tree species presence and frequency within each plot were recorded. Two overstorey habitat variables considered important were tree stem density and canopy cover. The circumference of trees having a diameter greater than 4.0cm at breast-height was measured and summed to give a value of tree stem density within the plot. Canopy cover was measured using a densiometer (Lemmon, 1956). Measurements, at 90^{o}, were recorded at the five permanently-pegged locations in each plot.

4.2.1.3 Understorey stratum

Ten $1m^2$ quadrats were randomly located within the larger overstorey plots for understorey species examination. The position of each quadrat was noted and fixed by reference to the tape. The perimeter of the quadrat was traced using a metal-sided frame, the sides of which were marked in 10cm units. Within each quadrat, species' presence and abundance were recorded. Annual species' presence was recorded on the basis of phenological growth stage and greenness of the leaves (Western, 1976). In several cases field identification of similar species within a genus proved difficult, such species were grouped at the genus level. Species of the families Stylidiaceae and Droseraceae proved difficult to identify and of dubious importance to the macropod species. These species were excluded from the vegetation analyses.

Differences in species' size and growth forms precluded the use of the number of individuals as a measure of abundance within a quadrat. A standard measure of species' cover was used to estimate species' abundance. Cover was defined as the vertical projection of above ground parts onto the ground (Brown, 1954). Abundance was subjectively assessed by the number of $100cm^2$ squares (i.e. 1% cover) that an individual species covered. If a species was present, but its total cover was less than $100cm^2$, its abundance was recorded as 1%. Average species' abundance across the plot was then calculated. Species' frequency was recorded as the percentage of quadrats occupied within the plot. Measurements of total ground cover and horizontal density were also recorded for each plot.

Total ground cover was subjectively assessed as the approximate number of $100cm^2$ squares covered by understorey vegetation in each quadrat. An average value of total ground cover was then determined for each plot.

The horizontal density component of cover was examined in each plot to assess the shelter value of different habitats. Horizontal density was measured using a vegetation profile board (Nudds, 1977). The board, 2.0m high and 0.3m wide, was marked in alternate colours, black and white, at intervals of 0-0.25m, 0.25-0.5m, 0.5-1.0m, 1.0-1.5m and 1.5-2.0m. The board was positioned in the centre of each plot and read at a distance of 15m along each side of the plot. At distances greater than 15m the board was usually obscured, and at distances less than 15m most of the board was visible, allowing no discrimination between habitat types. The proportion of each interval covered by vegetation was recorded as a single digit "density score" and graded 0 to 5 (1 = 1 - 20%, 5 = 81 - 100%). Horizontal density was recorded as the average cover for the respective intervals in each plot.

The nutritional quality of forage was expected to change on a seasonal basis. Therefore it was necessary to examine herbivore feeding patterns and habitat relationships over such time periods. Climatic data (see Appendix 1) suggested the presence of four distinct seasons. Pilot surveys during 1981 indicated little change in the measured vegetation components during the seasons winter and spring and during the seasons summer and autumn respectively. As such, vegetation surveys of the understorey stratum were conducted annually during spring and late summer and generally reflected differences in the annual component of the vegetation. Surveys during these two time periods were considered appropriate for the examination of the above herbivore relationships across all seasons.

4.2.2 Ordination and classification analysis

Examination of the floristics of the overstorey and understorey components of the vegetation on the reserve required the reduction of the dimensionality of the data set to manageable proportions, while preserving as much of the original structure as possible. Reduction of the data set into areas or classes also presented a convenient method of examining the effect of the manipulation experiments on the understorey stratum.

The question of whether vegetation communities are continuous or otherwise has been reviewed by Whittaker (1962). Classification analysis involves grouping similar entities together in clusters and assumes that such associations are discontinuous. Sites occupied by the various vegetation classes may then be mapped. If it is accepted that vegetation is continuous, and therefore cannot be classified, ordination analysis is the only alternative. Ordination may be examined directly on environmental ordinates or on ordinates derived from an analysis of the vegetation. Vegetation defined solely by ordination can only be represented by one or more series of isoclines, depending on the number of dimensions involved (Havel, 1975). However, the ordination framework may be subdivided into segments (Greig-Smith, 1964), which resemble classes, in that they can be named and mapped as discrete areas.

Present knowledge of vegetation indicates that it is neither one indivisible continuum, nor a mosiac of discrete units but rather a combination of both (Havel, 1975). Thus, analysis of vegetation data using both ordination and classification techniques is desirable for the most effective study and interpretation of vegetation communities.

A number of ordination and classification techniques have been developed and are reviewed in Gauch (1982). Several ordination techniques were available using ORDIFLEX of the Cornell Ecology Computer Programmes of Gauch (1973). Centred Principal Components Analysis (PCA) was selected as the most informative method for describing the floristics of the understorey associations.

PCA arranges the plots into sequential order which reflects their dissimilarity or ecological distances (Whittaker, 1978). The technique projects a multi-dimensional cloud of points into a space of fewer dimensions. Rigid rotations are used to derive successive orthogonal axes which maximize the variance accounted for (Gauch, 1982). The PCA axes represent linear combinations of the original variables. For each axis an eigenvalue is calculated, which represents the variance accounted for by that axis . The axes are ranked by their eigenvalues, the first PCA axis having the greatest eigenvalue. In a typical community study, the first three eigenvalues may account for 40 - 90% of the total variance (Gauch, 1982). However, assessment of PCA results must be in terms of their ecological utility, that is, the inter-relationship between species, stands and environmental gradients. Mere percentage of variance accounted for has not been found to be a reliable indicator of the quality of results (*Op. cit.*).

PCA has also been successfully employed in the analysis of vegetation change from repeated enumerations of the same plots over time (Swaine and Greig-Smith, 1980).

The MINFO Computer Programme of Orloci (1969) was used in the classification analysis of vegetation data. MINFO is a polythetic agglomerative classification technique. The technique uses information on all species; each sample is initially assigned to a cluster with a single member. These clusters are then agglomerated into a hierarchy of larger and larger clusters until finally a single cluster contains all samples.

Computer storage limitations necessitated reduction of the number of species used in the analyses prior to ordination and classification procedures. Reduction of species number was achieved using the matrix eident value system of Dale and Williams (1978). This system eliminates species or sites from large data matrices which have the least power to differentiate between populations.

A Cyber 180 - 825 Computer, at the Western Australian Regional Computing Centre in the University of Western Australia, was used for all computations associated with ordination and classification analyses.

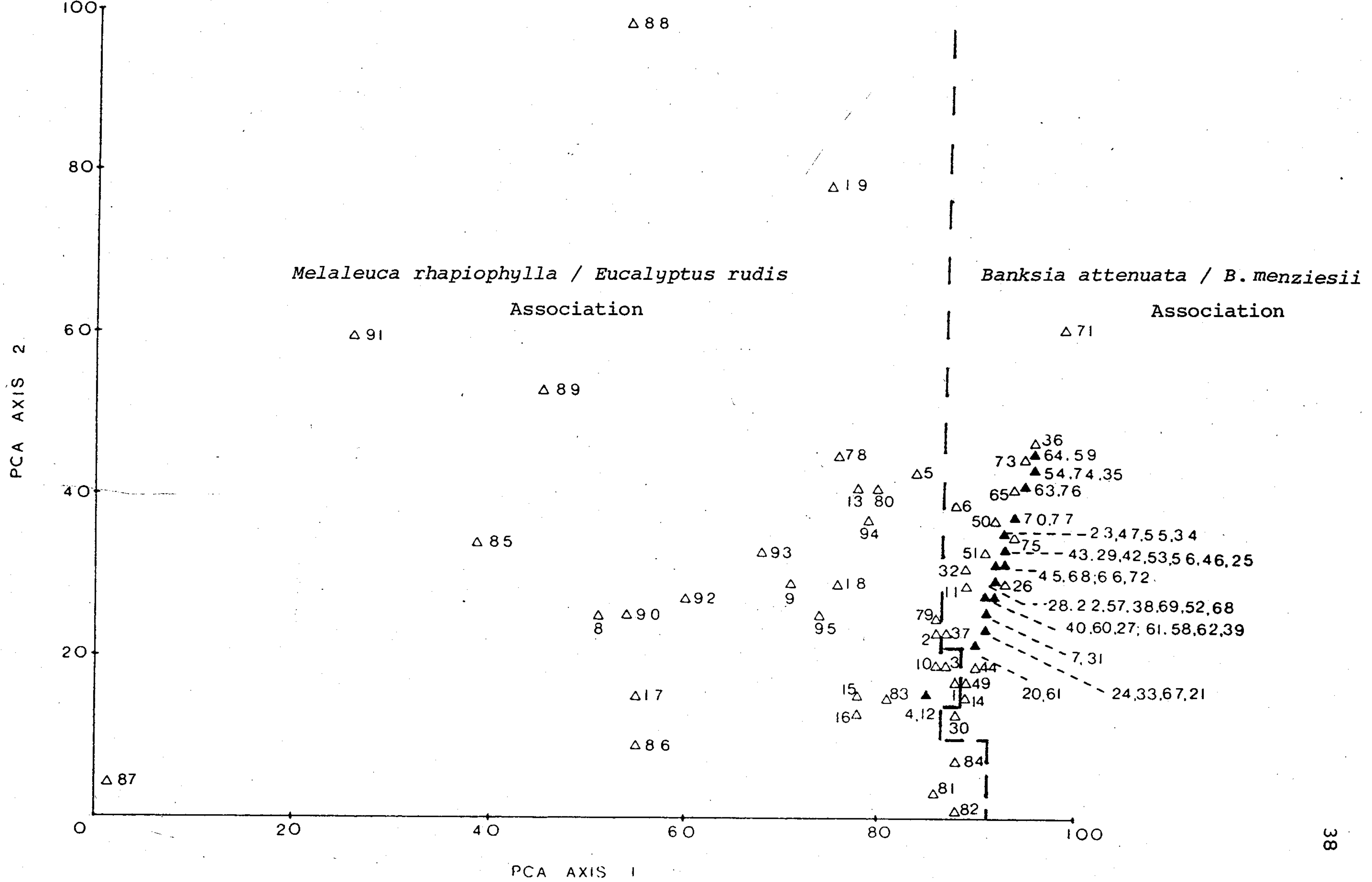
4.3 Results

4.3.1 Overstorey stratum

The overstorey stratum survey recorded the presence of 12 tree species within the reserve. The full tree matrix of species' abundance for each plot was subjected to ordination and classification analyses.

Centred PCA ordination of the overstorey stratum plots is presented (see Figure 4.2). PCA axis 1, which accounted for 58.6% of the total variance, indicates two plot clusters along an apparent soil moisture gradient. A broad cluster of sites from the axis origin represents those plots within and surrounding the lake and swamp areas. These sites are dominated by the species

Figure 4.2 Overstorey stratum ordination analysis (△ represents single plots, ▲ represents multiple plots, - - - represents classification divisions).



Melaleuca rhapiophylla and *Eucalyptus rudis*. The tight cluster of sites with a high loading on the first axis represent the more elevated, better drained plots within the reserve. The sites are dominated by the species *Banksia attenuata* and *B. menziesii*.

The other PCA axes show no apparent trend with respect to sites, floristics and/or ecological gradients, therefore are not considered further.

Classification analysis of the overstorey stratum plots is presented (see Figure 4.3). The analysis recognized two main classes of sites. These two classes were the same as those outlined by the ordination analysis. The class divisions have been superimposed on the ordination diagram (Figure 4.2).

The results suggest that for practical purposes two overstorey associations can be recognized within the reserve. These two associations have been named on the basis of their dominant species (see above). A summary of species' frequency, abundance and stem density (DBH) is presented (see Table 4.1). Also included in the summary are the mean values of total stem density and canopy cover for the respective associations.

4.3.2 Understorey stratum

Definition of understorey association was conducted using ordination and classification techniques on the plot data of the initial spring understorey survey. It was then possible to examine the impact of reduced grazing pressure and fire on species' composition, abundance and frequency over time with the reduced data set, that is, defined understorey association.

A total of 130 understorey species were recorded during the first survey. The number of species used in the analyses was reduced to 96 using the matrix reducing eident value system of Dale and Williams (1978).

Frequency and abundance data, of the eident value reduced

Figure 4.3 Classification analysis of overstorey stratum vegetation plots.

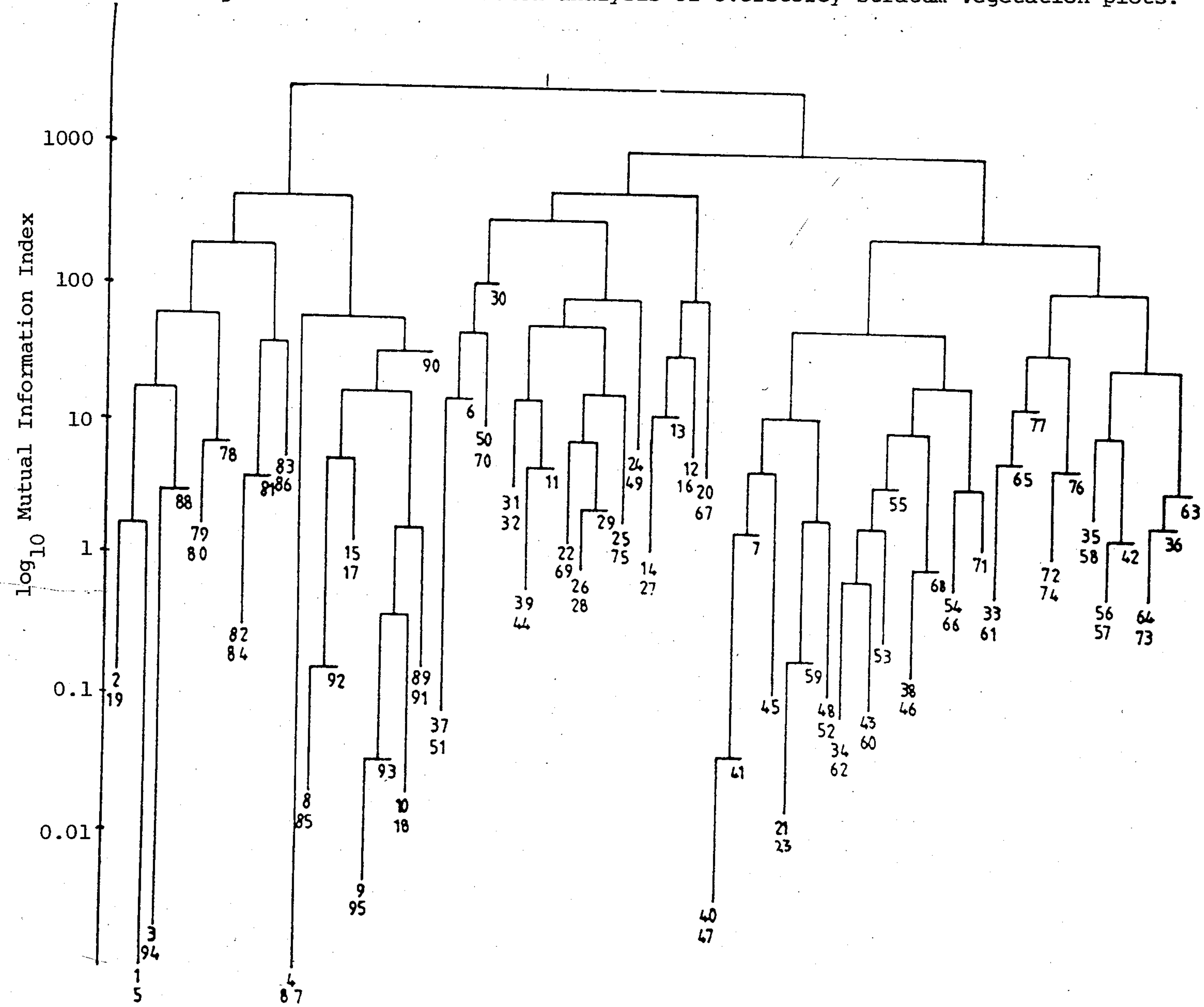


Table 4.1 Tree stratum association data summary ($\bar{x} \pm$ s.e.)

SPECIES	*Melaleuca rhapiophylla / E. rudis Assocn.*			*Banksia attenuata / B. menziesii Assocn.*		
	Frequency (% plots)	Abundance No. trees/plot	Stem Density (cm)	Frequency (% plots)	Abundance No. trees/plot	Stem Density (cm)
Nuytsia floribunda				20.0	0.5 ± 0.2	11.3 ± 4.2
Jacksonia furcellata				16.9	0.9 ± 0.3	1.6 ± 0.9
J. sternbergiana				23.1	1.4 ± 0.4	4.5 ± 1.4
Casuarina fraseriana	3.3	0.1 ± 0.1	0.5 ± 0.5	66.2	2.5 ± 0.4	42.3 ± 1.4
Eucalyptus marginata				9.2	0.5 ± 0.3	6.7 ± 3.1
E. rudis	90.0	8.8 ± 0.5	37.9 ± 12.1	4.6	0.2 ± 0.1	2.8 ± 1.8
Banksia attenuata				98.5	9.3 ± 0.7	164.8 ± 9.9
B. ilicifolia	6.7	0.3 ± 0.2	0.8 ± 0.6	40.0	1.2 ± 0.3	15.1 ± 4.7
B. littoralis	26.7	3.3 ± 1.2	47.7 ± 17.9			
B. menziesii				90.8	7.3 ± 0.6	88.1 ± 6.9
Melaleuca rhapiophylla	86.7	16.7 ± 1.1	268.5 ± 64.5	15.4	0.7 ± 0.3	23.5 ± 8.5
Viminaria juncea	13.3	0.7 ± 0.5	4.7 ± 2.9			
Total Stem Density		363.5 ± 60.1			355.3 ± 18.3	
Canopy Cover (%)		22.1 ± 2.5			17.1 ± 0.7	

matrix, were separately subjected to ordination analysis. Centred PCA of frequency and abundance data indicated that cluster assignments contained the same plots and that the distribution of these clusters with respect to each other within the component space was similar. However, centred PCA of abundance data tended to be polarized by the dominance of a few species in several plots. This reduced the component space available for the majority of plots and thus the clarity of the ordination. Therefore, only the centred PCA of frequency data is presented (see Figure 4.4). This ordination recognizes five plot cluster assignments.

PCA axis 1, which accounts for 22.3% of the total variance, represents an apparent moisture gradient. Cluster 1 plots (which reflect loadings resulting from the presence of species: *Hibbertia hypericoides, Mesomaleana stygia* and *Schoenus sublaxus)* and cluster 2 plots (which reflect loadings resulting from the presence of species: *Stirlingia latifolia, Lomandra spp.* and *Patersonia occidentalis)* were located on the elevated, better drained areas within the reserve. Cluster 3 plots (which reflect loadings resulting from the presence of species: *Hibbertia subvaginata, Scholtzia involucrata* and *Dasypogon bromeliaefolius)* represent areas of lower elevation. Cluster 4 plots (which reflect loadings resulting from the presence of annual grass species: *Aira spp., Vulpia spp., Ehrharta longiflora,* and *Bromus spp.)* represent low-lying areas adjacent to the lakes and swamps. Cluster 5 plots (which reflect loadings resulting from the presence of species: *Astartea fascicularis, Hypocalymma angustifolium, Melaleuca spp., Baumea articulata, B. juncea,* and *Centella cordifolia)* represent the moist sites located within the lakes and swamps.

PCA axis 2, which accounts for 10.6% of the total variance, locates plot clusters and plots within cluster assignments,

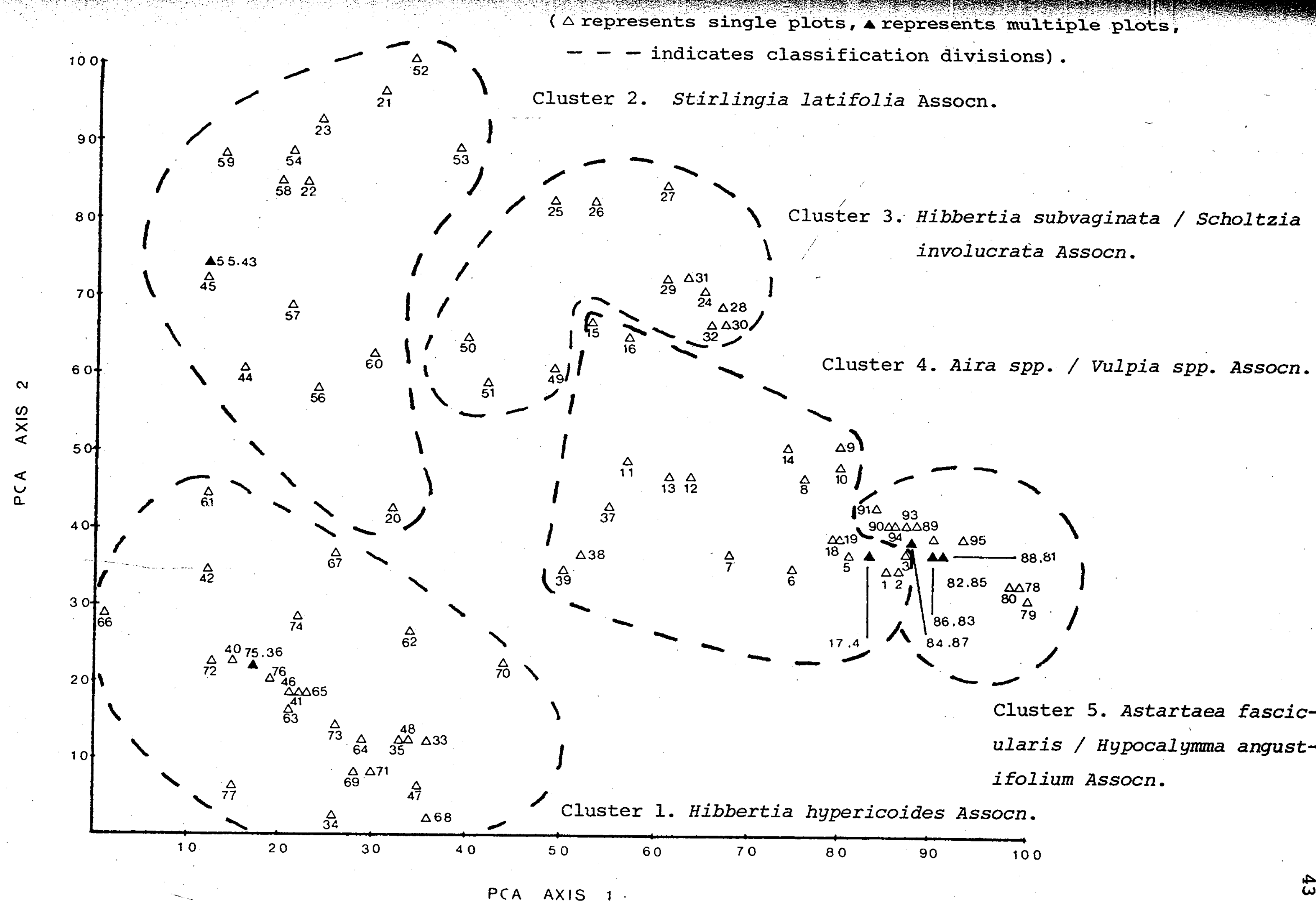


Figure 4.4 Understorey stratum ordination analysis.

in an apparent west/east gradient across the reserve. The reserve lies within a transition zone between the Spearwood and Bassendean Dune Systems. Soils occurring at the western end of the reserve are leached yellow and brown sands (podsolized sands) of the Karrakatta Soil Association, while soils at the eastern end are deep grey sands (iron podzols) of the Jandakot series. Therefore, PCA axis 2 locates plot clusters in an apparent gradient based on soil factors.

The remaining PCA axes show no apparent trend with respect to sites, floristics and/or ecological gradients, and are not considered further.

Frequency data of the understorey stratum were subjected to classification analysis. The polythetic agglomerative technique recognized two main classes; - plots located in the swamps and lakes and plots located across the rest of the reserve. The second class was then divided into four smaller classes. The plots within these first five classes are the same as those defined within the ordination clusters. The classification dendogram is presented (see Figure 4.5) and the class divisions have been superimposed on the ordination diagram (Figure 4.4).

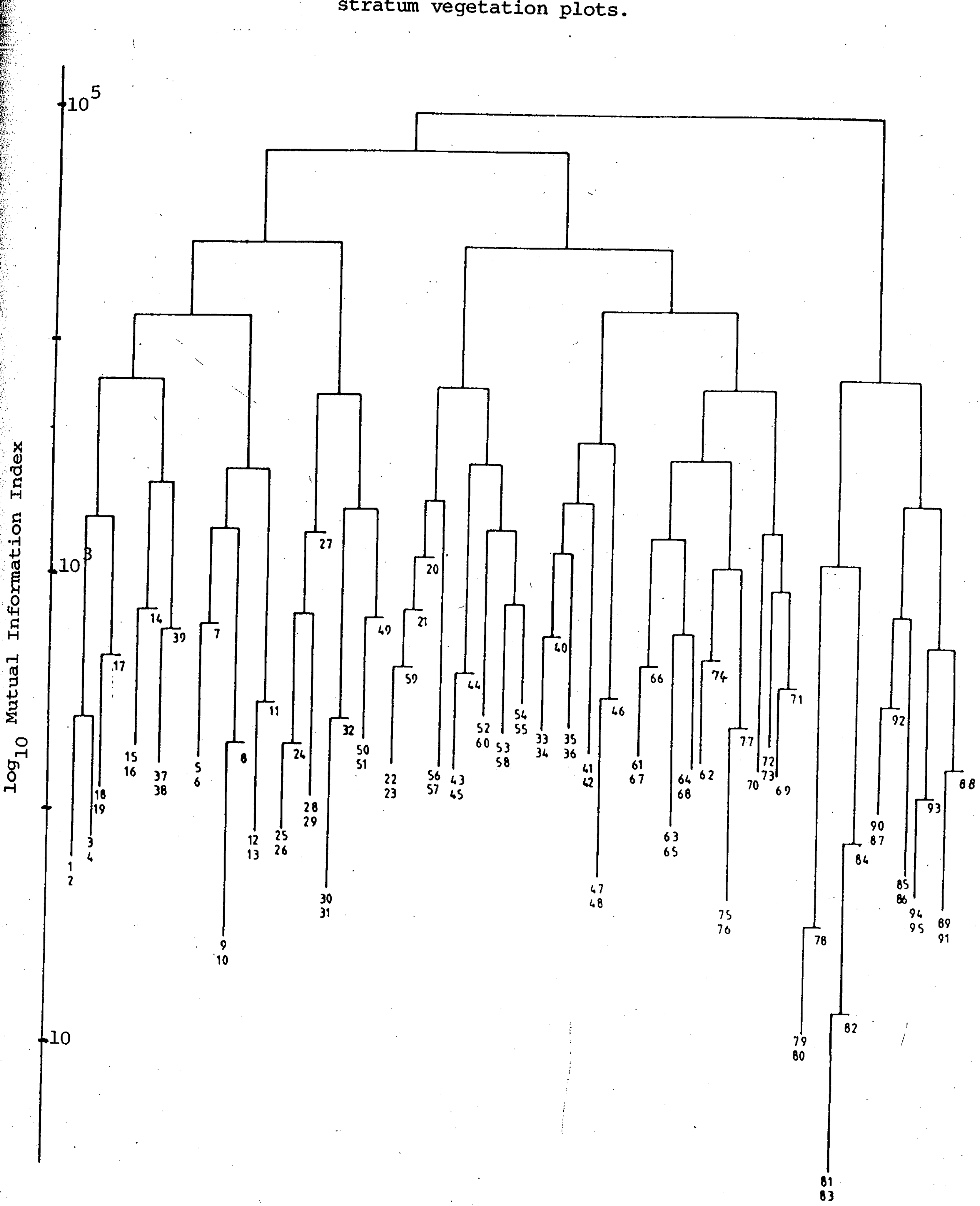
Although the ordination and classification analyses responded slightly differently to aspects of the data, the clusters and classes divided the community understorey in the same manner. As such, the community understorey could suitably be divided into five well defined associations. These understorey associations are named on the basis of species' importance in cluster and class assignments.

1.= *Hibbertia hypericoides* Association

2.= *Stirlingia latifolia* Association

3.= *Hibbertia subvaginata/Scholtzia involucrata* Association

Figure 4.5 Classification analysis of understorey stratum vegetation plots.



4. = *Aira spp./Vulpia spp.* Association

5. = *Astartea fascicularis/Hypocalymma angustifolium* Association

Banganup Lake, dominated by a dense thicket of *Baumea articulata,* represents the 6th understorey association because of its importance as quokka habitat. Representative areas within each of the above associations were photographed and are presented (see Photo 4.1 - 4.6).

A summary of understorey species' composition, abundance and frequency, during the initial survey for each of the defined associations, is presented as part of Section 4.3.3. The horizontal component of cover, for each association, is summarized in Figure 4.6. All plant species found during the surveys are listed (see Appendix 2). The plant species are recorded as native or introduced and are divided into 'floristic types' (discussed in Section 5.2.4.1).

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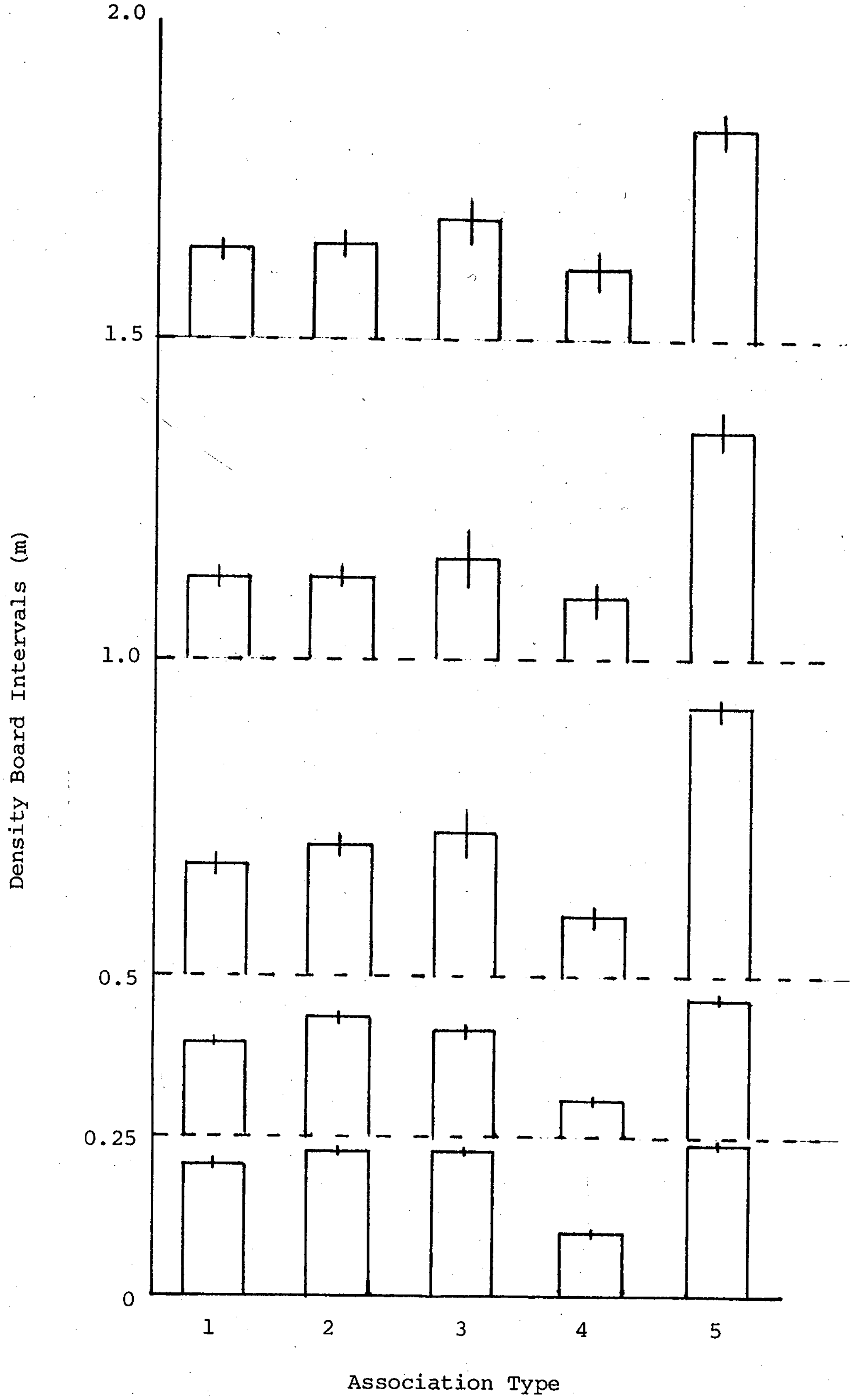


Figure 4.6 Horizontal density of the understorey associations

% Interval cover ($\bar{x} \pm$ s.e.).

4.3.3 Analysis of the understorey stratum over time: the impact of reduced grazing pressure.

Differences in the measured vegetation components during spring and summer surveys, within any one year, generally only reflected the absence of annual species. During the summer survey annual species were subjectively assessed as being 80 - 100% dry and therefore considered dead. As such, data is presented for the spring surveys only. Removal of the annual components in the data summaries indicate summer survey data.

Species' composition, abundance, frequency and total ground cover data are summarized for each understorey association over each survey (see Tables 4.2 to 4.6). Species' abundance is defined as species' mean cover within each plot averaged over all plots within a particular understorey association. Species' frequency is defined as its frequency of occurrence within a plot averaged over all plots within a particular understorey association. Plot data for the burnt and fenced sites, within the *Hibbertia hypericoides* association, are excluded from the data summary and examined in detail in Section 4.3.4.

Results are discussed in terms of the floristic types defined in Appendix 2. The majority of shrub species showed little change in abundance and frequency over the survey period. Small increases in abundance were generally a result of increased frequency rather than the result of any increase in individual cover. However, the number and occurrence of legume shrub species increased throughout the reserve over the study period. *Acacia pulchella,* present in the lake and annual grass associations increased in abundance and frequency. *Euchlopsis linearis* and *Sphaerolobium spp.* were first recorded in the lake association during the final survey. Similarly, *Bossiaea eriocarpa,* *Gompholobium tomentosum*, *Hardenbergia comptoniana* and *Hovea trisperma* increased in abundance and frequency within the other understorey associations over the survey period.

A number of grass species increased in occurrence over the surveys. *Briza maxima*, *Danthonia occidentalis* and *Stipa spp.* increased in abundance and frequency within most understorey associations. Increases in the occurrence of *Ehrharta longiflora* and *Cynodon dactylon* were recorded in the grass and lake associations respectively. *Briza minor* was the one exception to this general trend; its presence decreased in most associations.

The majority of perennial monocotyledons (other than grass species) showed small increases in abundance and frequency in successive surveys. Also, the number of species recorded increased over the survey period.

The occurrence of the few perennial herbaceous species recorded within the reserve fluctuated between surveys. *Centella cordifolia*, present in the lake association, increased in abundance and frequency between the 1982 and 1983 surveys. *Capobrotus spp.* increased in abundance and frequency during the first three surveys, however these measures decreased during the final survey. The presence of other perennial herbaceous species varied between surveys.

Small fluctuations were recorded in the occurrence of a number of annual herbaceous species. However, values for the majority of these species, in all associations, remained relatively static. Several species:- *Petrorhagia prolifera*, *Arctotheca calendula* and *Ursinia anthemoides* increased in abundance and frequency in the various associations over successive surveys.

The overall increase in species' richness and the abundance and frequency of many species is reflected in the increase in total ground cover, for the various associations, over successive surveys.

Table 4.2 *Hibbertia hypericoides* understorey association summary ($\bar{x} \pm$ s.e.).

SPECIES	1981		1982		1983		1984	
	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)
Hibbertia hypericoides	23.8 ± 2.2	94.4 ± 2.0	23.9 ± 2.2	94.4 ± 2.0	24.2 ± 2.1	93.3 ± 2.0	24.8 ± 2.1	93.3 ± 2.0
H. racemosa	0.2 ± 0.1	4.4 ± 1.7	0.2 ± 0.1	4.4 ± 1.7	0.3 ± 0.1	5.0 ± 2.0	0.3 ± 0.1	5.0 ± 2.0
Hypocalymma robustum	0.7 ± 0.2	10.0 ± 3.1	0.7 ± 0.2	10.0 ± 3.1	0.7 ± 0.2	10.0 ± 3.1	0.7 ± 0.2	10.0 ± 3.1
Scholtzia involucrata	0.9 ± 0.5	9.4 ± 5.4	0.9 ± 0.5	9.4 ± 5.4	0.9 ± 0.5	9.4 ± 5.4	0.9 ± 0.5	9.4 ± 5.4
Petrophile linearis	0.4 ± 0.1	7.2 ± 1.8	0.4 ± 0.1	7.2 ± 1.8	0.4 ± 0.1	7.2 ± 1.8	0.4 ± 0.1	7.2 ± 1.8
Hovea trisperma			*		0.2 ± 0.1	8.3 ± 2.3	0.2 ± 0.1	8.3 ± 2.3
Aira spp.	2.3 ± 0.3	50.0 ± 7.0	2.3 ± 0.3	50.0 ± 7.0	2.3 ± 0.3	50.0 ± 7.0	2.3 ± 0.3	50.0 ± 7.0
Briza maxima	5.8 ± 0.6	85.6 ± 4.1	5.8 ± 0.6	85.6 ± 4.1	5.8 ± 0.6	85.6 ± 4.1	5.8 ± 0.6	85.6 ± 4.1
B. minor	1.0 ± 0.3	27.2 ± 8.4	0.9 ± 0.3	24.4 ± 8.2	0.8 ± 0.3	24.4 ± 7.2	0.4 ± 0.1	11.7 ± 3.6
Danthonia occidentalis	*		*		0.3 ± 0.1	18.3 ± 4.2	0.7 ± 0.1	36.7 ± 6.7
Stipa spp.	0.1 ± 0.0	7.8 ± 2.5	0.1 ± 0.0	11.1 ± 2.5	0.2 ± 0.1	16.1 ± 4.5	0.7 ± 0.1	37.2 ± 5.5
Vulpia spp.	2.4 ± 0.3	50.0 ± 5.7	2.3 ± 0.3	34.1 ± 6.3	1.9 ± 0.4	38.9 ± 6.9	2.1 ± 0.3	45.6 ± 5.7
Lepidosperma costale	0.2 ± 0.1	23.3 ± 2.7	0.3 ± 0.1	25.6 ± 3.6	0.3 ± 0.1	28.9 ± 4.8	0.3 ± 0.1	29.4 ± 5.3
L. scabrum	*		0.1 ± 0.0	8.3 ± 2.2	0.1 ± 0.0	8.8 ± 2.1	0.2 ± 0.1	13.8 ± 3.2
Mesomelaena stygia	2.7 ± 0.8	27.8 ± 8.0	2.7 ± 0.8	27.8 ± 8.0	2.7 ± 0.8	27.8 ± 8.0	2.7 ± 0.8	27.8 ± 8.0
Schoenus sublaxus	2.2 ± 0.4	48.9 ± 7.3	2.2 ± 0.4	48.9 ± 7.3	2.4 ± 0.4	54.4 ± 7.6	2.3 ± 0.4	54.4 ± 7.6
Loxocarya pubescens	0.3 ± 0.1	13.9 ± 4.9	0.4 ± 0.1	19.4 ± 3.8	0.4 ± 0.1	21.7 ± 4.8	0.4 ± 0.1	21.7 ± 4.8
Burchardia umbellata	0.1 ± 0.0	9.4 ± 2.1	0.2 ± 0.1	19.4 ± 3.8	0.2 ± 0.1	15.6 ± 2.9	0.3 ± 0.1	21.1 ± 3.0
Lomandra spp.	0.2 ± 0.1	16.1 ± 3.4	0.2 ± 0.1	19.4 ± 3.8	0.3 ± 0.1	21.1 ± 4.1	0.3 ± 0.1	21.1 ± 4.1
Conostylis aculeata	0.6 ± 0.1	22.2 ± 3.8	0.6 ± 0.1	22.2 ± 3.8	0.7 ± 0.1	22.8 ± 3.5	0.9 ± 0.1	25.6 ± 4.0
Patersonia occidentalis	0.4 ± 0.2	7.8 ± 3.3	0.4 ± 0.2	8.3 ± 3.5	0.4 ± 0.2	9.4 ± 4.2	0.4 ± 0.2	9.4 ± 4.2
Petrorhagia prolifera	0.2 ± 0.1	16.1 ± 6.7	0.3 ± 0.1	17.2 ± 6.9	0.5 ± 0.2	20.0 ± 7.4	0.5 ± 0.2	21.1 ± 7.7
Homalosciadium verticillatum	0.3 ± 0.1	26.1 ± 4.9	0.3 ± 0.1	26.1 ± 4.9	0.3 ± 0.1	26.1 ± 4.9	0.3 ± 0.1	26.1 ± 4.9
Helipterum cotula	1.2 ± 0.4	11.7 ± 4.2	1.2 ± 0.4	11.7 ± 4.2	1.2 ± 0.4	11.7 ± 4.2	1.2 ± 0.4	11.7 ± 4.2
Hypochoeris spp.	4.9 ± 0.1	98.9 ± 0.8	4.9 ± 0.1	98.9 ± 0.8	4.9 ± 0.1	98.9 ± 0.8	4.9 ± 0.1	98.9 ± 0.8

Table 4.2 cont. *Hibbertia hypericoides* understorey association summary ($\bar{x} \pm$ s.e.).

SPECIES	1981		1982		1983		1984	
	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)
Ursinia anthemoides	0.3 ± 0.1	28.3 ± 5.0	0.3 ± 0.1	33.3 ± 5.5	0.4 ± 0.1	41.7 ± 6.0	0.6 ± 0.1	50.0 ± 5.7
Trachymene pilosa	0.6 ± 0.1	38.3 ± 8.3	0.6 ± 0.1	38.3 ± 8.3	0.6 ± 0.1	38.3 ± 8.3	0.6 ± 0.1	38.3 ± 8.3
Podolepsis canescens	1.7 ± 0.4	31.1 ± 5.8	1.7 ± 0.4	31.1 ± 5.8	1.7 ± 0.4	31.1 ± 5.8	1.7 ± 0.4	31.1 ± 5.8
Spp. type A	*		*		*		*	
Spp. type B			*		*		*	
Spp. type C					*		*	
Spp. type D					*			
Spp. type E							*	
Total Ground Cover	55.0 ± 2.6		55.2 ± 2.6		56.6 ± 2.8		58.5 ± 2.5	

* Species' abundance (less than 0.1%), frequency (less than 5.0%)

Spp. type A *Calytrix flavescens, Leupogon spp. Macrozamia riedlei, Dryandra nivea, Stirlingia latifolia, Capobrotus spp., Acacia pulchella, Phyllanthus calycinus, Ehrharta longiflora, Holcus setiger, Scirpus spp., Centrolepsis spp., Lyginia barbata, Dasypogon bromeliaefolius, Laxmannia spp., Conostylis setigera, Phlebocarya ciliata, Silene gallica, Crassula colarata, Trifolium dubium, Wahlenbergia capensis, Angianthus humifusus, Anagallis arvensis.*

Spp. type B *Gompholobium tomentosum, Caesia parviflora, Thysanotus spp., Platytheca verticillata.*

Spp. type C *Bossiaea eriocarpa, Amphipogon turbinatus, Avena barbata, Bromus spp., Calandrinia spp., Hybanthus calycinus, Cardus pycnocephalus.*

Spp. type D *Kennedia prostrata.*

Spp. type E *Gladiolus caryophyllaceus, Senecio lautus.*

Table 4.3 *Stirlingia latifolia* understorey association summary ($\bar{x} \pm$ s.e.).

SPECIES	1981 ABUNDANCE (%)	1981 FREQUENCY (%)	1982 ABUNDANCE (%)	1982 FREQUENCY (%)	1983 ABUNDANCE (%)	1983 FREQUENCY (%)	1984 ABUNDANCE (%)	1984 FREQUENCY (%)
Stirlingia latifolia	10.3 ± 2.0	56.9 ± 9.3	10.4 ± 2.0	56.9 ± 9.3	10.5 ± 2.0	56.9 ± 9.3	10.5 ± 2.0	56.9 ± 9.3
Petrophile linearis	1.2 ± 0.3	17.5 ± 4.1	1.2 ± 0.3	17.5 ± 4.1	1.2 ± 0.3	17.5 ± 4.1	1.2 ± 0.3	17.5 ± 4.1
Acacia cochlearis	1.5 ± 1.1	2.5 ± 1.7	1.5 ± 1.1	2.5 ± 1.7	1.5 ± 1.1	2.5 ± 1.7	1.5 ± 1.1	2.5 ± 1.7
Hibbertia hypericoides	3.2 ± 0.9	31.8 ± 4.8	3.2 ± 0.9	31.8 ± 4.8	3.5 ± 0.9	36.8 ± 6.0	3.5 ± 0.9	36.8 ± 6.0
H. racemosa	0.4 ± 0.2	10.6 ± 3.0	0.4 ± 0.2	10.6 ± 3.0	0.5 ± 0.2	12.5 ± 2.8	0.5 ± 0.2	12.5 ± 2.8
Calytrix flavescens	1.2 ± 0.2	29.4 ± 5.4	1.2 ± 0.2	29.4 ± 5.4	1.2 ± 0.2	29.4 ± 5.4	1.2 ± 0.2	29.4 ± 5.4
Eremaea pauciflora	1.1 ± 0.6	7.5 ± 3.8	1.3 ± 0.7	7.5 ± 3.8	1.5 ± 0.8	7.5 ± 3.8	1.5 ± 0.8	7.5 ± 3.8
Hypocalymma robustum	0.4 ± 0.2	5.6 ± 2.7	0.4 ± 0.2	5.6 ± 2.7	0.5 ± 0.2	6.9 ± 3.3	0.5 ± 0.2	6.9 ± 3.3
Aira spp.	3.2 ± 0.2	70.0 ± 5.7	3.2 ± 0.2	70.0 ± 5.7	3.2 ± 0.2	70.0 ± 5.7	3.2 ± 0.2	70.0 ± 5.7
Briza maxima	1.6 ± 0.5	33.8 ± 9.0	1.5 ± 0.5	31.3 ± 8.9	1.9 ± 0.5	39.4 ± 9.8	2.3 ± 0.6	36.9 ± 8.2
B. minor	0.3 ± 0.1	11.9 ± 3.6	0.2 ± 0.1	5.6 ± 2.4	0.2 ± 0.1	5.6 ± 2.2	0.1 ± 0.1	3.8 ± 2.0
Danthonia occidentalis	*		*		0.2 ± 0.1	11.9 ± 2.9	0.4 ± 0.1	19.4 ± 4.2
Stipa spp.	0.1 ± 0.0	9.4 ± 2.3	0.2 ± 0.1	9.4 ± 2.3	0.4 ± 0.1	18.1 ± 4.3	0.6 ± 0.1	33.1 ± 5.2
Vulpia spp.	2.8 ± 0.3	61.9 ± 5.8	2.8 ± 0.3	61.9 ± 5.8	2.8 ± 0.3	61.9 ± 5.8	2.8 ± 0.3	61.9 ± 5.8
Lepidosperma costale	0.4 ± 0.1	39.4 ± 7.2	0.4 ± 0.1	41.1 ± 7.1	0.5 ± 0.1	54.4 ± 6.3	0.6 ± 0.1	56.1 ± 6.1
L. scabrum	*		0.1 ± 0.0	6.9 ± 2.5	0.1 ± 0.0	8.8 ± 2.9	0.1 ± 0.0	11.3 ± 4.0
Mesomelaena stygia	0.5 ± 0.3	10.6 ± 5.7	0.5 ± 0.3	10.6 ± 5.7	0.6 ± 0.3	11.3 ± 6.1	0.6 ± 0.3	11.3 ± 6.1
Schoenus sublaxus	0.6 ± 0.2	15.0 ± 5.0	0.7 ± 0.3	16.3 ± 5.5	0.8 ± 0.3	21.3 ± 6.1	1.0 ± 0.3	21.3 ± 6.1
Loxocarya pubescens	0.4 ± 0.1	30.1 ± 6.0	0.6 ± 0.1	38.8 ± 6.2	0.7 ± 0.2	42.5 ± 6.1	0.7 ± 0.1	41.6 ± 6.1
Lyginia barbata	0.3 ± 0.1	11.9 ± 3.9	0.3 ± 0.1	13.1 ± 4.0	0.3 ± 0.1	12.5 ± 3.4	0.3 ± 0.1	12.5 ± 3.4
Burchardia umbellata	*		*		0.1 ± 0.0	11.9 ± 3.4	0.2 ± 0.0	20.0 ± 3.8
Dasypogon bromeliaefolius	1.0 ± 0.3	20.0 ± 3.9	1.0 ± 0.3	20.0 ± 3.9	1.0 ± 0.3	20.0 ± 3.9	1.0 ± 0.3	20.0 ± 3.9
Lomandra spp.	0.4 ± 0.1	41.3 ± 5.8	0.4 ± 0.1	42.5 ± 6.2	0.6 ± 0.1	62.5 ± 7.0	0.6 ± 0.1	62.5 ± 7.0
Conostylis aculeata	1.0 ± 0.2	43.8 ± 5.8	1.1 ± 0.3	45.0 ± 6.1	1.3 ± 0.3	55.0 ± 6.4	1.4 ± 0.3	56.3 ± 6.5
Phlebocarya ciliata	0.2 ± 0.2	2.5 ± 2.5	0.3 ± 0.2	3.1 ± 2.5	0.3 ± 0.2	3.8 ± 2.6	0.3 ± 0.2	3.8 ± 2.6

Table 4.3 cont. *Stirlingia latifolia* understorey association summary ($\bar{x} \pm$ s.e.).

SPECIES	1981 ABUNDANCE (%)	1981 FREQUENCY (%)	1982 ABUNDANCE (%)	1982 FREQUENCY (%)	1983 ABUNDANCE (%)	1983 FREQUENCY (%)	1984 ABUNDANCE (%)	1984 FREQUENCY (%)
Xanthorrhoea preissii	2.9 ± 1.0	15.0 ± 4.1	2.9 ± 1.0	15.0 ± 4.1	3.0 ± 1.0	15.0 ± 4.1	3.0 ± 1.0	15.0 ± 4.1
Patersonia occidentalis	4.9 ± 1.1	46.3 ± 8.0	4.9 ± 1.1	46.3 ± 1.1	5.1 ± 1.1	46.3 ± 8.0	5.2 ± 1.2	46.3 ± 8.6
Homalosciadium verticillatum	0.3 ± 0.1	25.0 ± 4.7	0.3 ± 0.1	25.0 ± 4.7	0.3 ± 0.1	25.0 ± 4.7	0.3 ± 0.1	25.0 ± 4.7
Angianthus humifusus	0.2 ± 0.1	19.4 ± 4.6	0.2 ± 0.1	19.4 ± 4.6	0.2 ± 0.1	19.4 ± 4.6	0.2 ± 0.1	19.4 ± 4.6
Helipterum cotula	0.9 ± 0.4	15.6 ± 5.2	0.7 ± 0.3	11.3 ± 4.6	0.6 ± 0.4	8.3 ± 4.9	0.5 ± 0.4	7.5 ± 4.1
Hypochoeris spp.	4.9 ± 0.1	98.1 ± 1.4	4.9 ± 0.1	98.1 ± 1.4	4.9 ± 0.1	98.1 ± 1.4	4.9 ± 0.1	98.1 ± 1.4
Ursinia anthemoides	0.1 ± 0.0	13.8 ± 3.2	0.2 ± 0.1	18.8 ± 3.9	0.4 ± 0.1	42.5 ± 6.4	0.5 ± 0.1	51.9 ± 6.0
Trachymene pilosa	0.9 ± 0.2	71.9 ± 7.1	0.9 ± 0.2	71.9 ± 7.1	0.9 ± 0.2	71.9 ± 7.1	0.9 ± 0.2	71.9 ± 7.1
Podolepsis canescens	1.2 ± 0.2	26.3 ± 4.8	1.1 ± 0.2	23.1 ± 4.7	1.2 ± 0.1	25.0 ± 4.4	1.5 ± 0.2	28.8 ± 4.5
Spp. type A	*		*		*		*	
Spp. type B			*		*		*	
Spp. type C					*			
Spp. type D					*		*	
Spp. type E							*	
Total Ground Cover	47.4 ± 2.0		47.1 ± 2.2		50.4 ± 1.8		52.2 ± 2.2	

* indicates species' abundance (less than 0.1%), frequency (less than 5.0%).

Spp. type A *Hibbertia huegelii, Leucopogon spp., Bossiaea eriocarpa, Hovea trisperma, Amphipogon turbinatus, Holcus setiger, Hypolaena exsulca, Centrolepis spp., Wahlenbergia capensis, Crassula colorata.*

Spp. type B *Kennedia prostrata, Laxmannia spp., Thysanotus spp., Conostylis setigera, Petrorhagia prolifera.*

Spp. type C *Capobrotus spp., Luzula meridionalis, Hybanthus calycinus.*

Spp. type D *Gompholobium tomentosum, Avena barbata, Scirpus spp., Gladiolus caryophyllaceus, Calandrinia spp., Silene gallica, Trifolium dubium.*

Spp. type E *Hardenbergia comptoniana, Ehrharta longiflora, Schoenus grandiflorus, S. curvifolius, Tricoryne elatior, Anigozanthos humilis, Platytheca verticillata, Eryngium pinnatifidum, Caladenia spp., Senecio lautus.*

Table 4.4 *Hibbertia subvaginata/Scholtzia involucrata* understorey association summary ($\bar{x} \pm$ s.e.).

SPECIES	1981		1982		1983		1984	
	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)
Hibbertia subvaginata	18.0 ± 3.7	74.2 ± 10.9	18.0 ± 3.7	74.2 ± 10.9	18.0 ± 3.7	74.2 ± 10.9	18.0 ± 3.7	74.2 ± 10.9
Astartea fascicularis	0.3 ± 0.3	4.2 ± 2.6	0.3 ± 0.3	4.2 ± 2.6	0.3 ± 0.3	4.2 ± 2.6	0.3 ± 0.3	4.2 ± 2.6
Calytrix flavescens	0.7 ± 0.3	16.7 ± 6.2	0.7 ± 0.3	16.7 ± 6.2	0.7 ± 0.3	16.7 ± 6.2	0.7 ± 0.3	16.7 ± 6.2
Scholtzia involucrata	9.9 ± 2.4	54.2 ± 8.6	9.9 ± 2.4	54.2 ± 8.6	9.9 ± 2.4	54.2 ± 8.6	9.9 ± 2.4	54.2 ± 8.6
Leucopogon spp.	0.2 ± 0.1	5.8 ± 2.6	0.2 ± 0.1	5.8 ± 2.6	0.2 ± 0.1	7.5 ± 2.8	0.2 ± 0.1	9.2 ± 3.6
Petrophile linearis	0.3 ± 0.2	4.2 ± 2.6	0.3 ± 0.2	4.2 ± 2.6	0.3 ± 0.2	4.2 ± 2.6	0.3 ± 0.2	4.2 ± 2.6
Bossiaea eriocarpa	*		*		0.1 ± 0.0	7.5 ± 3.3	0.1 ± 0.0	8.3 ± 2.7
Aira spp.	0.4 ± 0.1	29.2 ± 8.1	0.4 ± 0.1	28.3 ± 8.2	0.4 ± 0.1	25.8 ± 9.3	0.4 ± 0.1	27.5 ± 9.1
Briza maxima	1.6 ± 0.4	38.3 ± 6.5	1.6 ± 0.4	38.3 ± 6.5	2.4 ± 0.6	49.2 ± 9.0	2.5 ± 0.6	51.7 ± 9.2
B. minor	0.1 ± 0.1	4.2 ± 1.9	*		0.1 ± 0.1	5.0 ± 2.6	*	
Danthonia occidentalis	0.1 ± 0.1	7.5 ± 2.5	0.2 ± 0.1	12.5 ± 4.5	0.6 ± 0.2	30.0 ± 5.4	0.8 ± 0.2	34.2 ± 6.1
Stipa spp.	*		*		*		0.3 ± 0.1	15.0 ± 3.8
Vulpia spp.	0.4 ± 0.1	20.0 ± 5.2	0.4 ± 0.1	20.0 ± 5.2	0.5 ± 0.1	21.7 ± 5.1	0.5 ± 0.1	21.7 ± 5.1
Cladium riparium	0.7 ± 0.4	13.3 ± 8.0	0.7 ± 0.4	13.3 ± 8.0	0.7 ± 0.4	13.3 ± 8.0	0.7 ± 0.4	13.3 ± 8.0
Lepidosperma costale	0.3 ± 0.1	18.3 ± 6.3	0.3 ± 0.1	20.0 ± 6.5	0.4 ± 0.2	26.7 ± 6.8	0.4 ± 0.2	26.7 ± 6.8
Schoenus curvifolius	*		*		0.2 ± 0.1	10.0 ± 5.1	0.2 ± 0.1	13.3 ± 5.6
Hypolaena exsulca	0.2 ± 0.1	8.3 ± 3.9	0.2 ± 0.1	8.3 ± 3.9	0.3 ± 0.1	10.8 ± 4.2	0.3 ± 0.1	10.8 ± 4.0
Lyginia barbata	1.0 ± 0.4	27.5 ± 7.0	1.0 ± 0.4	30.0 ± 7.4	1.2 ± 0.4	34.8 ± 7.7	1.2 ± 0.4	34.8 ± 7.7
Burchardia umbellata	*		*		0.1 ± 0.1	12.5 ± 4.7	0.2 ± 0.1	19.2 ± 6.2
Dasypogon bromeliaefolius	7.6 ± 2.2	44.2 ± 11.9	7.6 ± 2.2	44.2 ± 11.9	7.6 ± 2.2	44.2 ± 11.9	7.6 ± 2.2	44.2 ± 11.9
Lomandra spp.	0.3 ± 0.1	25.8 ± 7.5	0.3 ± 0.1	26.7 ± 7.9	0.4 ± 0.1	28.3 ± 9.4	0.4 ± 0.1	30.8 ± 9.6
Xanthorrhoea preissii	3.4 ± 1.7	13.3 ± 6.1	3.4 ± 1.7	13.3 ± 6.1	3.8 ± 1.9	13.3 ± 6.1	3.9 ± 2.0	13.3 ± 6.1
Phlebocarya ciliata	3.5 ± 1.2	30.0 ± 9.7	3.5 ± 1.2	30.0 ± 9.7	3.5 ± 1.2	30.0 ± 9.7	3.5 ± 1.2	30.0 ± 9.7
Patersonia occidentalis	1.1 ± 0.3	15.8 ± 4.2	1.1 ± 0.3	15.8 ± 4.2	1.1 ± 0.3	15.8 ± 4.2	1.1 ± 0.3	15.8 ± 4.2
Angianthus humifusus	1.0 ± 0.5	19.2 ± 8.0	1.0 ± 0.5	19.2 ± 8.0	1.0 ± 0.5	19.2 ± 8.0	1.0 ± 0.5	19.2 ± 8.0

Table 4.4 cont. *Hibbertia subvaginata/Scholtzia involucrata* understorey association summary ($\bar{x} \pm$ s.e.).

SPECIES	1981		1982		1983		1984	
	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)
Helipterum cotula	1.0 ± 0.5	15.0 ± 7.6	1.0 ± 0.5	15.0 ± 7.6	1.0 ± 0.5	15.0 ± 7.6	1.0 ± 0.5	15.0 ± 7.6
Hypochoeris spp.	5.3 ± 0.6	88.3 ± 4.9	5.3 ± 0.6	88.3 ± 4.9	5.3 ± 0.6	88.3 ± 4.9	5.3 ± 0.6	88.3 ± 4.9
Ursinia anthemoides	0.3 ± 0.1	21.7 ± 5.4	0.3 ± 0.1	21.7 ± 5.4	0.3 ± 0.1	21.7 ± 5.4	0.3 ± 0.1	21.7 ± 5.4
Trachymene pilosa	1.0 ± 0.3	37.5 ± 9.3	1.0 ± 0.3	37.5 ± 9.3	1.0 ± 0.3	37.5 ± 9.3	1.0 ± 0.3	37.5 ± 9.3
Spp. type A	*		*		*		*	
Spp. type B			*		*		*	
Spp. type C					*		*	
Spp. type D					*			
Spp. type E							*	
Total Ground Cover	57.2 ± 6.5		57.2 ± 6.5		60.0 ± 6.4		61.5 ± 6.4	

* indicates species' abundance (less than 0.1%), frequency (less than 5.0%).

Spp. type A — *Hypocalymma robustum, Gompholobium tomentosum, Baumea juncea, Lepidosperma scabrum Schoenus grandiflorus, Conostylis aculeata, Crassula colorata, Homalosciadium verticillatum, Podolepsis canescens.*

Spp. type B — *Loxocarya pubescens.*

Spp. type C — *Laxmannia spp., Thysanotus spp., Gladiolus caryophyllaceus, Conostylis setigera, Platysace compressa.*

Spp. type D — *Capobrotus spp.*

Spp. type E — *Luzula meridionalis, Anigozanthus manglesii, Tricoryne elatior, Acacia stenoptera, Hovea trisperma, Calandrinia spp., Senecio lautus.*

Table 4.5 *Aira spp./Vulpia spp.* understorey association summary ($\bar{x} \pm$ s.e.).

SPECIES	1981 ABUNDANCE (%)	1981 FREQUENCY (%)	1982 ABUNDANCE (%)	1982 FREQUENCY (%)	1983 ABUNDANCE (%)	1983 FREQUENCY (%)	1984 ABUNDANCE (%)	1984 FREQUENCY (%)
Acacia pulchella	*		*		0.2 ± 0.1	6.8 ± 4.8	0.2 ± 0.1	6.8 ± 4.8
Capobrotus spp.	2.1 ± 1.4	5.9 ± 3.8	2.8 ± 1.6	7.3 ± 3.9	3.4 ± 1.9	14.1 ± 4.3	2.7 ± 1.8	11.8 ± 4.6
Aira spp.	7.4 ± 2.1	43.6 ± 7.6	7.4 ± 2.1	43.6 ± 7.6	6.3 ± 2.0	38.6 ± 8.3	7.6 ± 2.1	45.2 ± 8.5
Briza maxima	2.5 ± 1.2	17.3 ± 6.7	2.6 ± 1.2	17.1 ± 6.5	2.8 ± 1.4	19.6 ± 6.4	3.0 ± 1.4	25.5 ± 7.3
B. minor	1.4 ± 0.4	34.6 ± 6.8	1.3 ± 0.3	31.8 ± 6.4	1.4 ± 0.4	34.1 ± 7.1	1.5 ± 0.4	37.3 ± 7.2
Bromus spp.	0.5 ± 0.2	10.0 ± 4.1	0.6 ± 0.3	9.1 ± 3.9	0.4 ± 0.2	8.6 ± 4.0	0.5 ± 0.2	11.8 ± 4.5
Danthonia occidentalis	*		*		0.1 ± 0.1	10.0 ± 4.7	0.2 ± 0.1	6.8 ± 3.3
Ehrharta longiflora	5.9 ± 2.8	19.1 ± 7.2	6.2 ± 2.9	20.9 ± 7.1	7.4 ± 3.3	30.0 ± 8.1	7.7 ± 3.4	31.4 ± 8.2
Stipa spp.	0.2 ± 0.1	15.0 ± 4.2	0.3 ± 0.1	22.7 ± 6.0	0.3 ± 0.1	17.3 ± 4.7	0.5 ± 0.1	28.2 ± 6.0
Vulpia spp.	7.7 ± 1.4	64.6 ± 6.9	7.6 ± 1.4	64.6 ± 6.9	8.7 ± 1.7	66.4 ± 8.2	8.7 ± 1.7	70.5 ± 7.4
Holcus setiger	0.3 ± 0.1	5.9 ± 2.4	0.3 ± 0.1	5.0 ± 2.3	*		*	
Cladium riparium	0.7 ± 0.3	10.0 ± 4.9	0.7 ± 0.3	10.0 ± 4.9	0.8 ± 0.4	11.4 ± 5.3	0.8 ± 0.4	11.4 ± 5.3
Baumea juncea	1.0 ± 0.5	17.7 ± 6.4	1.0 ± 0.5	17.7 ± 6.4	1.0 ± 0.5	15.0 ± 5.8	1.0 ± 0.5	15.0 ± 5.8
Lyginia barbata	0.2 ± 0.2	1.8 ± 1.1	0.3 ± 0.2	2.7 ± 1.5	0.5 ± 0.4	2.7 ± 1.9	0.5 ± 0.4	2.7 ± 1.9
Dasypogon bromeliaefolius	2.2 ± 1.2	13.2 ± 7.3	2.2 ± 1.2	13.2 ± 7.3	2.2 ± 1.2	13.2 ± 7.3	2.2 ± 1.2	13.2 ± 7.3
Xanthorrhoea preissii	1.2 ± 0.7	4.1 ± 2.5	1.2 ± 0.7	4.1 ± 2.5	1.2 ± 0.7	4.1 ± 2.5	1.2 ± 0.7	4.1 ± 2.5
Conostylis aculeata	1.2 ± 0.6	11.9 ± 6.0	1.3 ± 0.7	12.7 ± 6.5	1.5 ± 0.8	12.7 ± 6.5	1.6 ± 0.8	12.7 ± 6.5
Phlebocarya ciliata	1.0 ± 0.4	10.9 ± 4.6	1.0 ± 0.4	10.9 ± 4.6	1.0 ± 0.5	10.9 ± 4.6	1.1 ± 0.5	10.9 ± 4.6
Cerastium glomeratum	*		*		0.3 ± 0.2	4.6 ± 2.4	0.4 ± 0.2	7.3 ± 3.2
Petrorhagia prolifera	0.3 ± 0.1	11.8 ± 4.1	0.4 ± 0.1	14.1 ± 4.9	0.6 ± 0.2	17.7 ± 5.2	0.8 ± 0.2	25.0 ± 6.5
Crassula colorata	4.1 ± 1.0	45.5 ± 7.1	4.0 ± 1.0	40.0 ± 5.9	3.9 ± 1.0	40.0 ± 5.9	3.9 ± 1.0	40.0 ± 5.9
Homalosciadium verticillatum	0.2 ± 0.1	20.5 ± 5.9	0.2 ± 0.1	20.5 ± 5.9	0.2 ± 0.1	20.5 ± 5.9	0.2 ± 0.1	20.5 ± 5.9
Arctotheca calendula	*		0.2 ± 0.1	3.6 ± 2.6	0.7 ± 0.5	9.1 ± 4.6	1.2 ± 0.8	11.8 ± 6.0
Angianthus humifusus	1.5 ± 0.7	26.8 ± 7.3	1.5 ± 0.7	26.8 ± 7.3	1.5 ± 0.7	26.8 ± 7.3	1.5 ± 0.7	26.8 ± 7.3
Hypochoeris spp.	11.6 ± 3.2	99.5 ± 0.5	11.6 ± 3.2	99.5 ± 0.5	11.6 ± 3.2	99.5 ± 0.5	11.6 ± 3.2	99.5 ± 0.5

Table 4.5 cont. *Aira spp./Vulpia spp.* understorey association summary ($\bar{x} \pm$ s.e.).

SPECIES	1981		1982		1983		1984	
	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)
Trachymene pilosa	0.1 ± 0.1	5.5 ± 3.3	0.1 ± 0.1	7.7 ± 3.7	0.3 ± 0.2	17.3 ± 6.0	0.3 ± 0.2	17.3 ± 6.0
Waitzia citrina	0.3 ± 0.2	4.1 ± 2.6	0.3 ± 0.2	4.1 ± 2.6	0.3 ± 0.2	4.5 ± 3.1	0.3 ± 0.2	5.5 ± 3.8
Spp. type A	*		*		*		*	
Spp. type B			*		*		*	
Spp. type C					*			
Spp. type D					*		*	
Spp. type E							*	
Total Ground Cover	72.7 ± 3.8		75.0 ± 3.9		79.4 ± 4.1		78.3 ± 3.5	

* indicates species' abundance (less than 0.1%), frequency (less than 5.0%).

Spp. type A — *Astartea fascicularis, Hypocalymma robustum, Melaleuca teretifolia, Hibbertia hypericoides, H. racemosa, H. subvaginata, Macrozamia riedlei, Avena barbata, Baumea articulata, Lepidosperma costale, Scirpus spp., Hypolaena exsulca, loxocarya pubescens, Centrolepis spp., Burchardia umbellata, Caesia parviflora, Trifolium dubium, Geranium molle, Euphorbia peplus, Centella cordifolia, Anagallis arvensis, Lobelia alata, Wahlenbergia capensis, Asteridea pulverulenta, Erigeron bonariensis, Millotia myosotidifolia, Podolepsis canescens, Ursinia anthemoides.*

Spp. type B — *Thysanotus spp., Laxmannia spp., Comesperma spp., Cardus pycnocephalus.*

Spp. type C — *Gladiolus caryophyllaceus, Platytheca verticillata.*

Spp. type D — *Sowerbaea laxiflora, Lomandra spp., Tricoryne elatior, Bossiaea eriocarpa.*

Spp. type E — *Senecio lautus.*

Table 4.6 *Astartea fascicularis/Hypocalymma angustifolium* understorey association summary ($\bar{x} \pm$ s.e.).

SPECIES	1981 ABUNDANCE (%)	1981 FREQUENCY (%)	1982 ABUNDANCE (%)	1982 FREQUENCY (%)	1983 ABUNDANCE (%)	1983 FREQUENCY (%)	1984 ABUNDANCE (%)	1984 FREQUENCY (%)
Astartea fascicularis	12.4 ± 4.5	35.6 ± 10.0	12.4 ± 4.5	35.6 ± 10.0	12.4 ± 4.5	35.6 ± 10.0	12.4 ± 4.5	35.6 ± 10.0
Hypocalymma angustifolium	7.2 ± 4.0	15.6 ± 8.5	7.2 ± 4.0	15.6 ± 8.5	7.2 ± 4.0	15.6 ± 8.5	7.2 ± 4.0	15.6 ± 8.5
Melaleuca nesophila	1.4 ± 1.0	7.4 ± 5.1	1.4 ± 1.0	7.4 ± 5.1	1.4 ± 1.0	7.4 ± 5.1	1.4 ± 1.0	7.4 ± 5.1
M. teretifolia	3.9 ± 1.9	17.2 ± 6.4	3.9 ± 1.9	17.2 ± 6.4	3.9 ± 1.9	17.2 ± 6.4	3.9 ± 1.9	17.2 ± 6.4
Acacia pulchella			*		0.3 ± 0.1	7.2 ± 3.0	0.4 ± 0.2	10.6 ± 4.2
Aira spp.	14.0 ± 3.6	58.3 ± 8.8	14.0 ± 3.6	58.3 ± 8.8	14.0 ± 3.6	58.3 ± 8.8	14.0 ± 3.6	58.3 ± 8.8
Briza minor					*		0.5 ± 0.2	23.3 ± 5.9
Cynodon dactylon	0.4 ± 0.2	7.8 ± 3.3	0.6 ± 0.2	10.6 ± 4.1	0.8 ± 0.3	17.8 ± 6.2	1.1 ± 0.4	25.6 ± 7.7
Vulpia spp.	1.1 ± 0.5	12.2 ± 4.6	1.1 ± 0.5	12.2 ± 4.6	1.1 ± 0.5	12.2 ± 4.6	1.1 ± 0.5	12.2 ± 4.6
Baumea articulata	5.6 ± 1.8	37.8 ± 9.8	5.6 ± 1.8	37.8 ± 9.8	5.6 ± 1.8	37.8 ± 9.8	5.6 ± 1.8	37.8 ± 9.8
B. juncea	5.8 ± 1.6	42.8 ± 9.2	5.8 ± 1.6	42.8 ± 9.2	5.8 ± 1.6	42.8 ± 9.2	5.8 ± 1.6	42.8 ± 9.2
Hypolaena exsulca	0.8 ± 0.5	6.1 ± 3.7	0.8 ± 0.5	6.1 ± 3.7	0.8 ± 0.5	6.1 ± 3.7	0.8 ± 0.5	6.1 ± 3.7
Centella cordifolia	2.9 ± 1.5	22.2 ± 6.7	2.9 ± 1.5	23.3 ± 7.0	4.4 ± 2.2	33.9 ± 8.4	4.4 ± 2.2	33.9 ± 8.4
Hypochoeris spp.	7.3 ± 1.9	53.3 ± 8.4	7.3 ± 1.9	53.3 ± 8.4	7.3 ± 1.9	53.3 ± 8.4	7.3 ± 1.9	53.3 ± 8.4
Spp. type A	*		*		*		*	
Spp. type B					*		*	
Spp. type C							*	
Total Ground Cover	62.9 ± 6.3		63.0 ± 6.2		64.6 ± 6.3		65.4 ± 6.2	

* indicates species' abundance (less than 0.1%), frequency (less than 5.0%).

Spp. type A *Cladium riparium, Erigeron bonariensis.*

Spp. type B *Comesperma spp., Cardus pycnocephalus.*

Spp. type C *Euchilopsis linearis, Sphaerolobium spp., Briza maxima, Holcus setiger, Polypogon monspeliensis, Stipa spp., Caladenia spp., Lobelia alata, Trachymene pilosa.*

4.3.4 Analysis of the understorey stratum with respect to fire

The burn was located within a section of the *Hibbertia hypericoides* association. A total of 62 understorey species were recorded in the 16 plots used to examine the effect of fire and subsequent grazing impact on species' composition, abundance and frequency. Two overstorey species: *Casuarina fraseriana* and *Jacksonia sternbergiana* were included in the above total because of their known importance as dietary sources (see Chapter 6) and seedling germination following fire.

Frequency and abundance data for each plot were separately subjected to ordination analysis. Centred PCA of abundance data tended to be polarized by the dominance of a few species in several plots; as was found in Section 4.3.2. As such, only the centred PCA of frequency data is presented (see Figure 4.7).

Ordination analysis indicated the presence of three cluster assignments and two significant, interpretable axes. Cluster 1 represents all non-burnt sites and includes nominated burn plots prior to the fire. The cluster assignment reflects loadings resulting from the presence of species: *Briza maxima*, *Mesomelaena stygia*, *Schoenus sublaxus*, *Loxocarya pubescens* and *Hibbertia hypericoides*. Cluster 2 represents the non-grazed (exclosure) burnt plots. The cluster assignment reflects loadings resulting from the presence of species: *Stipa spp.*, *Kennedia prostrata*, *Gompholobium tomentosum*, *Hovea trisperma*, *Jacksonia sternbergiana* and *Casuarina fraseriana*. Cluster 3 reflects loadings resulting from the presence of species: *Stipa spp.*, *Homalosciadium verticillatum*, *Scirpus spp.*, *Calandrinia spp.*, *Trachymere pilosa*, *Senecio lautus* and *Podolepsis canescens*.

PCA axis 1, which accounts for 23.7% of the total variance, indicates the impact of fire on the understorey species' composition and frequency. Plots within the burnt area (clusters 2 and 3) have

Legend for Figure 4.7

Vegetation plot No. (Figure 4.1)		PCA plot No. (Figure 4.7)	
67	Non-burnt plots	1	non-fenced
65		2	
77		3	
76		4	
63		5	fenced
64		6	
68		7	
66		8	
98*	Burnt plots	9	non-fenced
72		10	
97*		11	
70		12	
69		13	fenced
73		14	
71		15	
96*		16	

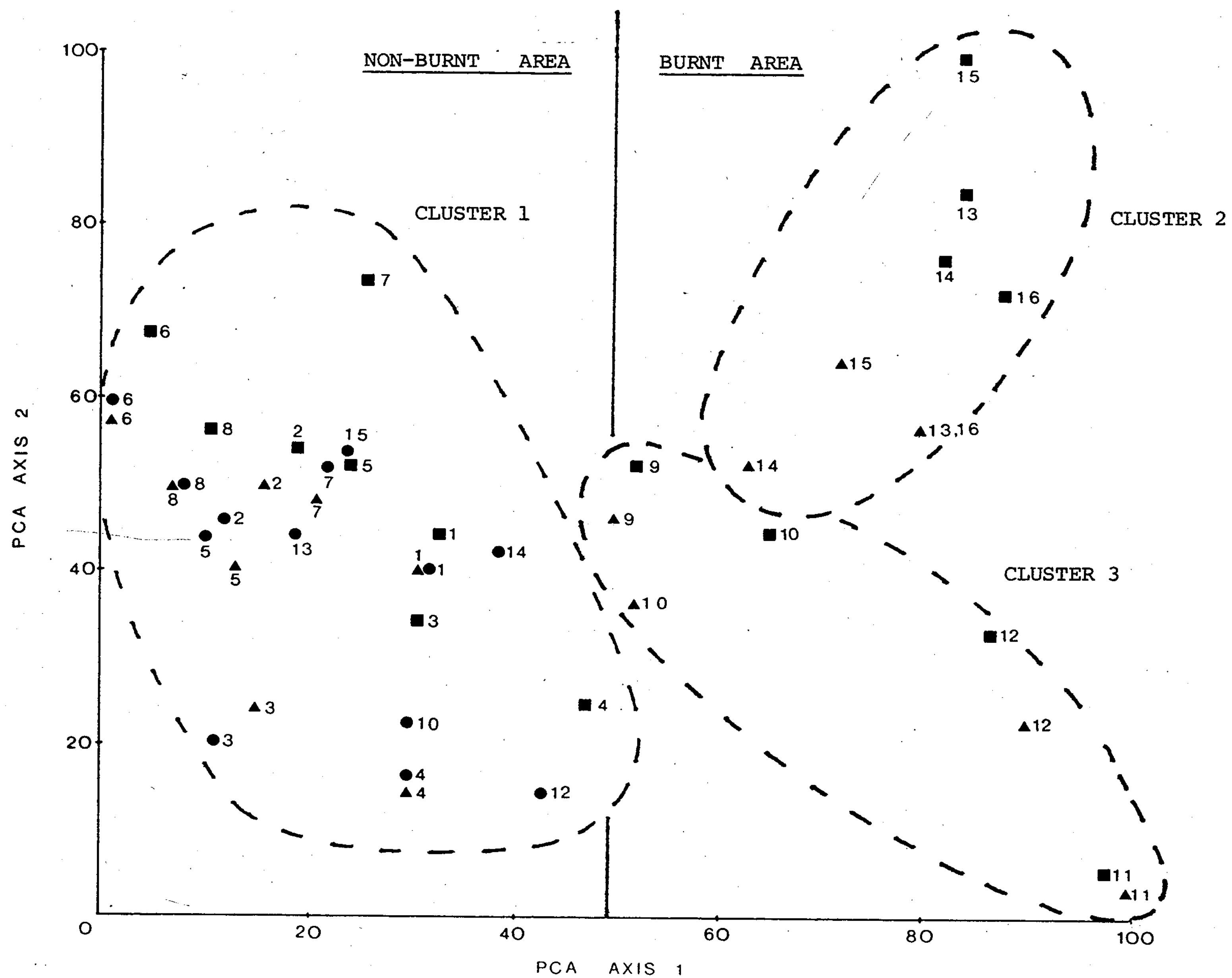
* indicates plot data unavailable for 1982

● 1982 survey plots

▲ 1983 survey plots

■ 1984 survey plots

Figure 4.7 Ordination analysis of fire plot data.



a high positive loading on the axis, while the non-burnt plots tend to a greater positive loading within the component space, particularly plot locations of the final survey. This plot movement suggests dispersal of fire induced/invading species into the non-burnt areas.

PCA axis 2, which accounts for 14.7% of the total variance, indicates the impact of grazing pressure, particularly following fire. Within the burnt area, cluster 2 plots have a high positive loading on the axis. The frequency and abundance of the species responsible for these loadings increased during the second year following the burn as indicated by the shift in plot locations within the component space. The grazed plots of cluster 3 are located closer to the axis origin. Changes in plot location within this cluster are less marked in successive years following the fire.

Regular examination of the burn prior to detailed surveying indicated that a number of leguminous species and the nitrogen-fixing *Casuarina fraseriana* had germinated throughout the area. However, intensive grazing within the area (see Chapter 5) significantly reduced the presence of these species. Resprouting growth from rootstocks of other shrub species was also the subject of intensive grazing pressure; as were the preferred dietary grass species: *Danthonia occidentalis* and *Stipa spp.* Reduction in the abundance and frequency of the above species in the burnt, non-fenced area enabled a dominant annual species component to occur, as reflected in the species' loadings of cluster 3. Representative photographs of grazed and non-grazed sites within the burn, over successive surveys, are presented (see Photo 4.7 to 4.13).

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Differences between grazed and non-grazed plots within the non-burnt zone were less marked. Plots within cluster 1 with a high positive loading on PCA axis 2 reflect the loadings of a number of dietary species: *Danthonia occidentalis, Burchardia umbellata, Loxocarya pubescens* and *Lepidosperma costale*. These plots, in general, represent the non-grazed (exclosure) plots. Plots located closer to the axis origin reflect loadings due to the presence of annual, mainly non-dietary, species: *Trachymene pilosa, Vulpia spp., Podolepsis canescens* and *Aira spp.* These plots generally represent the non-fenced, grazed sites.

All non-burnt plot locations, within the component space, have an increased positive loading, notably during the final survey. Within the exclosed plots, protection from grazing permitted species with a high positive loading to increase in frequency. However, outside these sites, the increased loading of grazed plots may possibly be attributable to the reduction of grazing pressure caused by

i) changes in macropod grazing sites, that is, species showing a preference to graze the burnt area.

and /or ii) reduction in the number of macropods within the reserve due to the culling programme.

A summary of species' composition, abundance and frequency data for the burnt/non-burnt, grazed/non-grazed plots is presented (see Tables 4.7 to 4.10).

Table 4.7 Non-burnt, grazed plots data summary ($\bar{x} \pm$ s.e.).

SPECIES	1982		1983		1984	
	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)
Hibbertia huegelii	0.8 ± 0.5	12.5 ± 9.5	0.8 ± 0.5	12.5 ± 9.5	0.8 ± 0.5	12.5 ± 9.5
H. hypericoides	40.3 ± 4.1	95.0 ± 2.9	40.8 ± 4.2	95.0 ± 2.9	42.0 ± 4.6	95.0 ± 2.9
Hypocalymma robustum	0.6 ± 0.5	7.5 ± 4.8	0.4 ± 0.2	5.0 ± 2.9	0.4 ± 0.2	5.0 ± 2.9
Macrozamia riedlei	0.3 ± 0.3	2.5 ± 2.5	0.3 ± 0.3	2.5 ± 2.5	0.3 ± 0.3	2.5 ± 2.5
Dryandra nivea	0.8 ± 0.8	7.5 ± 7.5	0.3 ± 0.3	5.0 ± 5.0	0.3 ± 0.3	5.0 ± 5.0
Petrophile linearis	1.0 ± 0.4	12.5 ± 6.3	1.0 ± 0.4	12.5 ± 6.3	1.0 ± 0.4	12.5 ± 6.3
Stirlingia latifolia	0.8 ± 0.8	5.0 ± 5.0	0.8 ± 0.8	5.0 ± 5.0	0.8 ± 0.8	5.0 ± 5.0
Phyllanthus calycinus	*		*		0.3 ± 0.3	5.0 ± 5.0
Xanthorrhoea preissii	0.6 ± 0.6	5.0 ± 5.0	0.6 ± 0.6	5.0 ± 5.0	0.6 ± 0.6	5.0 ± 5.0
Aira spp.	2.5 ± 0.7	50.0 ± 14.7	2.9 ± 0.8	57.5 ± 16.0	2.8 ± 0.8	57.5 ± 16.0
Briza maxima	4.6 ± 0.4	92.5 ± 7.5	5.4 ± 0.2	95.0 ± 5.0	5.6 ± 0.4	95.0 ± 5.0
Danthonia occidentalis					0.2 ± 0.1	12.5 ± 4.8
Stipa spp.	*		*		0.5 ± 0.3	27.5 ± 8.5
Vulpia spp.	1.3 ± 0.1	25.0 ± 2.9	1.5 ± 0.5	35.0 ± 8.7	1.4 ± 0.6	35.0 ± 8.7
Lepidosperma costale	0.3 ± 0.2	22.5 ± 9.5	0.2 ± 0.1	20.0 ± 7.1	0.3 ± 0.2	25.0 ± 6.5
L. scabrum			*		0.2 ± 0.1	15.0 ± 2.9
Mesomelaena stygia	8.5 ± 0.7	87.5 ± 4.8	8.8 ± 0.5	87.5 ± 4.8	9.8 ± 0.5	95.0 ± 5.0
Schoenus sublaxus	4.1 ± 0.8	55.0 ± 2.9	3.6 ± 0.6	50.0 ± 4.1	4.1 ± 0.7	57.5 ± 6.3
Loxocarya pubescens	0.7 ± 0.2	27.5 ± 4.8	0.6 ± 0.1	25.0 ± 6.5	0.6 ± 0.1	30.0 ± 7.1
Burchardia umbellata	0.2 ± 0.1	17.5 ± 2.5	0.2 ± 0.1	12.5 ± 4.8	0.6 ± 0.2	35.0 ± 6.5
Dasypogon bromeliaefolius	0.6 ± 0.4	10.0 ± 5.8	1.0 ± 0.7	15.0 ± 9.6	1.0 ± 0.7	15.0 ± 9.6
Lomandra spp.	0.3 ± 0.1	25.0 ± 11.9	0.2 ± 0.1	22.5 ± 8.0	0.2 ± 0.1	22.5 ± 8.0
Conostylis aculeata	0.7 ± 0.3	17.5 ± 8.5	0.6 ± 0.2	15.0 ± 6.5	0.6 ± 0.2	20.0 ± 4.1
C. setigera	0.4 ± 0.3	22.5 ± 13.1	0.4 ± 0.3	15.0 ± 8.7	0.4 ± 0.3	15.0 ± 8.7

Table 4.7 cont. Non-burnt, grazed plots data summary ($\bar{x} \pm$ s.e.).

SPECIES	1982		1983		1984	
	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)
Patersonia occidentalis	0.6 ± 0.6	7.5 ± 7.5	0.6 ± 0.6	7.5 ± 7.5	0.8 ± 0.8	10.0 ± 10.0
Eryngium pinnatifidum					0.1 ± 0.1	7.5 ± 7.5
Homalosciadium verticillatum	0.2 ± 0.1	15.0 ± 6.5	0.1 ± 0.1	10.0 ± 7.1	0.6 ± 0.5	10.0 ± 7.1
Angianthus humifusus	0.3 ± 0.3	7.5 ± 7.5	0.5 ± 0.5	10.0 ± 7.1	0.5 ± 0.5	10.0 ± 10.0
Helipterum cotula	2.6 ± 0.4	52.5 ± 8.5	1.9 ± 0.4	37.5 ± 7.5	2.9 ± 0.5	62.5 ± 6.3
Hypochoeris spp.	4.4 ± 0.5	92.5 ± 4.8	4.5 ± 0.5	95.0 ± 2.9	4.8 ± 0.3	95.0 ± 2.9
Ursinia anthemoides	0.6 ± 0.2	35.0 ± 15.5	0.8 ± 0.3	35.0 ± 15.5	1.8 ± 0.7	72.5 ± 11.1
Trachymene pilosa	0.8 ± 0.4	35.0 ± 15.5	1.2 ± 0.2	42.5 ± 19.3	0.8 ± 0.4	42.5 ± 19.3
Podolepsis canescens	0.3 ± 0.2	27.5 ± 9.5	0.1 ± 0.1	10.0 ± 10.0	0.1 ± 0.1	10.0 ± 10.0
Spp. type A	*		*		*	
Spp. type B	*		*			
Spp. type C			*		*	
Spp. type D					*	

* indicates species' abundance (less than 0.1%) and frequency (less than 5.0%).

Spp. type A *Hovea trisperma, Briza minor.*

Spp. type B *Bossiaea eriocarpa.*

Spp. type C *Acacia willdenowiniana.*

Spp. type D *Amphipogon turbinatus, Ehrharta longiflora, Gladiolus caryphyllaceus, Platytheca verticillata.*

Table 4.8 Non-burnt, exclosure plots data summary ($\bar{x} \pm$ s.e.).

SPECIES	1982 ABUNDANCE (%)	1982 FREQUENCY (%)	1983 ABUNDANCE (%)	1983 FREQUENCY (%)	1984 ABUNDANCE (%)	1984 FREQUENCY (%)
Hibbertia hypericoides	33.0 ± 1.5	95.0 ± 2.0	33.3 ± 1.4	95.0 ± 2.0	34.8 ± 1.8	95.0 ± 2.0
H. racemosa	0.3 ± 0.3	2.5 ± 2.5	0.3 ± 0.3	2.5 ± 2.5	0.3 ± 0.3	2.5 ± 2.5
Hypocalymma robustum	0.5 ± 0.4	7.5 ± 4.8	0.4 ± 0.2	10.0 ± 4.1	0.5 ± 0.4	12.5 ± 4.8
Petrophile linearis	0.6 ± 0.3	10.0 ± 4.1	0.6 ± 0.3	7.5 ± 4.8	0.5 ± 0.4	7.5 ± 4.8
Hovea trisperma	0.2 ± 0.1	12.5 ± 4.8	0.2 ± 0.1	12.5 ± 4.8	0.2 ± 0.1	12.5 ± 4.8
Xanthorrhoea preissii	1.3 ± 0.8	7.5 ± 2.5	1.3 ± 0.8	7.5 ± 2.5	1.3 ± 0.8	7.5 ± 2.5
Aira spp.	3.4 ± 0.6	62.5 ± 14.9	3.3 ± 0.8	62.5 ± 14.9	3.1 ± 0.8	62.5 ± 14.9
Briza maxima	4.0 ± 0.6	80.0 ± 11.5	4.5 ± 0.5	80.0 ± 11.5	4.0 ± 0.6	80.0 ± 11.5
B. minor	0.3 ± 0.2	10.0 ± 5.8	0.2 ± 0.1	7.5 ± 4.8	*	
Danthonia occidentalis	*		0.2 ± 0.1	7.5 ± 4.8	0.4 ± 0.3	30.0 ± 17.8
Stipa spp.	0.2 ± 0.1	10.0 ± 5.8	0.3 ± 0.2	15.0 ± 6.5	0.7 ± 0.3	35.0 ± 15.0
Vulpia spp.	2.9 ± 0.9	57.5 ± 18.9	2.8 ± 1.0	57.5 ± 18.9	2.8 ± 1.0	57.5 ± 18.9
Lepidosperma costale	0.2 ± 0.1	17.5 ± 7.5	0.2 ± 0.1	17.5 ± 7.5	0.2 ± 0.1	20.0 ± 7.1
Mesomelaena stygia	7.0 ± 1.2	70.0 ± 12.2	6.3 ± 1.7	70.0 ± 12.2	6.3 ± 1.7	70.0 ± 12.2
Schoenus sublaxus	2.2 ± 1.0	47.5 ± 18.9	2.2 ± 1.0	45.0 ± 19.4	2.2 ± 1.0	45.0 ± 19.4
Loxocarya pubescens	0.5 ± 0.2	17.5 ± 6.3	0.3 ± 0.1	17.5 ± 6.3	0.3 ± 0.2	22.5 ± 8.5
Burchardia umbellata	0.2 ± 0.1	12.5 ± 4.8	0.1 ± 0.1	10.0 ± 5.8	0.1 ± 0.1	10.0 ± 5.8
Dasypogon bromeliaefolius	0.4 ± 0.2	7.5 ± 4.8	0.5 ± 0.3	10.0 ± 5.8	0.5 ± 0.3	10.0 ± 5.8
Lomandra spp.	0.2 ± 0.1	20.0 ± 10.8	0.2 ± 0.1	20.0 ± 10.8	0.2 ± 0.1	22.5 ± 11.1
Conostylis aculeata	0.7 ± 0.4	20.0 ± 10.0	0.7 ± 0.4	20.0 ± 10.0	0.7 ± 0.3	22.5 ± 9.5
C. setigera	0.2 ± 0.1	5.0 ± 2.9	0.2 ± 0.1	5.0 ± 2.9	0.2 ± 0.1	7.5 ± 4.8
Patersonia occidentalis	0.5 ± 0.3	5.0 ± 2.9	0.5 ± 0.3	5.0 ± 2.9	0.4 ± 0.2	5.9 ± 2.9
Homalosciadium verticillatum	0.2 ± 0.1	17.5 ± 11.8	0.2 ± 0.1	17.5 ± 11.8	0.2 ± 0.1	17.5 ± 11.8
Angianthus humifusus	0.2 ± 0.2	7.5 ± 7.5	0.2 ± 0.2	10.0 ± 10.0	*	

Table 4.8 cont. Non-burnt, exclosure plots data summary ($\bar{x} \pm$ s.e.).

SPECIES	1982		1983		1984	
	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)
Helipterum cotula	0.5 ± 0.5	10.0 ± 10.0	0.8 ± 0.8	15.0 ± 15.0	1.0 ± 0.7	20.0 ± 14.1
Hypochoeris spp.	4.6 ± 0.4	90.0 ± 7.1	4.6 ± 0.4	90.0 ± 7.1	4.9 ± 0.1	90.0 ± 7.1
Ursinia anthemoides	0.4 ± 0.1	32.5 ± 4.8	0.6 ± 0.2	37.5 ± 8.5	1.2 ± 0.3	57.5 ± 4.8
Trachymene pilosa	1.0 ± 0.2	75.0 ± 9.6	0.8 ± 0.4	75.0 ± 9.6	1.6 ± 0.4	77.5 ± 8.5
Podolepsis canescens	0.3 ± 0.1	17.5 ± 10.3	0.9 ± 0.5	22.5 ± 8.5	0.9 ± 0.5	22.5 ± 8.5
Spp. type A	*		*		*	
Spp. type B					*	

* indicates species' abundance (less than 0.1%) and frequency (less than 5.0%).

Spp. type A *Dryandra nivea, Lepidosperma scabrum, Lyginia barbata.*

Spp. type B *Stirlingia latifolia, Bossiaea eriocarpa, Platytheca verticillata.*

Table 4.9 Burnt, grazed plots data summary ($\bar{x} \pm$ s.e.).

SPECIES	1982 ABUNDANCE (%)	1982 FREQUENCY (%)	1983 ABUNDANCE (%)	1983 FREQUENCY (%)	1984 ABUNDANCE (%)	1984 FREQUENCY (%)
Hibbertia hypericoides	35.3 ± 7.2	95.0 ± 3.5	8.5 ± 0.6	82.5 ± 6.3	14.8 ± 1.3	87.5 ± 4.8
H. racemosa			0.3 ± 0.3	5.0 ± 5.0	0.3 ± 0.3	5.0 ± 5.0
Hypocalymma robustum	1.0 ± 1.0	5.0 ± 3.5	0.4 ± 0.2	7.5 ± 4.8	0.6 ± 0.4	10.0 ± 5.8
Leucopogon spp.					0.1 ± 0.1	7.5 ± 7.5
Macrozamia riedlei			0.3 ± 0.3	3.0 ± 3.0	0.3 ± 0.1	5.0 ± 2.9
Dryandra nivea	0.8 ± 0.8	20.0 ± 14.1	0.4 ± 0.4	10.0 ± 10.0	0.7 ± 0.5	15.0 ± 9.6
Petrophile linearis	5.0 ± 5.0	20.0 ± 14.1	0.8 ± 0.6	12.5 ± 9.5	0.8 ± 0.6	12.5 ± 9.5
Xanthorrhoea preissii	8.0 ± 6.0	20.0 ± 7.1	1.8 ± 1.4	12.5 ± 6.3	2.4 ± 1.9	12.5 ± 6.3
Jacksonia sternbergiana			0.2 ± 0.1	10.0 ± 5.8		
Aira spp.	1.8 ± 0.3	35.0 ± 5.0	3.3 ± 1.0	40.0 ± 7.1	3.0 ± 0.4	47.5 ± 8.5
Briza maxima	2.8 ± 1.8	55.0 ± 35.0	2.4 ± 0.8	47.5 ± 14.9	2.5 ± 0.7	50.0 ± 14.7
Danthonia occidentalis					0.3 ± 0.1	25.0 ± 11.9
Stipa spp.	*		4.4 ± 0.3	85.0 ± 8.7	4.3 ± 0.3	95.0 ± 5.0
Vulpia spp.	1.4 ± 1.4	30.0 ± 30.0	1.5 ± 0.8	27.5 ± 13.8	2.1 ± 0.7	40.0 ± 14.7
Lepidosperma costale	0.1 ± 0.1	10.0 ± 10.0	0.1 ± 0.1	5.0 ± 5.0	0.2 ± 0.1	10.0 ± 5.6
Mesomelaena stygia	5.0 ± 0.0	50.0 ± 0.0	2.0 ± 0.9	42.5 ± 18.9	2.6 ± 1.0	50.0 ± 20.4
Schoenus sublaxus	0.8 ± 0.1	40.0 ± 3.0	1.6 ± 0.6	25.0 ± 3.0	2.0 ± 0.4	37.5 ± 7.5
Scirpus spp.			0.7 ± 0.4	27.5 ± 15.5	0.2 ± 0.1	17.5 ± 11.8
Loxocarya pubescens	0.3 ± 0.2	10.0 ± 0.0	*		*	
Burchardia umbellata	*		0.1 ± 0.1	10.0 ± 10.0	0.1 ± 0.1	7.5 ± 7.5
Dasypogon bromeliaefolius	0.5 ± 0.5	5.0 ± 5.0	0.7 ± 0.5	12.5 ± 9.5	1.0 ± 0.7	17.5 ± 11.8
Lomandra spp.	0.2 ± 0.1	20.0 ± 10.0	0.1 ± 0.1	10.0 ± 7.1	0.2 ± 0.1	17.5 ± 7.5
Conostylis aculeata			0.7 ± 0.3	7.5 ± 2.5	0.9 ± 0.2	22.5 ± 4.8
Patersonia occidentalis	0.5 ± 0.5	5.0 ± 5.0	0.1 ± 0.1	2.5 ± 2.5	0.3 ± 0.1	5.0 ± 2.9

Table 4.9 cont. Burnt, grazed plots data summary ($\bar{x} \pm$ s.e.).

SPECIES	1982 ABUNDANCE (%)	1982 FREQUENCY (%)	1983 ABUNDANCE (%)	1983 FREQUENCY (%)	1984 ABUNDANCE (%)	1984 FREQUENCY (%)
Calandrinia spp.			0.2 ± 0.1	22.5 ± 10.3	0.3 ± 0.1	27.5 ± 11.1
Platytheca verticillata			0.1 ± 0.1	7.5 ± 4.8	0.2 ± 0.1	15.0 ± 2.9
Homalosciadium verticillatum	0.4 ± 0.2	40.0 ± 20.0	0.5 ± 0.1	45.0 ± 13.2	0.5 ± 0.2	47.5 ± 18.0
Angianthus humifusus	*		0.5 ± 0.3	5.0 ± 2.9	0.5 ± 0.3	5.0 ± 2.9
Helipterum cotula			1.3 ± 1.3	25.0 ± 25.0	1.7 ± 1.3	32.5 ± 16.3
Hypochoeris spp.	4.3 ± 0.8	85.0 ± 5.0	5.4 ± 0.6	92.5 ± 7.5	4.6 ± 0.4	95.0 ± 5.0
Ursinia anthemoides	0.2 ± 0.2	15.0 ± 15.0	0.6 ± 0.2	40.0 ± 14.1	0.6 ± 0.2	50.0 ± 16.8
Trachymene pilosa	1.1 ± 0.3	85.0 ± 5.0	2.3 ± 0.3	85.0 ± 6.5	2.2 ± 0.5	90.0 ± 4.1
Podolepsis canescens	0.8 ± 0.5	40.0 ± 10.0	1.6 ± 0.3	32.5 ± 6.3	1.8 ± 0.6	25.0 ± 11.9
Senecio lautus					2.3 ± 0.3	40.0 ± 10.8
Spp. type A	*		*		*	
Spp. type B			*			
Spp. type C			*		*	
Spp. type D					*	

* indicates species' abundance (less than 0.1%) and frequency (less than 5.0%).

Spp. type A — *Briza minor, Lepidosperma scabrum, Lyginia barbata.*

Spp. type B — *Conostylis setigera, Wahlenbergia capensis.*

Spp. type C — *Capobrotus spp., Hovea trisperma, Eryngium pinnatifidum.*

Spp. type D — *Gompholobium tomentosum, Schoenus grandiflorus.*

Table 4.10 Burnt, exclosure plots data summary ($\bar{x} \pm$ s.e.).

SPECIES	1982		1983		1984	
	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)	ABUNDANCE (%)	FREQUENCY (%)
Hibbertia huegelii	0.3 ± 0.3	6.7 ± 5.8	*		*	
H. hypericoides	33.0 ± 5.0	96.7 ± 2.9	10.8 ± 0.6	85.0 ± 2.9	14.8 ± 0.6	92.5 ± 4.8
Casuarina fraseriana			0.9 ± 0.7	17.5 ± 14.4	1.8 ± 1.4	25.0 ± 18.5
Hypocalymma robustum	1.3 ± 1.0	6.7 ± 5.8	0.4 ± 0.2	7.5 ± 4.8	0.3 ± 0.1	5.0 ± 2.9
Leucopogon spp.	1.0 ± 0.6	6.7 ± 2.9			0.4 ± 0.2	20.0 ± 9.1
Macrozamia riedlei	0.3 ± 0.3	3.3 ± 2.9	0.5 ± 0.3	5.0 ± 2.9	0.5 ± 0.3	5.0 ± 2.9
Dryandra nivea	3.3 ± 1.8	33.3 ± 17.6	0.8 ± 0.6	22.5 ± 16.5	1.4 ± 0.9	25.0 ± 16.6
Petrophile linearis	1.3 ± 1.0	10.0 ± 8.7				
Gompholobium tomentosum					2.2 ± 0.3	62.5 ± 9.5
Hovea trisperma					0.7 ± 0.3	25.0 ± 11.9
Kennedia prostrata			0.8 ± 0.3	10.0 ± 4.1	10.3 ± 6.6	45.0 ± 11.9
Jacksonia sternbergiana			0.9 ± 0.4	17.5 ± 4.8	1.7 ± 0.8	27.5 ± 7.5
Kunzea ericifolia					0.9 ± 0.9	5.0 ± 5.0
Xanthorrhoea preissii	0.3 ± 0.3	3.3 ± 2.9	0.8 ± 0.3	7.5 ± 2.5	0.9 ± 0.3	10.0 ± 4.1
Aira spp.	1.3 ± 0.2	16.7 ± 8.8	0.7 ± 0.2	20.0 ± 5.8	0.8 ± 0.3	22.5 ± 7.5
Briza maxima	3.5 ± 1.0	66.7 ± 17.7	2.4 ± 0.2	47.5 ± 4.8	4.9 ± 0.9	77.5 ± 10.3
Danthonia occidentalis	0.1 ± 0.1	6.7 ± 6.7	0.4 ± 0.2	12.5 ± 6.3	1.5 ± 0.5	50.0 ± 17.8
Stipa spp.	0.1 ± 0.1	6.7 ± 6.7	18.3 ± 1.4	92.5 ± 7.5	17.3 ± 1.1	100.0 ± 0.0
Vulpia spp.	1.5 ± 0.0	30.0 ± 0.0	0.4 ± 0.1	17.5 ± 6.3	0.5 ± 0.2	17.5 ± 6.3
Lepidosperma costale	0.2 ± 0.0	20.0 ± 0.0	0.2 ± 0.1	17.5 ± 4.8	0.2 ± 0.1	17.5 ± 4.8
L. scabrum	0.1 ± 0.0	10.0 ± 0.0	*		*	
Mesomelaena stygia	9.0 ± 0.9	90.0 ± 10.0	3.9 ± 0.4	75.0 ± 5.0	6.0 ± 1.4	82.5 ± 7.5
Schoenus sublaxus	1.8 ± 0.4	33.3 ± 6.7	1.7 ± 0.3	35.0 ± 5.0	2.4 ± 0.2	45.0 ± 5.0
Scirpus spp.			0.3 ± 0.1	17.5 ± 7.5	0.2 ± 0.1	12.5 ± 4.8

Table 4.10 cont. Burnt, exclosure plots data summary ($\bar{x} \pm$ s.e.).

SPECIES	1982 ABUNDANCE (%)	1982 FREQUENCY (%)	1983 ABUNDANCE (%)	1983 FREQUENCY (%)	1984 ABUNDANCE (%)	1984 FREQUENCY (%)
Loxocarya pubescens	1.1 ± 0.1	33.3 ± 8.8	0.8 ± 0.3	35.0 ± 5.0	0.8 ± 0.3	45.0 ± 5.0
Burchardia umbellata	0.2 ± 0.1	16.7 ± 3.3	0.3 ± 0.1	30.0 ± 10.8	0.5 ± 0.2	32.5 ± 11.8
Dasypogon bromeliaefolius			0.2 ± 0.1	2.5 ± 2.5	0.2 ± 0.1	2.5 ± 2.5
Laxmannia spp.					1.0 ± 0.7	20.0 ± 14.1
Lomandra spp.	0.3 ± 0.1	26.7 ± 13.3	0.2 ± 0.1	17.5 ± 8.5	0.4 ± 0.2	30.0 ± 12.9
Anigozanthos humilis			*		0.2 ± 0.2	7.5 ± 7.5
Conostylis aculeata			0.3 ± 0.2	5.0 ± 2.9	0.7 ± 0.2	17.5 ± 2.5
C. setigera	0.4 ± 0.3	10.0 ± 5.8	0.2 ± 0.1	17.5 ± 6.3	0.5 ± 0.2	25.0 ± 9.6
Patersonia occidentalis					0.3 ± 0.1	5.0 ± 2.9
Calandrinia spp.			0.1 ± 0.1	10.0 ± 7.1	0.1 ± 0.1	12.5 ± 9.5
Platytheca verticillata			0.2 ± 0.1	12.5 ± 2.5	0.3 ± 0.1	32.5 ± 10.3
Homalosciadium verticillatum	0.1 ± 0.1	5.0 ± 5.0	0.3 ± 0.1	25.0 ± 10.4	0.3 ± 0.1	27.5 ± 11.1
Hypochoeris spp.	4.2 ± 0.4	90.0 ± 5.8	4.8 ± 0.5	82.5 ± 2.5	4.6 ± 0.5	95.0 ± 5.0
Ursinia anthemoides	0.9 ± 0.4	30.0 ± 0.0	1.9 ± 0.5	72.5 ± 11.1	2.5 ± 0.3	90.0 ± 7.1
Trachymene pilosa	0.6 ± 0.1	63.3 ± 0.1	1.3 ± 0.2	52.5 ± 7.5	0.8 ± 0.1	52.5 ± 7.5
Podolepsis canescens	0.6 ± 0.3	16.7 ± 12.0	0.8 ± 0.5	15.0 ± 9.6	0.8 ± 0.5	15.0 ± 9.6
Senecio lautus					0.8 ± 0.3	25.0 ± 8.7
Spp. type A	*		*		*	
Spp. type B			*		*	
Spp. type C					*	

* indicates species' abundance (less than 0.1%) and frequency (less than 5.0%).

Spp. type A — *Briza minor, Centrolepis spp.*

Spp. type B — *Capobrotus spp., Gladiolus caryophyllaceus, Eryngium pinnatifidum.*

Spp. type C — *Acacia stenoptera, A. willdenowiniana, Hardenbergia comptoniana, Luzula meridionalis, Helipterum cotula, Caladenia spp.*

4.4 Discussion

Plant species in any community differ greatly in palatability and accessibility to herbivores and in their response to defoliation. Some species are greatly reduced by herbivory, while others,which are excluded (or suppressed) by competition may invade (or increase in abundance) when grazing pressure is increased (Main, 1981b; Noy-Meir, 1981; Crawley, 1983). Within the objectives outlined for the reserve, management policies must provide a balance between the requirements of herbivores for food and shelter and the requirements of the plant species for persistence.

Main (1968) considered that much of the diet of kangaroos and wallabies was derived from perennial species, as such it was possible to look at food resources in two ways:

i) The total quantity of dietary plant species present at any one time - the standing crop.

ii) The annual growth of these species - the annual crop.

It was thus possible to consider the upper limit of prudent management as being set by the maximum harvest possible, while leaving sufficient of the annual crop to replace mortality and wastage of the standing crop.

The application of the above statement depends on the values of the following variables:

a) population size

b) nutritional status of the population in relation to the maintenance level

c) size of the annual crop

d) size of the standing crop

Main (1968, 1970) further suggested that the amounts of nitrogen fixed in a system would determine the "carrying capacity" of the land with respect to certain marsupials.

Initial management policies for the reserve (see Section 3.1) permitted an increase in herbivore population levels. This increase resulted in overutilization of the annual crop and nett reduction of the standing crop. The locally overabundant herbivore populations caused a reduction in plant species richness and diversity, as noted by earlier research workers on the reserve. Over-exploitation of these plant resources accentuated the annual late summer nutritional stress (Main, 1968), which led finally to a heavy mortality of certain macropod species' populations on the reserve (see Chapter 5).

During the study period, fluctuations in rainfall, temperature and water table levels may have had an effect on plant species characteristics. However, manipulations of species' population levels, to reduce total grazing pressure, are believed to be primarily responsible for increases in plant species richness and increases in abundance and frequency of many species. Justification of the above statement stems from the increase in species' richness and occurrence of palatable species, particularly during the later surveys. Initial surveys indicated leguminous species, preferred dietary grass species such as, *Cynodon dactylon, Danthonia occidentalis* and *Stipa spp.* and various sedges when present,were observed to be heavily browsed/grazed or inaccessible. During later surveys species' richness and occurrence of these palatable forms increased despite their increased importance in the diets of the study species (see Chapter 6).

The results and the above discussion emphasize the importance of regulating hervivore population levels in reserves of limited size, to maintain existing vegetation species' richness and diversity.

Examination of the impact of fire and subsequent grazing pressure on plant species composition and occurrence suggested a number of important considerations if fire is to be used as an effective management technique.

The widespread germination of leguminous species following fire indicated the presence of a considerable seed store. This seed bank would have been built up over a period of time as legume species were not particularly prevalent in surveys prior to the fire. Shea et *al.* (1979) indicated the importance of high intensity burns for broad-scale germination of leguminous species. Apparently in the northern jarrah forest the bulk of legume seed is located below the zone of soil which is heated during 'normal' low to moderate intensity prescription burning. During high intensity fires sufficient heat is conducted to the zones of the soil where the seed is stored. Soil depth-temperatures and fire intensity recorded on the reserve during the burn were consistent with the above findings. The use of fire is also important in nutrient recycling, invasion of palatable grass species and the rejuvenation of fire-resistent species through vigorous resprouting from rootstocks and lignotubers.

Following fire the above species were subjected to intensive grazing pressure in non-fenced areas. Shea *et al.* (1979) and Main (1981a) noted that when the area burnt is small, the large mobile macropods shelter in the unburnt areas and graze on the post-burn regeneration. Thus in small burns grazing pressure is increased or remains high enough to prevent regeneration of palatable species. On the other hand, large intense burns will have no shelter for herbivores and as a consequence regeneration is likely to proceed unaffected by their grazing pressure.

On reserves of limited size, only small area burns are practical. Large burns would reduce the total area available for shelter and food resources prior to germination. Such factors would limit the well-being and survival of herbivore species present. The burn area should be fenced to permit species' germination and establishment, which would otherwise be the subject of intense grazing pressure. The length of time these areas need to be exclosed was beyond the scope of this study, but would be dependent on adequate species establishment.

The frequency of fire is also an important consideration in the use of fire as a management technique. Frequent fires will have a deleterious effect on obligate seeder species. The time interval between fires must be of such a duration as to permit seedling establishment, sexual maturity and seed production if these species are not to be lost from the community. The frequent occurrence of wildfires on the reserve has most likely contributed to the decline of these species. The possibility of broad-scale reintroduction of such species using heat pretreatment seeds requires examination.

Exclosure of non-burnt areas does not contribute greatly to an increase in species' richness, but it does permit certain palatable species present,to increase in frequency and abundance. However, it seems more appropriate to regulate herbivore population levels within the framework of Main (1968), than reduce the space available to higher density populations through exclosure plots.

CHAPTER 5

SPECIES' SPATIAL DISTRIBUTIONS

5.1 Introduction

Understanding the relationships between a species and its environment is the basic premise for wildlife management (Carey, 1981). The concept of the niche is predicated on the theory that there is some basic configuration or pattern in the environment that is selected by a species (Rotenberry, 1981). A community may be regarded as a multivariate complex, with the distribution of any species therein being a function of the distribution of one or more biotic and/or physical community factors (Hirst, 1975). Species which exhibit heterogenous distributions over a given area are responding qualitatively and quantitatively to habitat factors which relate directly or indirectly to their well-being and survival (*Op. cit.*).

Within ungulate communities, plant species composition, abundance and frequency have been found to be of central importance in determining species' distributions and feeding patterns while, vegetation structure was of consequence as shelter and in avoidance of predation (Lamprey, 1964; Bell, 1971; Ferrar and Walker, 1974; Hirst, 1975; Hudson, 1977; Leuthold, 1978).

A number of studies have examined macropod habitat preferences, particularly the larger, primarily grazing species in arid and semi-arid areas. The majority of these studies have used frequency of occurrence within broad, well-defined habitat types as a measure of habitat preference.

Broad scale surveys of red kangaroo (*Macropus rufus*) populations have indicated the importance of food quality, food quantity and shelter on their distribution (Frith, 1964; Newsome, 1965a, 1965b; Bailey *et al.*, 1971). The climatic influence on forage quality and the availability of water also have a significant effect on distribution and dispersion (Newsome, 1975).

Euros normally occur in association with rocky outcrops and ranges, which provide important heat refuges (Ealey, 1967; Russell, 1969). Location of permanent bores in pastoral areas has reduced the euros dependence on the rocky heat refuges and allowed them to disperse into areas where adequate drought forage is available (Newsome, 1975). Also, during periods of adequate rain, euros may disperse outwards from heat refuges but return as the country dries out (Ealey, 1967).

Eastern grey kangaroos (*Macropus giganteus*) occupy extensive geographical ranges and exist in high densities in widely dissimilar ecotypes (Hill, 1981). Caughley (1964) found that the density of this species to be correlated with lateral cover. The density and height of undergrowth and food abundance were also shown to be important in influencing distribution (Taylor, 1980).

Very few studies have used multivariate techniques in the analysis of single species macropod habitat preferences. Hill (1981) used multiple regression and cluster analysis in the analysis of eastern grey kangaroo distribution with reference to habitat structural attributes and food resources. Results suggested preferred habitats were a balance between food resources and lateral cover. Subsequent work (Hill, 1982) demonstrated that patterns of habitat use were not constant. Seasonal environmental changes and their influence on pasture status was found to be the most important factor governing eastern grey kangaroo distribution. Christensen (1977), using principal components analysis, indicated the importance of plant species composition and various vegetation structural attributes in determining woylie (*Bettongia penicillata*) and tammar (*Macropus eugenii*) habitat preferences.

Detailed studies, using multivariate techniques, of multi-species macropod communities have not occurred. Where species occur in sympatry it has been suggested that they occupy essentially different habitat types (Ealey, 1962; Caughley, 1964; Storr, 1968; Frith and Calaby , 1969; Kaufmann, 1974; Coulsen, 1978).

From the above discussion the importance, primarily, of vegetation attributes in determining species' habitat preferences is apparent. Within the limited extent of the Harry Waring Marsupial Reserve, physical community factors change little. Restriction of available habitat use because of species' water requirements would not occur due to the provision of permanent watering points and the number and size of lakes and temporary soaks. As such, the relationships between species and their habitats, in this study, are examined by focusing on the differences in the floristic and structural aspects of the vegetation within the community which may allow species to co-exist.

In this chapter factors of niche separation which influence the distribution of species in space and the degree of separation of each niche are examined.

5.2 Method

The activity pattern of macropodid marsupial species is generally described as nocturnal, although a crepuscular tendency has been noted in many species (Kaufmann, 1974; Coulsen, 1978; Taylor, 1981). Personal observations of the four study species suggested that the brush wallaby, euro and western grey kangaroo commenced feeding activity from late afternoon and continued until several hours after dawn; depending on the climatic conditions of the day. Quokkas tended to be nocturnal commencing feeding activity after dark and ceasing prior to dawn. After these periods the respective species moved from preferred feeding areas to areas preferred for sheltering.

In order to fulfill the objectives of this study it was necessary to determine the extent of covariance between the occurrence of each species and the habitat variables considered to have a possible influence on the location of feeding and sheltering areas. Of the various possible approaches to the collection of data, two methods were chosen as suitable. Systematic surveys along the tracks and firebreaks, across the reserve, were used to determine the locations of the brush wallaby, euro and western grey kangaroo. Because of the quokkas' smaller size, nocturnal activity pattern and the density of vegetation in and around the lakes and swamps, seasonal trapping data was used in analyses of quokka spatial distributions and habitat preferences.

5.2.1 Animal capture

The research programme required an accurate determination of the population levels of the four study species. Seasonal trapping and marking of captured animals was satisfactory for the examination of quokka population levels. Recognition of individuals in the other study species, during surveys, would have been difficult because of their lack of distinguishing marks. Repeated sightings of non-recognizable individuals during surveys would significantly reduce the accuracy of any population census. As such, it was desirable to capture and mark as many animals, during the study, as possible to permit individual identification. Monitoring species' population levels where the majority of animals were tagged would also provide additional information on sex and age class structures, recruitment and mortality.

Small macropod species, such as the quokka, are readily caught in box traps, hand nets and long nets (Dunnet, 1956). A number of techniques has been used to capture larger macropod species with varying degrees of success. Drugs such as chloral hydrate (Marlow, 1956) and a derivative - alpha-chloralose (Oliver, 1968), which are added to water, have been successful in the capture of euros and red kangaroos respectively. Arnold *et al.* (in press) using alpha-chloralose in food baits and water were able to capture large numbers of western grey kangaroos. Driving animals in long nets has met with little success and usually resulted in a high mortality of captured animals (Keep and Fox, 1971; Wapstra, 1976). Cage traps (Wapstra, 1976) and cage traps around watering points (Gooding and Harrison, 1955; Frith, 1964; Ealey, 1967; Bailey, *et al.*, 1971) have been more successful. Dart guns have been used by a number of workers (Keep and Fox, 1971; Wilson, 1975; Shepherd, 1981) with variable results. The use and effect of drugs available for the capture and restraint of macropods have been comprehensively reviewed by a number of authors (Wilson, 1975; Finnie, 1978; Keep, 1978a). A 'stunning' technique where animals are disorientated by a combination of light and sound has been particularly successful in the capture of macropods (Shepherd, 1981; Robertson and Gepp, 1982). The problems of post-capture complications in macropods, in particular capture myopathy, have been reviewed by a number of authors (Keep, 1978b; Shepherd, 1981; Chalmers and Barrett, 1982).

5.2.1.1 Capture techniques, handling and measurements

The above techniques were evaluated to determine their suitability, in terms of capture success, handling and post-capture stress, for the study species.

Inability to control alpha-chloralose intake in food baits, with respect to the study species and non-target species, of differing body size, prevented its use on the reserve. The small target area available, that is the hindquarters, together with obscured vision and dart flight deflection in the dense undergrowth on the reserve, similarly excluded the use of dart guns.

A number of cage trap types, shapes and sizes were examined. A trap design of dimensions 2 x 1.8 x 0.8m was found to be the most satisfactory for the capture of the three larger macropod species. The traps were constructed of rabbit-netting panels, padded at the corners, an operator access gate and trap mechanism. The trap mechanism consisted of a one-way swinging gate held open by an upright- supporting pole. A length of string was stretched across the width of the trap and 'bow-strung' around the pole. As an animal entered the trap it touched the string causing the pole to move and the gate to drop. This relatively simple trap design prevented access by more than one animal and restricted the animal's movement while in the trap; both important factors in preventing injury. Also animals within these traps could be handled by one operator.

Extensive cage-trapping of brush wallabies, euros and western grey kangaroos was conducted during the latter part of 1981 in the evaluation of the above traps and to maximise the number of tagged animals prior to the detailed survey programme. In 1982 and 1983 large cage trapping of animals was usually conducted twice during each season. Only one trapping season occurred during the autumn of 1984 because the majority of animals were tagged and field work was nearing completion.

Eight cage traps, located across the reserve (see Figure 5.1), were used in each trapping session. Traps were prebaited with bread for three days prior to each trapping period. During trapping, bread baits were laid approximately two hours before sunset and the traps checked two hours after dark. Any animals caught were processed, the traps being reset and examined two hours later. Trapping periods were of three to five days duration, depending on the number of animals captured and how 'trap-happy' individuals became. Following each trapping session all traps were wired open.

Animals caught in these traps were restrained by means of a hand net and placed in hessian bags to reduce stress. Particularly aggressive female euros, western grey kangaroos and males in excess of 40kg required tranquilization prior to measurement. A combination of the drugs Ketamine: 2- (O-chloro-phenyl) -2- (methylamino) cyclo hexanone - hydrochloride, 100 mg/ml (Trade mane Ketalar, Parke Davis Ltd.) and Xylazine: 2 - (2,6 - xylidino) - 5,6 - dihydro - 4H - 1,3 - thiazine hydrochloride, 100mg/ml (Trade name Rompun, Bayer Australia Ltd.) were used. Animals weighing less than 40kg were injected intra-muscularly with 1.0 ml ketamine : 0.5ml Xylazine. Animals greater than 40. kg were injected intramuscularly with 2.0ml ketamine

1.0 ml Xylazine. The drug combination used had an induction time of approximately five minutes and tranquilization effect for up to one hour, with no noticable post-release complications.

All animals were weighed and had pes and tibia lengths recorded. The pes was measured from the insertion of the claw on the first phalange to the back of the calcaneum. The tibia was measured from the tuberosity on the proximal end of the tibia to the lateral ridge on the calcaneum of the foot at the distal end. Female pregnancy status and the sex of the offspring were also noted.

Sub-adult and adult brush wallabies, euros and western grey kangaroos were collared and ear-tagged. Juvenile animals were ear-tagged but not collared because of the possibility of strangulation during growth. The collars were constructed of a 4cm wide, white plastic belting. The width of the collar was reduced to 2.5cm for the smaller brush wallaby. Plastic coded symbols were attached to each collar to permit individual identification. Numbered cattle eartags (Stockbrands Ltd., Perth, W.A.) were attached to the front of each collar to further aid identification. Coloured Chicken wing tags (Stockbrands Ltd.) were used as eartags. Although the eartags did not permit individual identification during census runs, they were visible up to 50m and allowed assigning the individual to 'tagged' or 'non-tagged' populations.

Restraint and processing of individuals captured in cage traps usually took less than 15 minutes. Prior to restraint the animals did not appear to be particularly stressed, self-inflicted injuries were seldom observed and mortality (discussed in Section 5.3.1) was low.

The 'stunning' technique proved very successful in the capture of brush wallabies and juvenile/sub-adult western grey kangaroos. The animals were caught by a team of one catcher, a shooter, two spotlighters and a vehicle driver. The equipment consisted of two (100 watt) spotlights, a 0.22 calibre rifle, fitted with a 'variable' telescopic sight and supersonic ammunition. An animal, up to a distance of 50m, was held in the spotlights, while a shot was fired between its ears about 2cm above the top of its skull. The catcher would then sprint along the margin of the light beam and grab the animal by the tail. The animal was then bagged and processed, as described above. Processing took less than five minutes and although slightly disorientated no post-capture complications were apparent.

The 'stunning' technique proved inadequate for the capture of large animals. Adult male and female western grey kangaroos and euros showed little sign of disorientation when 'stunned' and the density of vegetation hindered extensive chases.

The 'stunning' of animals was conducted across the reserve during the new moon phase, on nights of low wind and no rain. During 1982 and 1983 the method was employed several times each season. Its use was curtailed during 1984 because of the reduced brush wallaby population.

Quokkas were readily captured in box traps of dimensions 32 x 33 x 72 cm (Viking Wire Ind., Perth W.A.), baited with bread. One trapping session was conducted each season during the study period. Trap locations are discussed later (see Section 5.2.3) Traps were set and checked as for the large cage traps, however, only one trap run was conducted each night. Each trapping session was conducted over three days. Extended trapping sessions resulted in a large number of recaptures. Animals were processed as before however, fingerling tags (Salt Lake Stamp Co. Utah, U.S.A.) were used as ear tags. All quokkas were anal swabbed as part of a *Salmonella* research programme conducted by the Western Australian Health Department.

5.2.2 Brush wallaby, euro and western grey kangaroo surveys

Three basic assumptions were taken into consideration when designing the survey method to determine the preferred feeding and sheltering areas of the brush wallaby, euro and western grey kangaroo:-

1. No animal was counted more than once
2. Animals were seen in the location from which they were disturbed by the observer, that is, animals did not move from the observer's path before they broke cover and were seen.
3. There was no difference between species, sexes and age classes in animal responses to the observer.

Preliminary surveys indicated that the study species, across sex and age classes, showed little sign of disturbance to low speed vehicle movement within the reserve.

Visibility was examined at 20m intervals at right angles to the tracks using the vegetation profile board method (see Section 4.2.1.3). Results suggested that all species would generally be visible from 60 to 100 m depending on the vegetation association.

The number of tracks and firebreaks within the reserve provided good access across its extent. Thus it was possible to design a survey route to give maximum coverage and visibility of the reserve with minimum road overlap. Parallel tracks were surveyed systematically to improve sightability, minimize disturbance in other areas and thus reduce possible error because of animals flushing ahead. Possible errors in counting animals more than once were reduced because of the large number of animals tagged.

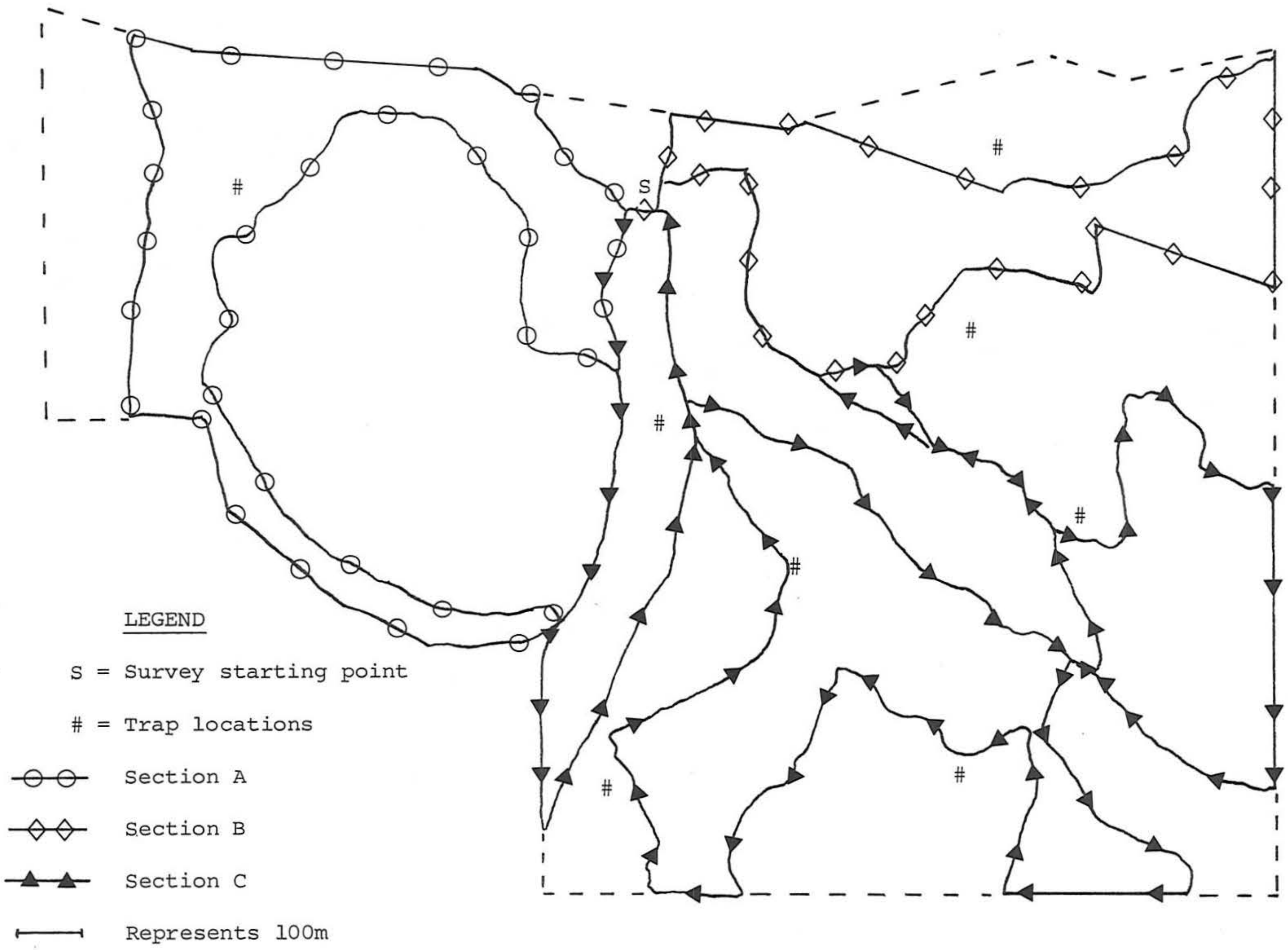
The survey route (see Figure 5.1) was divided into three sections and the survey of each section could be made in either direction. The survey route was 17.4km in length (section A = 4.9km; B = 3.2km; C = 9.3km). The section sequence and direction of each section was chosen at random prior to each survey to avoid any possible time bias effects.

Two survey sessions were conducted each month. Each session consisted of a dawn and dusk survey to examine areas of feeding activity and a noon survey to examine areas preferred for sheltering. The dawn survey was undertaken the day following the dusk run to detect possible large scale movements that may have occurred overnight.

Prior to each survey, temperature and relative humidity data were recorded. Cloud cover, wind strength and rainfall were subjectively assessed on a scale 0 to 5. Surveys were not conducted during heavy rain and/or high wind.

Surveys were conducted by one operator driving a 4WD vehicle at approximately 10km/h. During each survey both sides of the track/firebreak were scanned. All observations were made using 10 x 50 magnification binoculars. Each individual sighted was assigned to a vegetation plot reference (see Figure 4.1) being closest and similar to the vegetation type in which the animal was observed feeding or sheltering. Animals were recorded as non-tagged or tagged and the collar number noted. Whenever possible the sex of each animal was recorded

Figure 5.1 Survey route and large kangaroo trap locations.



and the pregnancy status of females noted. The age class of each individual, broadly defined as juvenile, sub-adult or adult, was recorded.

The detailed recording of the above factors, group associations and extensive capture records enabled an accurate estimation of species' population levels during the study.

5.2.3 Quokka surveys

A preliminary trapping programme was initiated in late spring/ early summer 1981 to examine the distribution and abundance of quokkas on the reserve. Over a two month period traps were set across the extent of the reserve. A total of 91 animals was captured. Of these 96 percent were trapped in and around Banganup Lake and the remaining four percent were located in Melaleuca Swamp. Following the 1981 census a further 99 quokkas were introduced onto the reserve, all animals being released within Banganup Lake. Thus, at the beginning of the study a known population of 190 quokkas was present on the reserve.

On the basis of the above capture results and introduction programme it was decided to concentrate trapping effort in and surrounding Banganup Lake. During the extensive surveys and trapping programmes conducted throughout the study, quokkas were very rarely observed or captured outside this area. Trapping sessions were conducted each season during the study period. Traps were located at each of the vegetation plots 85 to 95 (see Figure 4.1). Four traps were placed 25m apart at each of these sites.

To establish areas preferred for shelter by quokkas the reserve was intensively searched on foot during the day throughout the preliminary trapping period. Evidence of sheltering activity was confined to the dense *Baumea articulata* thickets within Banganup Lake. Inability to accurately census animals within this vegetation type made it necessary, for the purposes of this study, to assume that these thickets represent preferred quokka sheltering areas. Quokkas' use of these thickets will be discussed further (see Section 5.4).

5.2.4 Discriminant function analysis

The community niche is considered as the parent space within which species' niches are located at characteristic distances from one another, with varying degrees of overlap (see Chapter 1). Discriminant function analysis (DFA) provides an appropriate multivariate statistical method for the separation of groups (species) according to their characterization by a series of environmental variables (Green, 1971, 1979; Ferrar and Walker, 1974; Hutchinson, 1978; Page and Walker, 1978; Shugart, 1981).

Species' abundance and species' presence are not usually related to environmental variables in a linear additive manner (Green, 1971). The curve of species' abundance, and therefore probability of occurrence along an environmental gradient is usually unimodal, with the maximum at some ecological optimum. In DFA species are groups, separated in ecological space by linear additive functions of ecological variables, rather than the dependent variables related to the ecological variables in a linear additive manner. That is, the linear additive relationship is among the ecological variables and not between the species and the ecological variables (*Op. cit.*).

DFA examines all variables simultaneously and reduces them to a number of new, uncorrelated variables called discriminant functions on which the between - group variation is maximized relative to the within - group variation (Seal, 1964; Hope, 1968). Thus discriminant functions are a linear combination of the environmental variables, weighted by a discriminant function coefficient, in accordance with their relative contribution to separation in the new dimension. The new dimensions DFA produces are independent and species' separation along them is maximal.

Each discriminant function is defined by its eigenvalue and the vector of discriminant coefficients (the eigenvector). The eigenvalue gives the proportion of the total variance extracted. It is used to calculate Wilks' Lambda statistic which, when transformed, is distributed approximately as an F statistic and provides a test of the discriminating power of the discriminant function. The eigenvector can be standardized by multiplying each coefficient by the standard deviation of the variable. This implies that the size of the standardized coefficient is a measure of the relative importance of the corresponding variable in achieving discrimination, with the sign denoting the direction of that contribution.

Association of the variance from each variable with the gradients represented by the discriminant functions may be shown as communalities. The communalities are calculated as the sum of squares on the factor patterns (standardized weights) for each discriminant function. Thus, the communalities indicate the importance of each variable with respect to their overall influence on the animals sampled (Ferrar and Walker, 1974).

The discriminant function mean scores indicate which group is being separated by the corresponding discriminant function. The group means of these scores are known as the species' centroids and may be considered as the niche centres (Ferrar and Walker, 1974). Plotting the species' centroids on each discriminant function separates the species along what are regarded as the dimensions of the community habitat niche (*Op. cit.*).

A geometric view of the separation between species' centroids may be obtained using confidence limits. As the discriminant functions are scaled to reflect the variance of each variable, confidence circles are appropriate. The radius for an approximate $(1 - \alpha) \times 100\%$ confidence circle, for group i, is obtained by:

$$r_{\alpha} = \sqrt{\frac{\chi^2_{\alpha, 2}}{n_i}}$$

(Mardia *et al.*, 1979; Chatfield and Collins, 1980).

Significance of separation between species' centroids may be tested using Mahalanobis distances. These distances are a guide to the amount of separation between groups. An F statistic may be calculated using Mahalanobis distances, in the following way (*Op. cit.*).

$$F = \frac{n_i + n_j - p - 1}{p(n_i + n_j - 2)} \times \frac{n_i . n_j}{n_i + n_j} \times d^2_{ij} \quad F\ (p, n_i + n_j - p - 1)$$

where d_{ij} is the Mahalanobis distance between groups i and j,

n_i and n_j are the group sizes,

p is the number of variables in the discriminant function.

DFA is a technique which has the following underlying assumptions (Hope, 1968; Mardia et. al., 1979; Chatfield and Collins, 1980):

1. The distribution of the data for each group is multivariate normal.
2. The groups have the same dispersion (matrix).

In an attempt to meet the first assumption, transformations were performed on variables to approximate normal distributions. It was not desirable to equalise dispersions around the group means as this would have altered the between-groups variance to within - groups variance relationship, upon which the analysis depends. In practice, DFA is a robust technique, even to quite large deviations from normality and homogenity (Cooley and Lohnes, 1971), and if group separation is highly significant and the discriminant functions are biologically meaningful, the separation can be regarded as real (Green, 1971).

The GENSTAT programme package (Alvey *et al.*, 1980) on the DEC 10 computer at the Western Australian Regional Computing Centre at the University of Western Australia was used for all computations associated with DFA.

5.2.4.1 Habitat variable selection

Whether the discriminant functions are biologically meaningful or not depends mainly on the relevance of the original variables. Discriminant functions are weighted combinations of the original variables and can only summarise, rather than add to, the information they contain. DFA cannot correct for the omission of important variables and given large sample sizes, may produce significant separation based on a set of irrelevant ones (Green, 1971). To overcome these problems Green (1971) suggested environmental variables should be selected on the basis of four criteria:-

1. The variable should have a reasonable chance of directly affecting the organisms, or should be correlated with such a variable.
2. It should be possible to measure the variable in the field or to collect a sample for analysis without the delay causing error.
3. The seasonal variation in the variable should be insignificant compared with its variation between all samples collected at any one time.
4. The variable should describe the environment in direct contact with the organisms.

In this study, relationships between species and their habitats were examined following the above criteria by focusing on the differences in the floristic and structural aspects of vegetation within the community (see Section 5.1). Systematic surveys of brush wallabies, euros, western grey kangaroos and quokka trapping programmes associated animal locations with vegetation plots. Thus the environment, in contact with any individual animal, in terms of floristic and structural vegetation components, could be described.

To facilitate analysis of sighting and trapping data and to allow for seasonal comparisons, data collection was pooled within seasons for each year during the study period. Measurement of vegetation components during the seasons winter and spring and during the seasons summer and autumn experienced little change (see Section 4.2.1.3), although the nutritional quality of the forage may have (see Chapter 6). As such, vegetation surveys during the spring and late summer each year were considered appropriate for the examination of the above herbivore relationships across all seasons.

Plant species could not be used as variables because of their excessive number and the dubious importance of many in individually determining macropod habitat preferences. However, when plant species were grouped into a number of floristic types, the abundance of these floristic types within vegetation plots, differed considerably across the reserve. Thus the reduction of the data set to floristic type abundances as habitat variables, was considered more appropriate. Six floristic types were recognized, within the reserve, and are listed below:-

1. Shrubs - Perennial dicotyledons greater than 30cm tall and less than 3m tall with secondary woody thickening.
2. Perennial herbs - perennial dicotyledons less than 30cm tall with no secondary woody thickening.
3. Annual/biennial herbs - annual/biennial dicotyledons less

than 30cm tall.

4. Grasses - all perennial and annual grass species.
5. Perennial sedges - all perennial monocotyledons, excluding grass species.
6. Annual sedges - all annual monocotyledons, excluding grass species.

Classification of all plant species, on the reserve, into the above six categories is shown in Appendix 2.

The mean abundance (cover) of the respective floristic types, for each vegetation plot, was calculated by summing the abundances of individual species within each quadrat and then obtaining the mean abundance for the plot. The remaining habitat variables considered important reflect the structural components of vegetation within each plot. Detailed descriptions and methods of measurement of these variables are given in Sections 4.2.1.2 and 4.2.1.3. The structural and floristic variables used in the analysis are listed in Table 5.1. In total, 13 habitat variables were used to examine macropod habitat preferences.

Macropod species presence, within the experimental burn area following fire, was omitted from the multivariate analysis. Fire has a dramatic effect on plant species composition, frequency and abundance (see Chapter 4). Fire is also responsible for increases in the nutrient status and palatability of regenerating species. As such, environmental variables considered important in non-burnt areas are not necessarily compatible with those in post-burn regenerating areas. Quantifying factors such as nutrient status and palatability of species within burnt and non-burnt areas was beyond the scope of this study. Macropod preference for post-burn regenerating areas is inferred from observed changes in the proportion of species' population levels therein, before and after fire.

Table 5.1 Summary of the 13 variables used in the multivariate analysis.

Variable No.	Mnemonic	Variable description
1	SHB	Shrub abundance (% cover)
2	PHD	Perennial herb abundance (% cover)
3	AHD	Annual herb abundance (% cover)
4	GRS	Grass abundance (% cover)
5	PSM	Perennial sedge abundance (% cover)
6	ASM	Annual sedge abundance (% cover)
7	COV	Total ground cover (% cover)
8	DBH	Tree stem density (m)
9	DNI	Horizontal density 0-0.25m (% cover)
10	DN2	Horizontal density 0.25 - 0.5m (% cover)
11	DN3	Horizontal density 0.5 - 1.0m (% cover)
12	DN4	Horizontal density 1.0 - 1.5m (% cover)
13	DN5	Horizontal density 1.5 - 2.0m (% cover)

5.3 Results

5.3.1 Species' capture records, population level and structures

Species' capture records and trap mortality are presented for the study period (see Table 5.2). For western grey knagaroos, euros and brush wallabies, the column titled 'Mortality' includes animals found dead in traps plus those animals not sighted again following trap release. As it was not possible to ascertain whether trapping had a significant effect on the loss of these animals, following release, the mortality levels may be considered elevated.

The majority of trap-associated mortalities occurred during the preliminary period of capture method and trap type evaluation. The trial use of alpha-chloralose accounted for the majority of western grey kangaroo and euro capture mortalities, while the use of small weldmesh traps (35 x 60 x 80 cm) was responsible for the three brush wallaby deaths.

Species' population levels and structures, on a seasonal basis throughout the study, are presented below. The number of animals tabulated indicates the population levels at the end of each season. The population structure is divided into sex and age classes. Three broad age classes are recognized:-

1. Juveniles - joeys at foot. As a general rule joeys, of all species, leave the pouch in late spring and remain at heel until the following spring.
2. Sub-adults - animals no longer at heel and not sexually mature.
3. Adults - sexually mature animals.

Adult females are divided into a series of classes depending on their pregnancy status. For the two larger species, the western grey kangaroo and euro, observation data permitted females to be

Table 5.2 Species' capture records and trap mortality

SPECIES	TOTAL CAPTURES	INDIVIDUALS CAPTURED	MORTALITY (%)
Western grey kangaroo	158	55	4
Euro	72	23	8
Brush wallaby	86	56	3
Quokka	607	194	< 1

divided into four classes:

Class 1. non-pregnant females

Class 2. females with a joey in the pouch

Class 3. females with a juvenile at heel

Class 4. females with a joey in the pouch and a juvenile at heel.

Female pregnancy status for the brush wallaby and quokka was restricted to two classes:

Class 1. females without a joey in the pouch

Class 2. females with a joey in the pouch.

5.3.1.1 Western grey kangaroo population level and structure

Western grey kangaroo population level and structure, on a seasonal basis, is presented (see Table 5.3a). The initial population of 82 animals was reduced over the study period to a population of 33 animals by spring 1984. A total of 47 animals was removed as a result of the culling programme (see Section 3.2.1). Twenty animals were lost from the population as a result of natural mortality. The majority of deaths, attributable to natural mortality, occurred during the late autumn periods. Mortality of pouch young was very low. Recapture data indicated losses of pouch young usually occurred early in pouch life in females pregnant for the first time.

5.3.1.2 Euro population level and structure

Euro population level and structure, on a seasonal basis, is presented (see Table 5.3b). During the study period, the euro population declined from 18 to 6 animals. Dramatic population declines occurred during the autumn/winter periods with mortality of 50% of the population in 1982/83. Euro mortality was across sex and age classes.

5.3.1.3 Brush wallaby population level and structure

Brush wallaby population level and structure, on a

Table 5.3a Western grey kangaroo population level and structure.

YEAR	SEASON	ADULT					SUB-ADULT		JUVENILE		Total Population	Tagged Population (%)
		Male	Female				Male	Female	Male	Female		
			Class 1	Class 2	Class 3	Class 4						
1981/82	Summer	15	2	2	1	16	8	16	13	9	82	24
	Autumn	14 (1)	2	2	0	8 (7)	3 (3)	11 (5)	9 (2)	7 (2)	55 (20)	44
	Winter	12	2	4	0	6	3	10	9	7	53	42
	Spring	12	2	4	0	6	3	10	9	7	53	42
1982/83	Summer	14	2	9	1	10	10	6	6	5	63	59
	Autumn	8 (3)	0 (1)	7 (2)	1	9 (1)	5 (2)	3 (1)	6	5	44 (10)	80
	Winter	8	0	7	0	9	5	3	5	5	42	74
	Spring	8	0	7	0	9	5	3	5	5	42	74
1983/84	Summer	11	1	7	0	10	7	5	5	6	53	75
	Autumn	5 (4)	1	5 (3)	0	7 (3)	5 (2)	3 (1)	3 (2)	4 (2)	33 (17)	76
	Winter	5	1	5	0	7	5	3	3	4	33	76
	Spring	5	1	5	0	7	5	3	3	4	33	76

( ) indicates number of animals culled in each category.

Table 5.3b Euro population level and structure.

YEAR	SEASON	ADULT					SUB-ADULT		JUVENILE		Total	Tagged
		Male	Female				Male	Female	Male	Female	Population	Population
			Class 1	Class 2	Class 3	Class 4						(%)
1981/82	Summer	6	0	4	1	3	0	0	2	2	18	67
	Autumn	6	2	2	1	3	0	0	2	2	18	78
	Winter	5	2	1	1	2	0	0	1	2	14	86
	Spring	4	2	1	1	2	0	0	1	2	13	85
1982/83	Summer	4	2	1	1	2	1	0	1	2	14	93
	Autumn	1	2	1	0	1	1	0	1	0	7	100
	Winter	1	1	1	0	1	1	0	1	0	6	100
	Spring	1	1	1	0	1	1	0	1	0	6	100
1983/84	Summer	2	2	0	0	1	1	0	0	1	7	86
	Autumn	2	1	0	0	1	1	0	0	1	6	83
	Winter	2	1	0	0	1	1	0	0	1	6	83
	Spring	2	1	0	0	1	1	0	0	1	6	83

seasonal basis, is presented (see Table 5.3c). The brush wallaby population level declined from 79 animals at the beginning of the study to a population of 24 animals at the end. Natural mortality accounted for the majority of these losses. Mortality was greatest during the first two years, the majority of these losses occurring during the autumn/winter periods. During 1983/84 the population appeared to stabilize. Mortality was across sex and age classes. Mortality of pouch young was particularly high.

5.3.1.4 Quokka population level and structure

Quokka population level and structure, on a seasonal basis, is presented (see Table 5.3d). The preliminary trapping programme, discussed in Section 5.2.3, resulted in the capture of 91 animals. Following the above census, a further 99 quokkas were introduced onto the reserve. A total of 40 introduced animals were recaptured during the autumn, 1982 census, four of which survived to the spring, 1982 census.

Results of the trapping sessions during 1981/82 suggested a high mortality, particularly between the summer and spring surveys, of both resident and introduced animals. To establish whether the reduction in the population level was due to mortality rather than dispersal from the lake area, the preliminary trapping programme was employed again during spring, 1982. No additional animals were captured during this survey thus, confirming the decline in the quokka population level was due to heavy mortality. The quokka population level stabilized during 1982/83 however, recruitment of juveniles was low.

A number of factors, either acting singly or in concert, were proposed responsible for the population crash observed in 1981/82:

Table 5.3c Brush wallaby population level and structure.

YEAR	SEASON	ADULT			SUB-ADULT		JUVENILE		Total	Tagged
		Male	Female		Male	Female	Male	Female	Population	Population
			Class 1	Class 2						(%)
1981/82	Summer	28	4	16	9	7	5	10	79	3
	Autumn	17 (8)	4 (2)	13 (1)	8 (1)	7	5	9	63 (12)	32
	Winter	12	1	11	6	4	5	8	47	11
	Spring	12	1	10	5	4	5	8	45	7
1982/83	Summer	17	5	10	5	7	2	2	48	25
	Autumn	12	3	5	5	5	2	2	34	79
	Winter	8	3	5	3	4	2	2	27	59
	Spring	8	2	4	3	4	2	2	25	76
1983/84	Summer	11	2	5	2	2	2	2	26	69
	Autumn	10	1	5	2	2	2	2	24	71
	Winter	10	1	5	2	2	2	2	24	71
	Spring	10	1	5	2	2	2	2	24	71

( ) indicates number of animals culled in each category.

Table 5.3d Quokka population level and structure.

YEAR	SEASON	ADULT Male	ADULT Female Class 1	ADULT Female Class 2	SUB-ADULT Male	SUB-ADULT Female	JUVENILE Male	JUVENILE Female	Total Population	Captured Population (%)
1981/82	Summer	33	49	0	8	2	7	4	103	88
	Autumn	31	7	36	1	1	0	2	77	90
	Winter	No trapping session conducted								
	Spring	9	4	3	0	0	0	2	18	100
1982/83	Summer	8	6	0	0	2	0	1	17	76
	Autumn	7	3	2	0	1	0	1	14	100
	Winter	7	2	3	0	1	0	1	14	79
	Spring	7	1	4	0	1	0	1	14	93
1983/84	Summer	13	37	0	2	3	2	2	59	49
	Autumn	12	5	31	2	2	1	1	54	83
	Winter	10	4	27	2	2	1	1	47	89
	Spring	10	7	21	2	3	3	4	50	90

1) Competition with rabbits, limiting available food and shelter resources, especially at critical seasonal times of the year.
2) Reduction of quokka gut flora during quarantine, inhibiting utilization of food resources when the animals were released onto the reserve.
3) Predation.
4) *Salmonella* infections.

In an attempt to successfully re-establish a quokka colony onto the reserve due consideration was given to the above factors prior to animal release. Reduction of rabbit population levels was conducted as discussed in Section 3.2.1. Regular 1080 baiting and shooting programmes were implemented to reduce possible predation pressure by foxes, cats and dogs. As part of the on-going management policy, quokkas to be introduced onto the reserve were quarantined and examined for *Salmonella* infections prior to release. Five *Salmonella* types (*S. typhimurium, S. cerro, S. javiana, S. bredeney* and *S.rottnest)* were subject to restriction from the reserve. Animals *Salmonella* positive for any of the above types were not introduced onto the reserve. Resident or introduced qookkas found suffering the above *Salmonella* infections during the course of surveys were recaptured and removed from the population. During the period of quarantine, quokkas were fed a high fibre diet in an attempt to maintain their gut flora.

A total of 60 quokkas were introduced onto the reserve in summer,1984. Of these animals, 36 were recaptured on a regular basis during the final year of study. Five animals were removed from the population because of *Salmonella* infections and two were found dead within a month of release. The fate of the remaining 17 animals is not known however, several quokkas were occasionally sighted in Melaleuca and Russel Swamps. As such, dispersal from Banganup Lake may have accounted for their disappearance.

The number of animals recaptured during 1984, survival of these animals and recruitment of juveniles during 1985 (Reserve Warden, pers. comm.) would appear to suggest the initial success of improved re-establishment procedures.

5.3.2 DFA of species' spatial distributions

In total, 178 systematic surveys were undertaken in the examination of brush wallaby, euro and western grey kangaroo habitat preferences. The number of surveys each season per year are presented (see Table 5.4). Eleven trapping programmes were conducted in the examination of quokka feeding area preferences. During winter 1982 traps were unavailable and as such this represents the only season during the study period for which data are unavailable.

The number of variables used to describe species' locations was reduced after examination of the raw data. DFA requires the computational matrices be non-singular. Singularities occur when a group has zero variance for any one variable. This situation can arise in the data matrix when only zero scores are achieved by any one species for any one variable (Hope, 1968; Ferrar and Walker, 1974). Thus, variables PHD and ASM, where zero scores predominated, were discarded. AHD was invariant and deleted from the data set. Of the original 13 variables, six were selected to be subjected to DFA. These variables and their transformations are presented in Table 5.5.

Variables that were measured as percentages of area were found to have skewed (non-normal) distributions. A number of transformations were attempted and the square-root transform (Snedecor and Cochran, 1967) adopted as the most suitable. The

Table 5.4 The number and time of surveys each season during the study period

Dawn Surveys

	1981/1982	1982/1983	1983/1984
Summer	7	6	5
Autumn	4	4	4
Winter	4	3	6
Spring	5	5	4

Noon Surveys

	1981/1982	1982/1983	1983/1984
Summer	7	6	3
Autumn	4	3	3
Winter	6	5	6
Spring	6	4	3

Dusk Surveys

	1981/1982	1982/1983	1983/1984
Summer	7	6	5
Autumn	4	5	5
Winter	6	5	6
Spring	6	6	4

Table 5.5 Variables selected for DFA and their transformations.

VARIABLE	MNEMONIC	TRANSFORMATION
Tree stem density	DBH	-
Canopy cover	CPY	$\sqrt{}$ of original variable
Sum of horizontal density (0 to 2.0m)	SHD	$\sqrt{}$ of original variable
Shrub abundance	SHB	$\sqrt{}$ of original variable
Perennial sedge abundance	PSM	$\sqrt{}$ of original variable
Grass abundance	GRS	$\sqrt{}$ of original variable

transformation improved the symmetry of the resulting distributions. Also, the group variances were more stable after transformation, thus further improving the data with respect to the assumption of groups having the same dispersion. Previously, the group variances were found to be proportional to the group means. Finally, the square-root transformation choice was made because the resulting data were in a scale which had some physical interpretation. Taking the square root of a measurement, which is proportional to an area is equivalent to passing to a variable which is proportional to length.

The first step in the multivariate analysis was to examine the possibility of pooling data across seasons within years or across years. Also, it was desirable to see whether data could be combined across dawn and dusk surveys.

Results from preliminary analyses indicated similarities in terms of the importance of certain variables separating species' locations across seasons and years. However, subtle differences in patterns and trends within seasons and across years, due to manipulation of species' population levels, suggested the importance of examining the results on a seasonal basis for each year. DFA results for dawn and dusk surveys were very similar thus, for convenience, data were pooled for these two activity periods.

The inclusion of the variable GRS (grass abundance) posed a number of problems in the analyses. The large standardized coefficient of GRS suggested that GRS was primarily responsible for the separation of quokka feeding locations from the other species, particularly during the seasons summer and autumn. Over the study period the factor weighting on GRS was attributable to the increasing abundance of the perennial grass *Cynodon dactylon*, present in the quokka sites only. The perennial grasses

Stipa spp. and *Danthonia occidentalis*, present across the rest of the reserve, tended to be heavily grazed and difficult to detect during the late summer vegetation surveys. Thus, perennial grass presence within the quokka feeding areas was artificially high compared with the other species' feeding locations. It is therefore suggested that the importance of GRS in the analyses is an artifact. Quokkas are present in areas where perennial grass is abundant, however they are not actively selecting feeding areas on the basis of this grass dominance.

The presence of annual grass species in macropod diets during the seasons summer and autumn (see Chapter 6) further complicated the use of GRS as a variable in the examination of species' preferred feeding locations. During the vegetation surveys annual grass species' presence was recorded, on the basis of phenological growth stage and greeness of the leaves. During the late summer surveys these species, being greater than 90% dry, were considered dead and thus omitted from the data matrix.

For the above reasons, it was decided to discard the variable GRS from the analyses. Sites which reflect the importance of grass cover in species' feeding locations may be interpreted from the remaining variables. Grass cover predominates in open sites surrounding Banganup Lake and the swamps, that is, the *Aira spp/ Vulpia spp.* vegetation association (see Section 4.3.2). Sites within this association may be summarized, in terms of the measured habitat variables, as having: low tree stem density; very low vegetation horizontal density; very low shrub abundance; variable perennial sedge abundance and variable canopy cover.

For subsequent DFA's, discriminant functions were extracted until at least 90% of the among-species variance was accounted for. In all cases, the first two discriminant functions accounted for more than 90% of variance extracted.

5.3.2.1 Habitat variable preferences in species' feeding activity areas

The distribution of species' centroids (niche centres) and their 95% confidence circles are plotted for the first two discriminant functions for all seasons during the study period (see Figures 5.2 to 5.12). Variable patterns (standardized weights), communalities and the extracted percentage of among-species variance are presented for the discriminant functions (see Tables 5.6 to 5.16).

In terms of the variables measured, a general pattern of habitat selection or niche occupancy, across seasons and years, is evident from the analyses. The distances between the species centroids and their locations, relative to the two axes, indicate the extent and nature of species separation.

The primary dimension, separates quokka feeding activity areas from the remaining study species. This dimension may be interpreted as a specific site type, reflecting structural and horizontal density components of vegetation, rather than a gradient. Quokka feeding activity areas are principally located in association with areas of high canopy cover with a very dense horizontal component of vegetation. These variables reflect the vegetation type and structure along the eastern and north-eastern edges of Banganup Lake, where the sedge, *Baumea articulata* forms a dense continuous thicket. The feeding activity site preferences of the other study species are variably clustered distant from those of the quokka and permit no further satisfactory interpretation on this primary dimension.

The second discriminant function suggests that separation of species' feeding site preferences is based on floristic-type habitat variables. The discriminant function represents a gradient from sites of low shrub abundance, low horizontal density and where canopy cover and perennial sedge abundance are variable. This combination of variables reflects the open sites where grass species dominate (see Section 5.3.3). At the far end of the gradient woodland sites of high shrub abundance are located. Species' separation indicates euro feeding activity areas were positively associated with grass dominated sites while, the woodland sites of high shrub abundance were associated with brush wallaby and western grey kangaroo feeding sites. Quokka feeding sites were located intermediate along the gradient.

Confidence circles proved inappropriate as measures of species' niche widths. The confidence circles tended to be inversely proportional to the number of sightings of each species. However, calculation of F statistics, using Mahalanobis distances, indicated two significant trends in the extent of separation between species' centroids, when results were examined seasonally within and across years.

Results suggested a seasonal cycle in species' centroid separation. Separation was greatest between all species during spring and at a minimum during autumn. Reduction in the brush wallaby, western grey kangaroo and euro population levels caused niche separation, between these species, to increase for each season over successive years. Niche separation was greatest between the quokka and the other study species. The extent of separation increased over the years 1982 and 1983 but decreased in 1984. The reduction in niche separation between quokkas and the other species in 1984 may be attributable to the introduction of an additional 60 quokkas onto the reserve. These animals selected feeding areas along the north-eastern edge of Banganup Lake, sites not used to any great extent by quokkas previously.

Figure 5.2 Summer 1982, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.

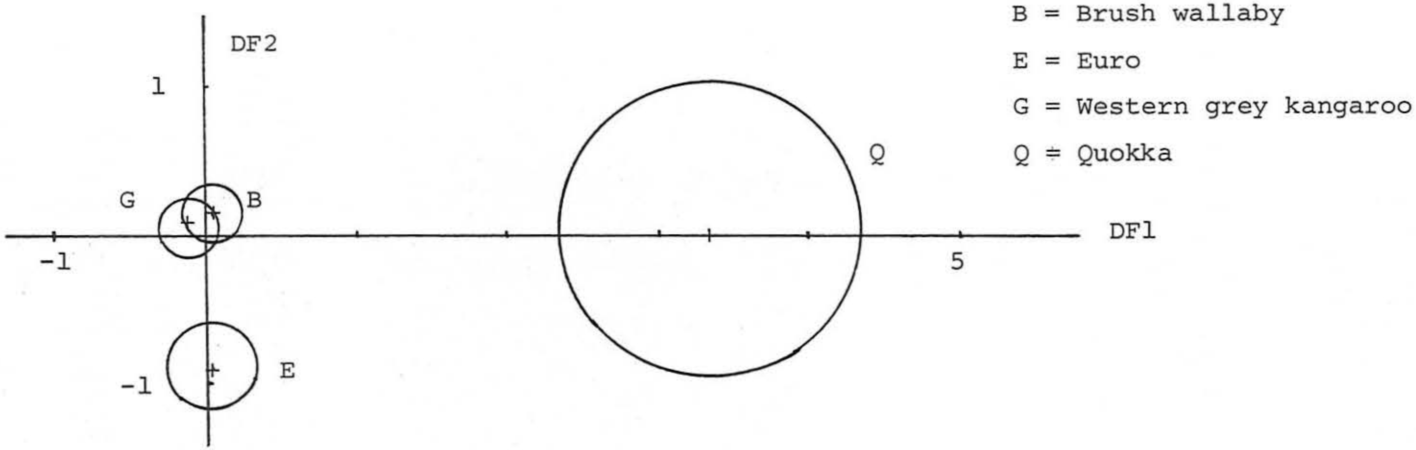


Table 5.6 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

	DISCRIMINANT FUNCTIONS		COMMUNALITIES
VARIABLES	DF1	DF2	
DBH	-0.3506	0.0012	0.1229
CPY	0.3753	-0.0030	0.1409
SHD	0.8891	0.0064	0.7905
SHB	-0.8954	0.0152	0.8020
PSM	0.5314	-0.0018	0.2824
% among-species variance extracted	60	30	

Figure 5.3 Autumn 1982, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.

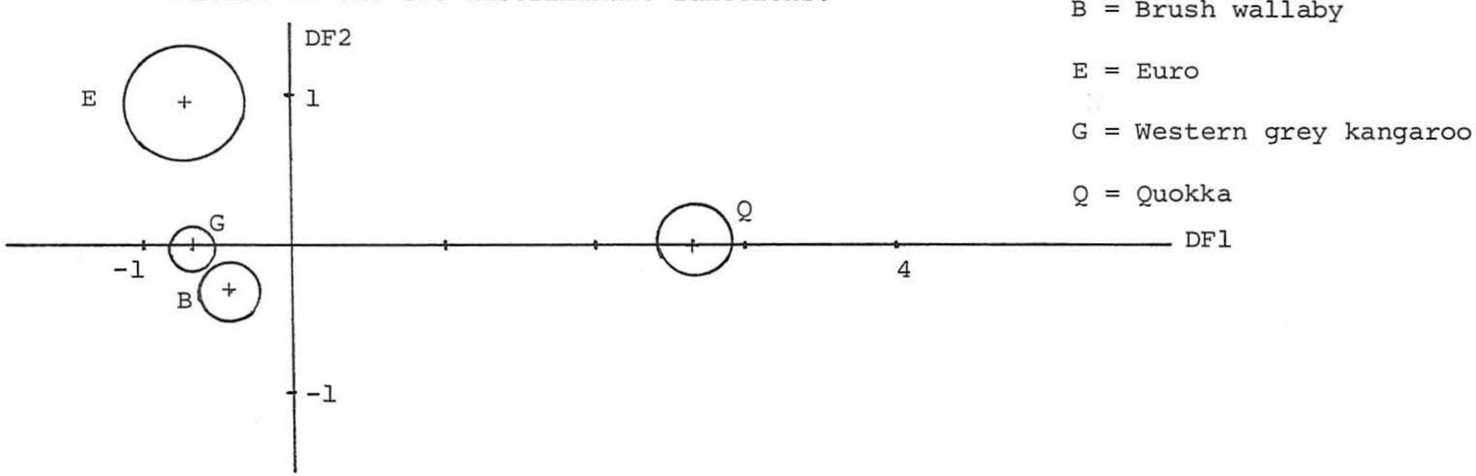


Table 5.7 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

VARIABLES	DISCRIMINANT FUNCTIONS		COMMUNALITIES
	DF1	DF2	
DBH	-0.6584	-0.0032	0.4335
CPY	0.8111	0.0272	0.6586
SHD	0.8882	-0.0119	0.7890
SHB	-0.7034	-0.0005	0.4948
PSM	-0.1505	-0.0070	0.0227
% among -species variance extracted	92	6	

Figure 5.4 Spring 1982, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.

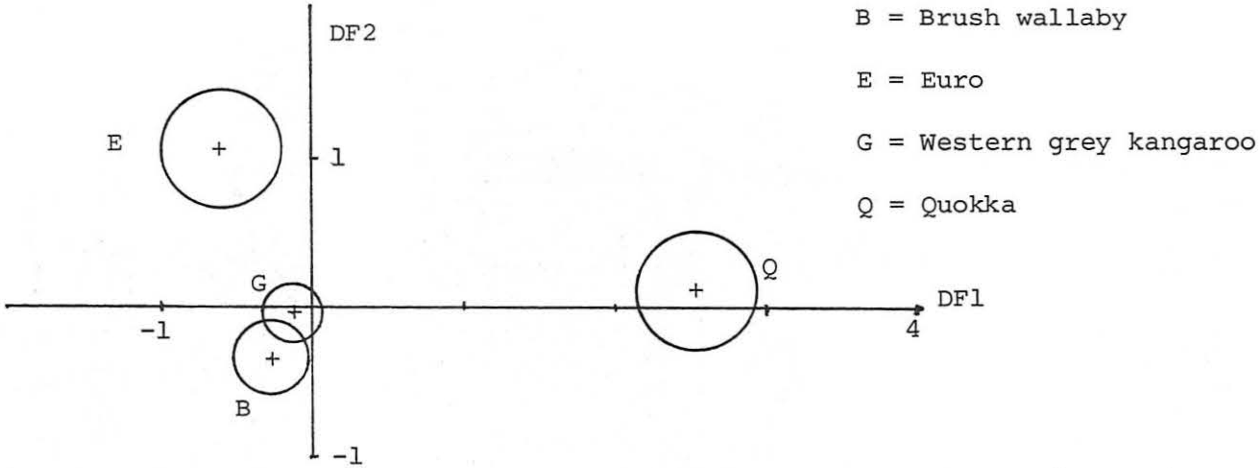


Table 5.8 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

	DISCRIMINANT FUNCTIONS		COMMUNALITIES
VARIABLES	DF1	DF2	
DBH	-0.6288	-0.0018	0.3954
CPY	0.9410	0.0100	0.8856
SHD	0.9250	-0.0088	0.8557
SHB	-0.7458	-0.0171	0.5565
PSM	0.2483	0.0080	0.0617
% among-species variance extracted	77	19	

Figure 5.5 Summer 1983, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.

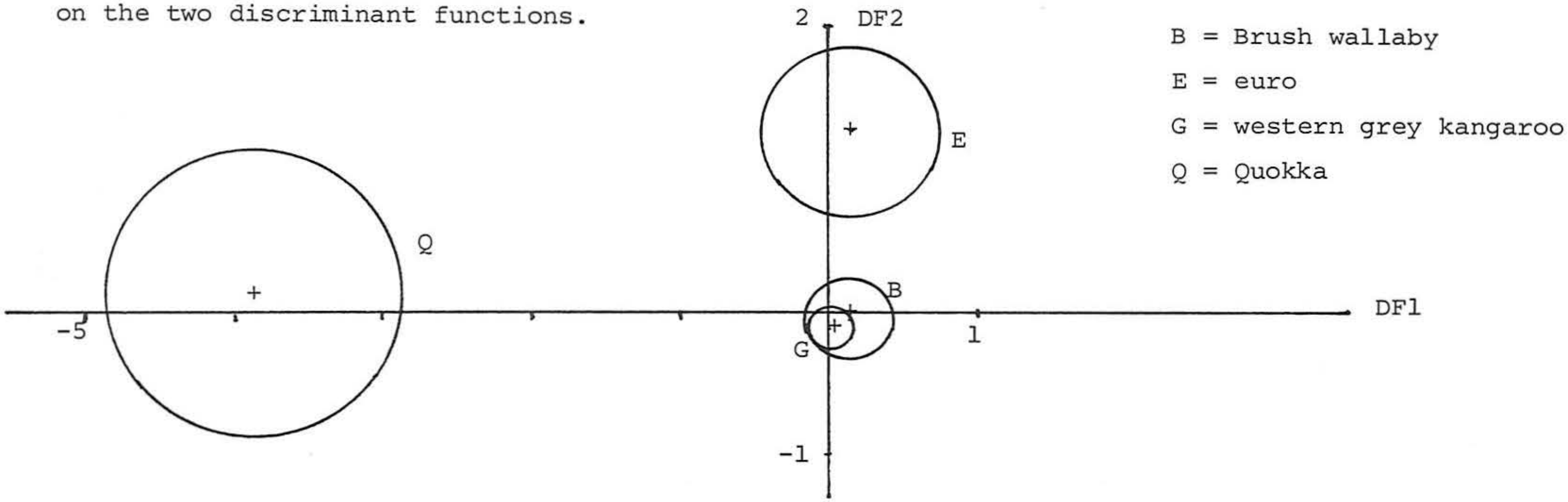


Table 5.9 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

VARIABLES	DISCRIMINANT FUNCTIONS DF1	DF2	COMMUNALITIES
DBH	0.2342	0.0017	0.0549
CPY	-0.8604	-0.0376	0.7417
SHD	-0.2463	-0.0027	0.0607
SHB	0.3469	-0.0250	0.1210
PSM	-0.3804	0.0020	0.1447
% among-species variance extracted	71	26	

Figure 5.6 Autumn 1983, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.

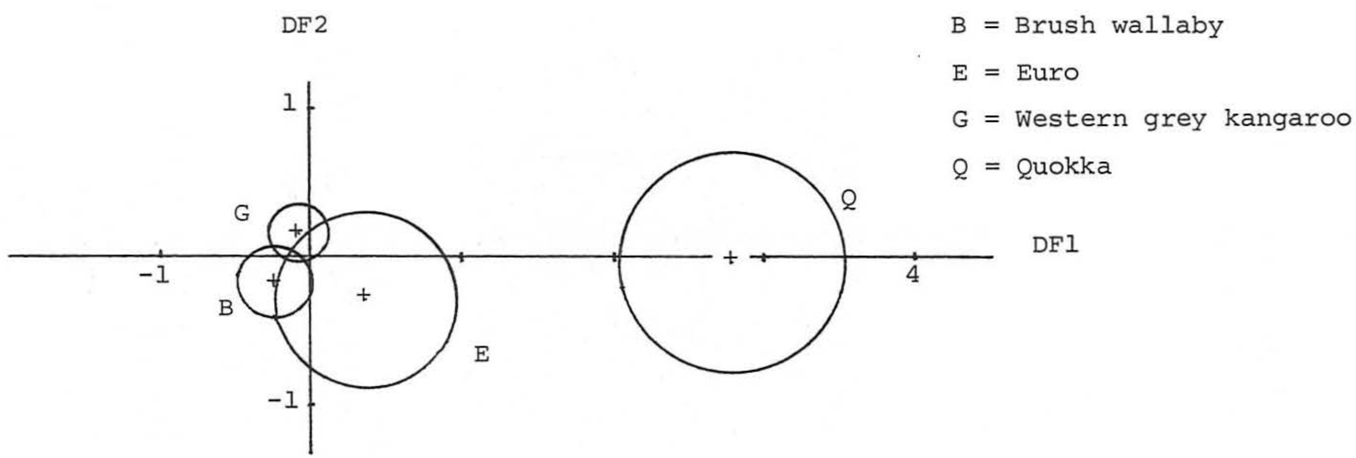


Table 5.10 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

VARIABLES	DISCRIMINANT FUNCTIONS DF1	DF2	COMMUNALITIES
DBH	-0.2419	0.0027	0.0585
CPY	0.7531	0.0058	0.5672
SHD	0.5395	0.0051	0.2911
SHB	-0.4472	0.0321	0.2010
PSM	0.4296	-0.0007	0.1846
% among -species variance extracted	92	7	

Figure 5. 7 Winter 1983, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.

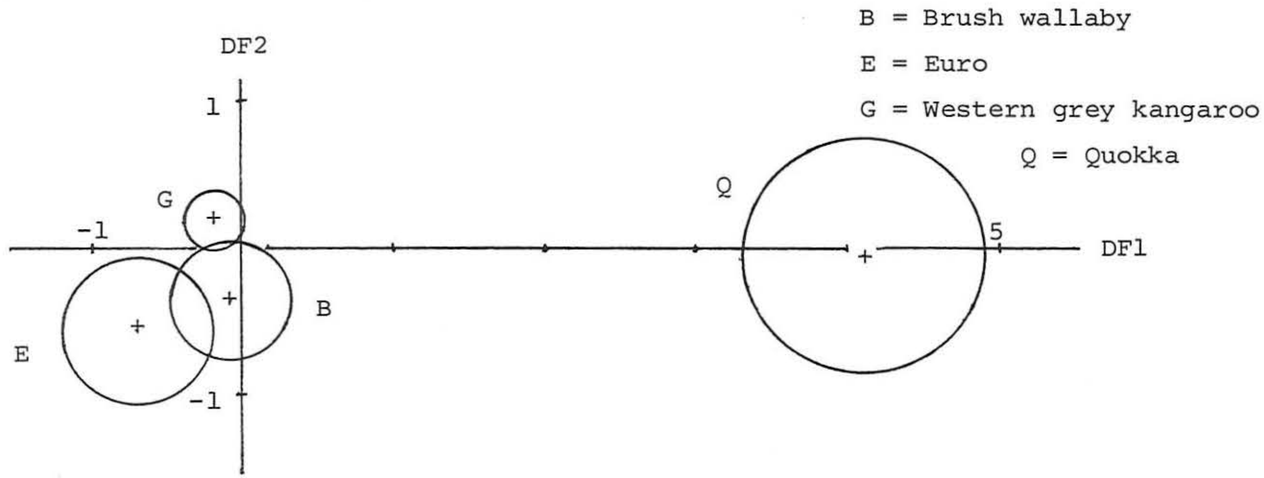


Table 5.11 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

VARIABLES	DISCRIMINANT FUNCTIONS DF1	DF2	COMMUNALITIES
DBH	-0.4364	-0.0011	0.1904
CPY	0.9825	0.0422	0.9671
SHD	0.8113	0.0049	0.6582
SHB	-0.7395	0.0424	0.5487
PSM	0.4477	-0.0006	0.2004
% among-species variance extracted	91	8	

Figure 5.8 Spring 1983, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.

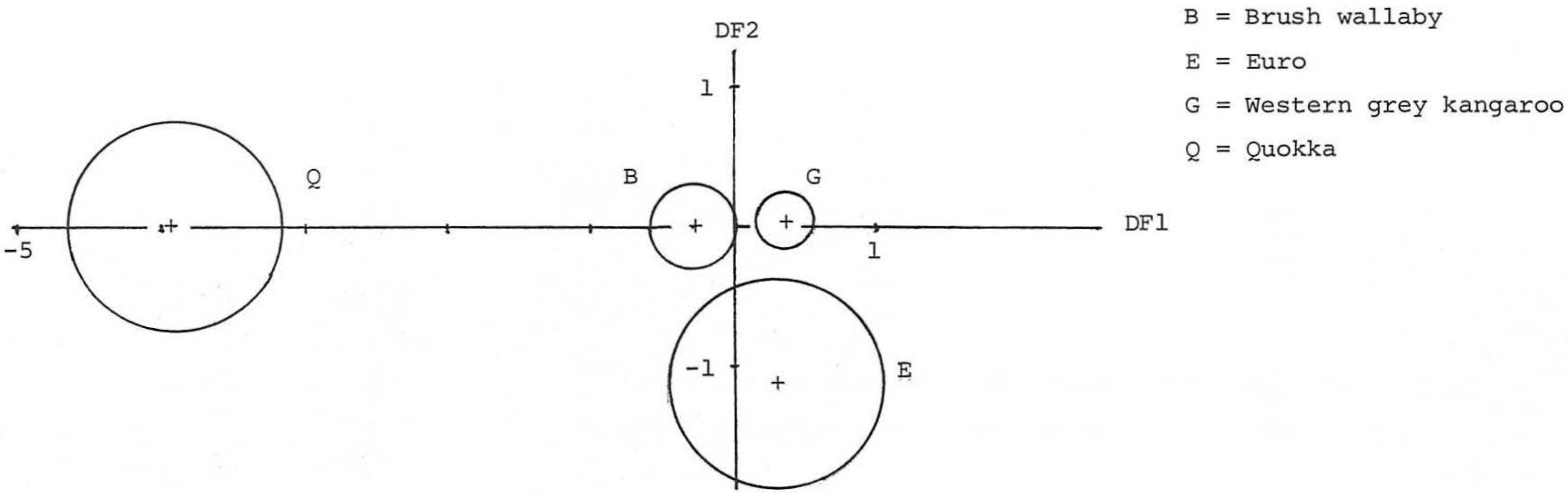
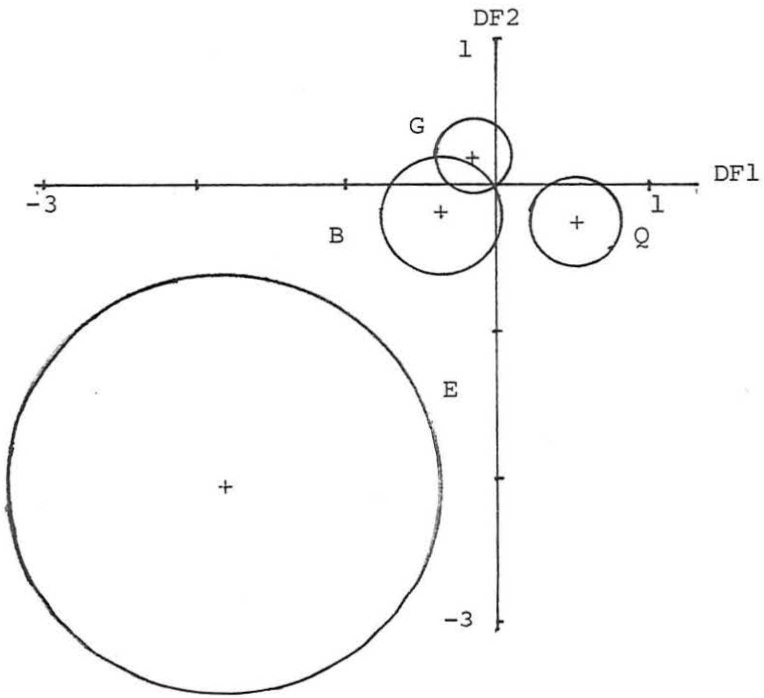


Table 5.12 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

VARIABLES	DISCRIMINANT FUNCTIONS DF1	DF2	COMMUNALITIES
DBH	-0.2146	0.0038	0.0461
CPY	-0.3073	-0.0136	0.0946
SHD	-0.4897	0.0259	0.2405
SHB	0.8091	0.0232	0.6552
PSM	-0.6518	0.0220	0.4253
% among-species variance extracted	94	6	

Figure 5.9 Summer 1984, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.



B = Brush wallaby

E = Euro

G = Western grey kangaroo

Q = Quokka

Table 5.13 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

	DISCRIMINANT FUNCTIONS		COMMUNALITIES
VARIABLE	DF1	DF2	
DBH	0.0271	0.0032	0.0007
CPY	0.4096	-0.0199	0.1682
SHD	0.7794	0.0050	0.6075
SHB	0.0809	0.0365	0.0079
PSM	-0.3925	-0.0173	0.1544
% among-species variance extracted	60	32	

Figure 5.10 Autumn 1984, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.

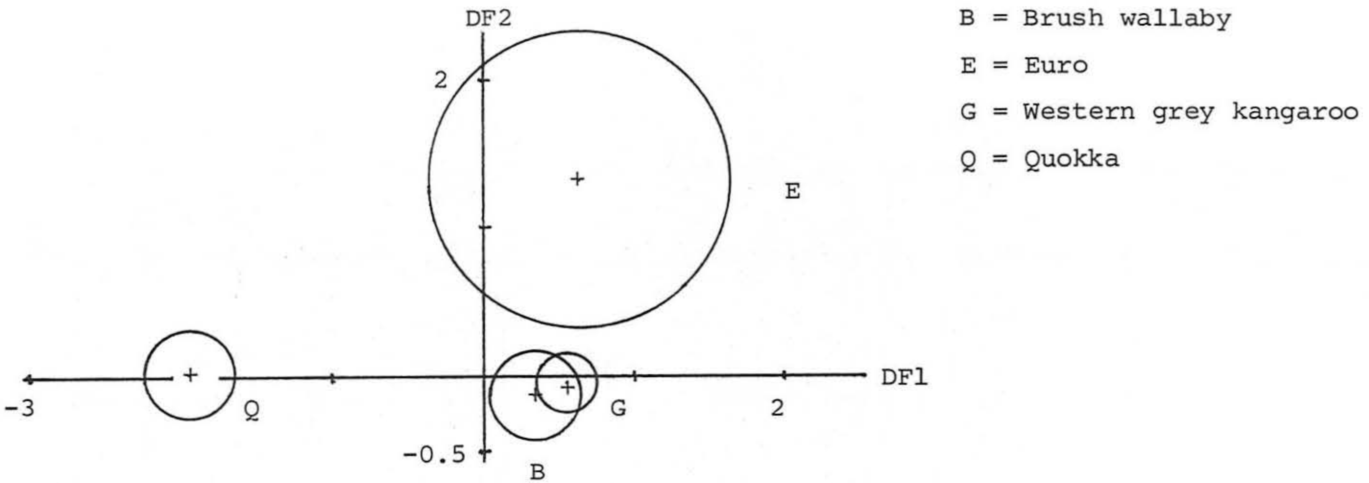


Table 5.14 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

VARIABLE	DISCRIMINANT FUNCTION DF1	DF2	COMMUNALITIES
DBH	0.2020	0.0015	0.0408
CPY	-0.7796	0.0199	0.6082
SHD	-0.7607	-0.0128	0.5788
SHB	0.5527	-0.0272	0.3062
PSM	-0.5845	0.0043	0.3417
% among-species variance extracted	88	8	

Figure 5.11 Winter 1984, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions

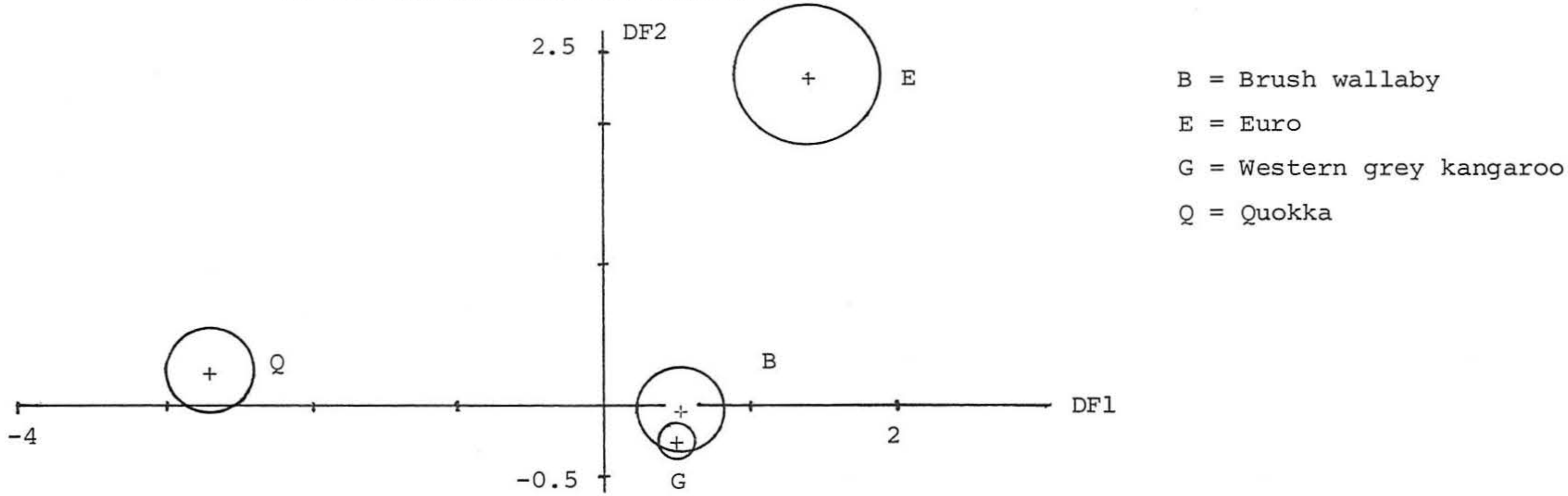


Table 5.15 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

	DISCRIMINANT FUNCTIONS		COMMUNALITIES
VARIABLES	DF1	DF2	
DBH	0.3649	-0.0021	0.1332
CPY	-0.9181	0.0052	0.8429
SHD	-0.6831	-0.0046	0.4666
SHB	0.5813	-0.0265	0.3386
PSM	-0.8279	-0.0153	0.6857
% among-species variance extracted	79	21	

Figure 5.12 Spring 1984, a two-dimensional graph of species' centroid locations and 95% confidence circles on the two discriminant functions.

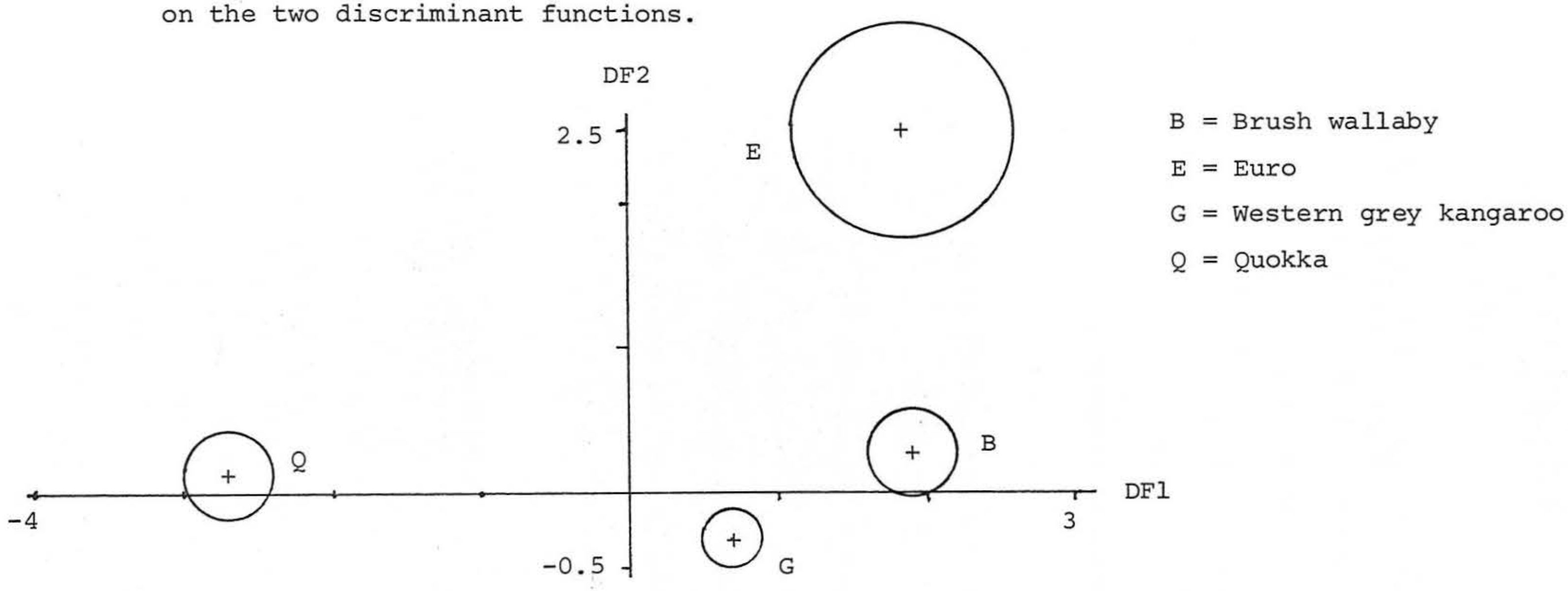


Table 5.16 Variable patterns, communalities and extracted % of among-species variance for the discriminant functions.

VARIABLES	DISCRIMINANT FUNCTIONS DF1	DF2	COMMUNALITIES
DBH	0.2297	-0.0018	0.0528
CPY	-0.5314	0.0144	0.2826
SHD	-0.7602	-0.0167	0.5782
SHB	0.6572	-0.0305	0.4328
PSM	-0.5770	0.0127	0.3331
% among-species variance extracted	88	10	

5.3.2.2 Habitat variable preferences in species' sheltering sites

DFA of variable preferences for brush wallaby, euro and western grey kangaroo shelter sites proved difficult. Preliminary analyses indicated little difference in variable selection by the three species within and across seasons. Shelter areas were selected on the basis of shrub abundance and canopy cover. However, insufficient observations of sheltering animals, particularly of euros and brush wallabies in the later stages of the study when their respective population levels were low, prevented detailed analysis.

In the absence of an adequate data base for detailed DFA over the study period, shelter site preferences are inferred from the preliminary analyses and personal observations. Brush wallaby and western grey kangaroos selected shelter sites, within their feeding activity areas, based on the variables shrub abundance and canopy cover. Euros selected areas for shelter that are adjacent, or in close proximity, to their feeding site preferences of open, grass-dominated areas. These shelter sites reflected those of the other two species, being woodland with a dominant shrub understorey. Quokka shelter areas have been described earlier (see Section 5.2.3).

5.3.3 Macropod preference for post-burn regenerating areas

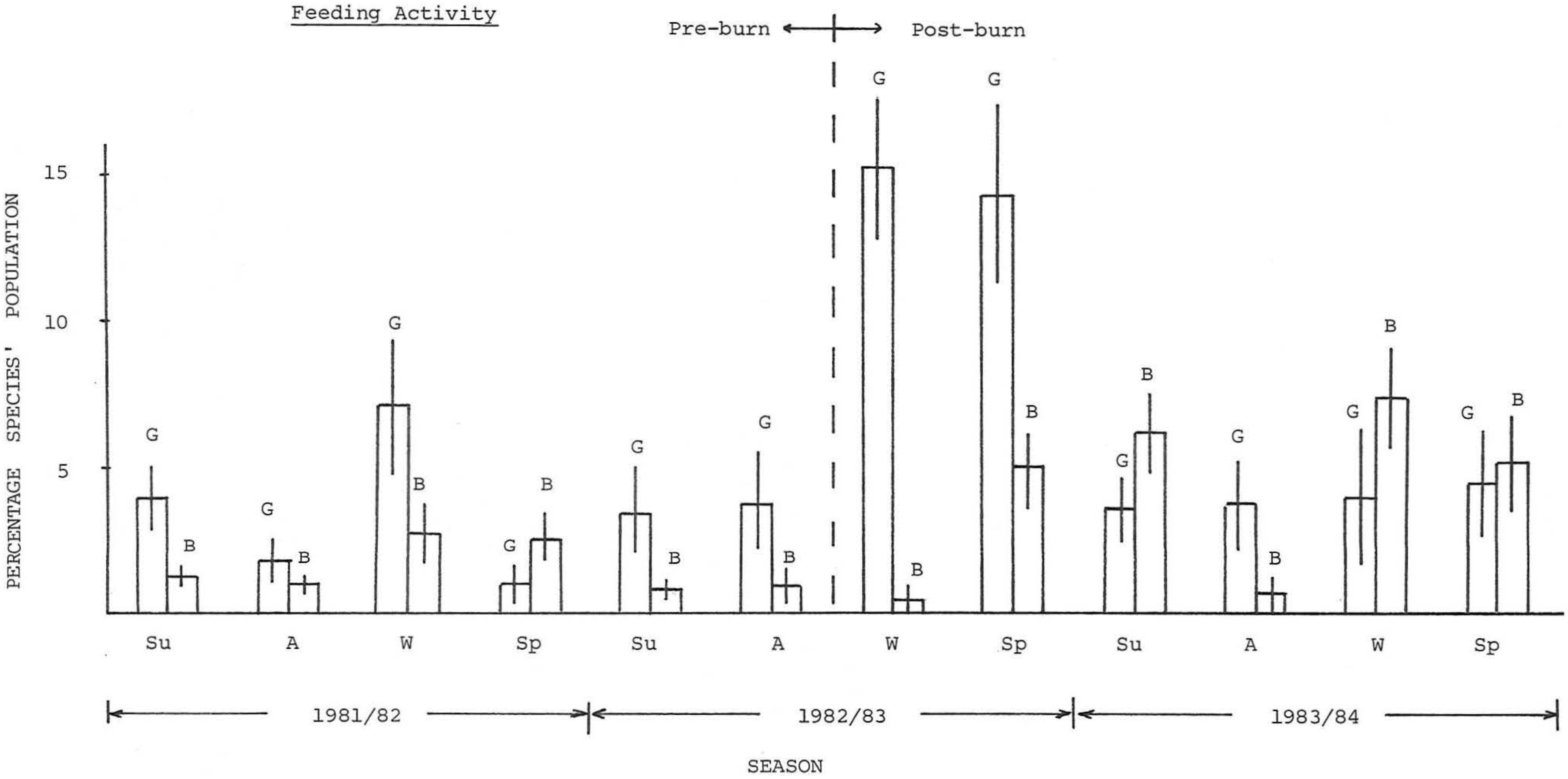
Macropod preference for post-burn regenerating areas was inferred from observed changes in the proportion of species' population levels therein, before and after fire. An area of approximately 10ha (see Figure 3.1), located within a section of the *Hibbertia hypericoides* Association, was selected for a hot, late autumn burn in 1983.

Western grey kangaroos and brush wallabies were the only macropod species observed to utilize the area before and after the fire. The seasonal percentage of each species' population level ($\bar{x} \pm$ s.e.) within the area during feeding activity periods, is shown (see Figure 5.13). The seasonal percentage of each species' population level ($\bar{x} \pm$ s.e.) observed sheltering within the area is shown in Figure 5.14.

Prior to the burn the proportion of the western grey kangaroo population using the area for feeding and/or sheltering activity, tended to be variable within and across seasons. Many individual animals were observed within the area however, the presence of any particular individual tended to be periodic. Such evidence suggests that the area formed a part of a much larger home range for many western grey kangaroos. The proportion of the brush wallaby population feeding and/or sheltering within the area was less variable than for the western grey kangaroo population. The majority of these animals were regularly sighted both feeding and sheltering within the area and were considered residents of the area.

A large increase was observed in the percentage of the western grey kangaroo population feeding on the germinating/regenerating plant species post-burn. Following spring, this percentage declined to a relatively constant level. Although the percentage of the species' population within the burnt area

Figure 5.13 Seasonal percentage of species' populations ($\bar{x} \pm$ s.e.) within the burn area.

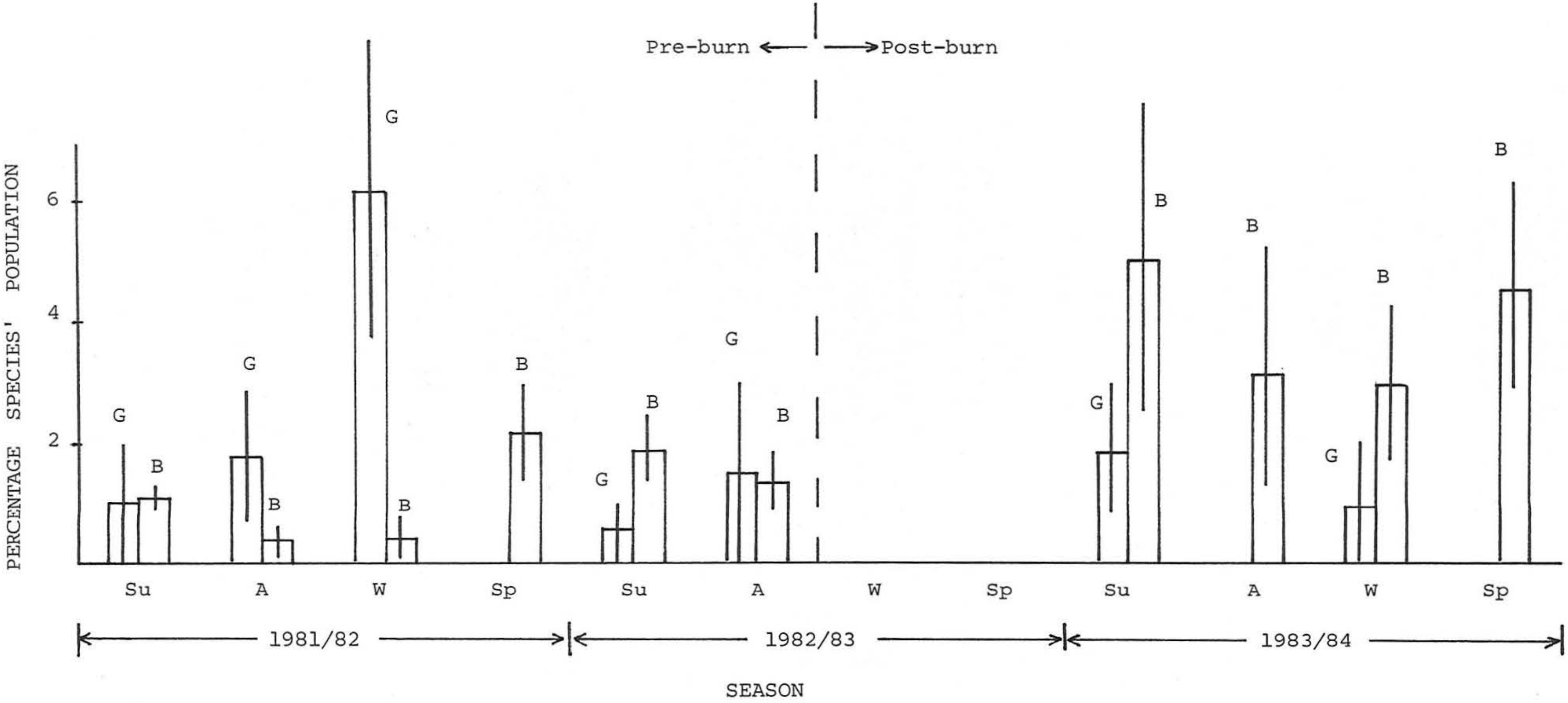


Su = Summer, A = Autumn, W = Winter, Sp = Spring.

G = Western grey kangaroo, B = Brush wallaby

Figure 5.14 Seasonal percentage of species' populations ($\bar{x} \pm$ s.e.) within the burn area.

Sheltering Activity



Su = Summer, A = Autumn, W = Winter, Sp = Spring.

G = Western grey kangaroo, B = Brush wallaby.

was relatively constant, individual use of the area continued to fluctuate. The percentage of the species' population observed sheltering in the area continued to vary within and across seasons. The percentage of the brush wallaby population observed feeding within the area declined immediately post-burn however, it remained relatively constant from spring onwards. The proportion of the species' population observed sheltering within the area was relatively constant from summer post-burn onwards. The percentage of the brush wallaby population feeding and sheltering within the post-burn area was greater than for the pre-burn surveys. However, the number of individual animals present in the area remained constant. Thus, the increase in the percentage of the species' population, within the post-burn area, was due to heavy mortality of the brush wallaby population experienced across the rest of the reserve, rather than a greater number of animals present.

5.4 Discussion

Herbivore overpopulation, within the reserve, is believed primarily responsible for the heavy mortality observed in the euro, brush wallaby and quokka populations. Regulation of population density, through dispersal was prevented by erection of the boundary fence. Control of predators also enabled populations of certain species to increase. The increase in animal density locally created browsing and grazing in excess of the vegetation's rate of renewal. Thus, the herbivore density reached a peak and eventually crashed because of the reduced food availability.

There was a distinct seasonal influence on macropod mortality. Natural mortality in western grey kangaroos and the dramatic declines in the other study species' population levels occurred during late autumn/early winter periods. Main (1986) summarized the nature of the mediterranean seasonal cycle as perceived by ruminant and ruminant-like animals:-

1) A long decline in the quality of the environment through summer. During this period the quality of food declines, water becomes scarce, salt loading and dehydration may be present and heat loading may be intense.
2) As summer progresses into autumn, temperatures decline, heat loading is less intense but the quality of diet and availability of water are usually still inadequate.
3) An abrupt transition from summer/autumn drought to winter wet. The intensity of the transition is governed by the abruptness of the break in the season and the intensity and duration of the preceding drought. Water is now abundant but food quality does not immediately improve and cold, windy conditions pose new problems.
4) As spring approaches a relatively short (shorter than

the summer decline) improvement in environmental quality occurs, culminating in spring. During spring the environment approximates to optimum conditions, with a gradual turn-over from spring to summer conditions.

Thus, perturbations to which herbivores respond are firstly, those within seasons, for example, temperature fluctuations, water shortage and the change in the nutrient status of forage throughout the season. Secondly, they are forced to respond to the particularly abrupt and massive perturbation consequent upon the winter break of season following the summer/autumn drought (*Op. cit.*). Results of studies measuring water and electrolyte metabolism in populations of tammar wallabies (Bakker, Bradshaw and Main, 1982) and quokkas (Miller and Bradshaw, 1979) confirm a number of other studies, indicating that the period of maximum environmental stress coincides with the change at the end of the hot, dry season to the cold, wet winter.

On the reserve, the environment (in the form of plants providing nitrogen and energy during the summer drought) was allowed to deteriorate. Thus it is reasonable to assume that inadequacies in the diet accentuated the seasonal nutritional stress. Macropod resilience to within and across seasons change in the quality of forage through their symbiotic relationship with a complex of protistan, fungal and bacterial symbionts in their foregut was adversely affected. Thus, urea recycling (Brown and Main, 1967; Kinnear and Main, 1975), in response to inadequate dietary nitrogen would have been limited because of inadequate dietary energy. The inadequacies in the diet would have led to weight loss and malnutrition. Thus, the poor condition of animals at the onset of the cold, wet winter, when environmental stress is at a maximum, resulted in the observed population crashes.

Interpretation of results from the discriminant function analyses will be approached from a broad, holistic viewpoint. Data were recorded quantitatively however, subjective assessment of certain measures, and the inclusion of the variable SDN, which was recorded as a graded, single digit "density score", suggest that it is inappropriate to place a rigorous statistical interpretation on the results of the study. The technique does however provide a valid approach to understanding and defining the nature and strength of those factors involved in macropodid species/habitat relationships on the reserve relative to the dimensionality of the overall community niche.

Macropodid species/habitat relationships and the pattern of separation suggested here is specific to the study area. Erection of the boundary fence, which restricted animal movement and the limited types of habitat variables for which animals could select would lead to niche compression and increased niche overlap. The degree of separation observed would also be restricted by the exclusion of data from the burnt site.

The results of species' spatial distributions indicated habitat variable combinations reflecting three habitat types were responsible for species' separation within the community niche. The primary DFA dimension, which separated quokka distributions from the other species, represented a specific site type reflecting the importance of the vegetation structural components: vegetation horizontal density and canopy cover. Quokka feeding sites were restricted to areas in close proximity to the dense thickets of *Baumea articulata* surrounding Banganup Lake. These thickets provided the only substantial area of dense continuous cover on the reserve.

On Rottnest Island, where predation pressure on quokkas may be considered negligible, Kitchener (1972) found quokkas to be aggregated about clumps of vegetation that provided dense cover. Shelter was considered important for protection from climatic conditions and the operation of certain social organization factors. The above study revealed that quokkas had a well-organized society, composed of family groups. Adult males were dominant and the male dominance hierarchy was age based and relatively stable. Aggression was most frequently witnessed between adult males in conjunction with an adult male's defense of its shelter site. The shelter area defended by males was approximately 2m in diameter. Away from shelter, males were seen feeding side by side without any obvious aggression. A number of other studies on Rottnest Island and personal observations on the reserve suggest quokkas often congregate on preferred feeding areas without obvious aggression.

It is therefore reasonable to suggest that quokka habitat preferences on the reserve reflect firstly, sites where dense continuous cover (the *Baumea articulata* Association, see Section 4.3.2) provides shelter from the vagaries of weather, minimizes aggressive encounters between adult males and thus, promotes stability for social organization factors to operate within the family group. Secondly, the habitat preferences reflect feeding sites adjacent to shelter (the *Astartae fascicularis/ Hypocalymma angustifolium* Association, see Section 4.3.2), where community factors may operate. These findings have important management implications if the establishment of a quokka colony, on the reserve, is to be successful in the long term, and will be discussed in detail later (see Chapter 7, General Discussion).

Euro habitat preferences were separated from those of brush wallabies and western grey kangaroos along the secondary DFA dimension. Along this axis, separation was based predominately on habitat variables reflecting site dominant floristic types. The open, grass-dominated sites were preferred by the euros as feeding activity areas, while the woodland sites of high shrub abundance were preferred by brush wallabies and western grey kangaroos.

DFA indicates co-variance between species' presence and particular habitat variables however, it does not identify specific components of the environment for which the animals are actively selecting. Thus, species' separations on the basis of floristic types may be interpreted as reflecting the importance of certain forage classes in determining species' feeding site preferences. The floristic types, on the other hand, may correspond to site specific vegetation associations, within which fine divisions of preferred dietary resources are responsible for niche separation. Clarification of the above relationship will be conducted following examination of species' diet preferences (see Chapter 6).

Distinct, interpretable seasonal changes in species' habitat use were not evident from the DFA results. However, the degree of separation between species' niche centroids followed a seasonal cycle both in years before and after reduction of grazing pressure intensity. Although it was not possible to measure niche widths, it is suggested that the seasonal changes in species' separation were a result of an expansion, rather than change, in species' feeding site preferences. Niche separation was lowest in autumn, when seasonal nutritional stress (discussed earlier) was greatest. It is suggested that the decline in forage nutritional status, during this period, caused certain species to increase their feeding site preferences in order to maintain their nutritional requirements. Analysis of species' dietary preferences (see Chapter 6) indicated the increased importance on all diets, of certain plant species during autumn. These plant species were found predominately in areas surrounding the lakes and swamps and in the open, grass dominated sites; feeding site preferences of the quokka and euro respectively. Therefore, during the seasonal periods affecting reduced food resource availability and/or declines in the nutritional status of certain preferred foods, brush wallabies and western grey kangaroos expanded their feeding areas to include those of the quokka and euro.

Inability to quantify niche widths made it difficult to interpret changes in niche separation for respective seasons over successive years. Overpopulation, leading to reduced food resource availability, would have caused species to expand their feeding activity areas within seasons in order to maintain nutritional requirements. Such a situation would have resulted in increased niche overlap and reduced species' niche separation. Reduction in grazing pressure, due to decreases in species' population levels, resulted in increases in plant species richness, abundance and frequency both within and across vegetation associations (see Chapter 4). This increased food resource availability would have enabled the macropod species to be more selective in their choice of dietary items and thus preferred feeding activity areas. It is therefore proposed that within the broadly defined species' habitat preferences increased resource availability enabled the reduced population levels to be more selective for specific components. This resulted in the increased species' niche separation observed for respective seasons over consecutive years.

Fire induced regenerating areas had a considerable impact on certain species' habitat preferences. Main (1986) suggests that there are two opposing consequences of fire with respect to macropod populations:-

Consequence a) The destruction of shelter and consequent exposure to environmental extremes.

Consequence b) The provision of improved palatable and nutritious plant growth.

A large increase in the proportion of the western grey kangaroo population was observed feeding within the designated burn area during the winter and spring months immediately following fire. These large, mobile animals sheltered in non-burnt areas across the reserve and aggregated on the post-burn area during feeding activity periods as a consequence of b (above). As such, this species exerted intensive grazing pressure on many of the regenerating/germinating plant species and is primarily responsible for the significant differences observed between exclosed and non-exclosed burnt areas (see Section 4.3.3).

The response of the brush wallaby, the only other macropod species present in the burnt area, differed from that of the western grey kangaroo. Large scale movement of this species into the post-burn area did not occur. Animals present in the pre-burn area were observed in adjacent areas following the fire. As such these animals, considered residents of the area, were initially responding to consequence (a). Feeding and sheltering activity resumed in the burn site during the spring and summer months. The low natural mortality of these animals compared with the general decline in the population across the rest of the reserve suggests a response to consequence (b), that is, following fire the provision of increased, palatable and nutritious plant growth improved survival of these animals. Similar results were obtained by Christensen (1980); woylie and tammar populations (territorial species), feeding on post-burn regenerating areas were significantly heavier than animals feeding outside these areas.

The importance of specific fire regimes to plant communities has been discussed earlier (see Chapter 3). Changes in feeding activity area preferences of western grey kangaroos and increased survival of resident brush wallabies highlight the value of fire induced regenerating areas, as sites providing palatable and nutritious plant growth. However, the resulting intense grazing pressure was of serious consequence to the regenerating plant community. Thus, if fire is to be used as an effective, environmental management technique for the long-term conservation of both flora and fauna communities the problem of overgrazing on regenerating growth must be considered. This factor is discussed further in the final chapter.

CHAPTER 6

SPECIES' FEEDING PATTERNS

6.1 Introduction

Ecological separation within multi-species herbivore communities may be based on; differences in the habitats in which they feed (examined in the previous chapter), differences in feeding strategies or, a combination of the two (Gwynne and Bell, 1968; Geist, 1974; Jarman, 1974; Schwartz and Ellis, 1981; Hanley, 1982). Contemporary theory, relating to body size, mouth morphology, metabolic requirements and rumen physiological considerations, suggests that differences in feeding strategy are more likely between species which differ in body size. As the metabolic needs of an animal are a function of their body weight raised to the power of 0.75, the larger the animal the lower the metabolic needs per unit body weight. Thus, large herbivores are able to utilize diets which are nutritionally inadequate for smaller species. Larger species tend to be bulk or roughage feeders, feeding on diets of lower nutritional value compared with the diets of smaller species which feed principally on foods of high nutritional quality (Bell, 1971; Hofmann and Stewart, 1972; Jarman, 1974; Hanley, 1982).

The digestive system of macropodid species is considered ruminant-like(Moir *et al.*,1956; Brown, 1964; Brown and Main, 1967; Kinnear and Main, 1979). Most studies examining macropodid diets have been conducted in arid, semi-arid environments and the vast majority of these dietary studies have focused on the larger kangaroo species. Such studies have shown red kangaroos, euros and eastern grey kangaroos to be almost exclusively grazers. Their diets consist of a high proportion of grass species with a variable dicotyledon component depending on seasonal conditions and pasture composition (Kirkpatrick, 1965; Griffiths and Barker, 1966; Storr, 1968).

The above studies were conducted in open grasslands where dicotyledonous species generally constituted a minor vegetation component. A study of western grey kangaroos in a woodland habitat indicated the dietary importance of a number of shrubby dicotyledons, particularly legume species (Halford *et al.*, 1984).

Dietary studies of smaller macropodid species have received scant attention within scientific literature. Examination of quokka diets on Rottnest Island indicated differences in the forage classes consumed and the plant species composition of the forage classes in different areas on the Island (Storr, 1964). These differences were explained partly by reference to the relative availability of the plants and partly by the water requirements of the animals in different habitats.

Knowledge of the composition of diets selected by wildlife is necessary for an understanding of their forage needs and the underlying basis of competitive interactions between them. In this chapter the plant species composition of the diets of the four macropodid species on the reserve are determined. The factors responsible for the separation of the species' feeding niches and the degree of separation of each niche are also examined.

6.2 Method

6.2.1 Faecal analysis

Procedures used to evaluate the botanical composition of a grazing animal's diet have included direct observation of the animal while feeding, utilization techniques, stomach analysis, fistula techniques and faecal analysis. Associated with each of these methods are a number of advantages and disadvantages which have stimulated discussion as to which is most useful in interpreting food habits of large herbivores.

In this study faecal analysis was chosen as the most appropriate method for species' diet analysis. Inability to accurately observe and thus identify plant species on which the animals were feeding, not wishing to disturb animal's movement or their normal habits and the undesirability of sacrificing large numbers of animals for stomach analysis prevented the use of other techniques.

Faecal analysis is based on the recognition and identification of plant particles which have survived the process of digestion. The principal structurally identifiable component of herbivore faeces consists of fragments of undigestible plant epidermis. Epidermis contains cutin-impregnated cell walls which render it, to a large extent, resistant to the action of digestive enzymes. The structure and composition of plant cuticle has been described by Skoss (1955). The cell configuration of epidermis is characteristic for each plant species. Thus, it is possible to identify faecal plant fragments with the aid of reference slides prepared from known fresh material. Epidermal cell anatomy and diagnostic characteristics have been reviewed by Metcalfe and Chalk, (1950); Esau, (1962); Metcalfe, (1960); Storr, (1961) and Stevens, (1977).

Faecal analysis has a number of unique advantages as a research tool, these are discussed by Crocker, (1959); Ward, (1970);

Anthony and Smith, (1974); Scotcher, (1979) and are reviewed by Holechek *et al.*, (1982).

Faecal analysis methodology assumes that:

1/. Fragments of ingested plant species are recoverable and identifiable in faecal samples.

2/. Recovery or identification rates of plant fragments are consistently proportional to ingestion rates of plant species and/or plant parts, or that digestion correction factors can be developed to account for differential digestion bias (Dearden *et al.*, 1975, Fitzgerald and Waddington, 1979).

3/. There is a predictable relationship between frequency of occurrence of dietary items in the sample and the weight or density of those items (Sparks and Malechek, 1968).

Ivins, (1960); Ward, (1970) and Dearden *et al.*, (1975) have shown that differences in digestive ability between animals are less than their digestibilities of different plant species. Therefore, assuming that species' diets are not sufficently different to cause differences in their digestive ability, plant species dietary composition can be compared between animals. Several authors have suggested that differential digestibility and discernability of plant species causes certain species, particularly those of thin and fragile epidermis, to be unidentifiable in faeces (Slater and Jones, 1971; Westoby *et al.*, 1976). However, research by Todd and Hansen, (1973); Dearden *et al.*, (1975) and Vavra and Holechek, (1980) has suggested that the discernability of plant species was influenced less by digestion than subsequent unnecessarily harsh preparatory techniques employed during micro-histological analysis. The above authors suggested that digestion may reduce the mean weight of fragments, rather than eliminating the whole fragment.

The major disadvantage of faecal analysis is that preference indicies cannot be accurately assigned because the location where food items were consumed cannot be determined.

6.2.2 Analysis technique

Within the scientific literature a number of material preparation techniques and faecal cuticle analysis methods have been described and are reviewed by Stevens (1977). The method of faecal analysis adopted in this study followed exploratory trials, testing a number of chemical and microbial faecal preparation methods and slide evaluation techniques at L.R.M. Laboratories, CSIRO W.A. Hand - compounded diets, which included a range of species of varying epidermal thicknesses and fragility were fed to penned western grey kangaroos and quokkas. The degree of similarity between the actual and estimated species' composition for each diet was calculated using Kulcyznski's formula (Oosting, 1956). Each estimated species' mean was compared to the actual mean by use of a t-test (Steel and Torrie, 1960). The chosen technique (described below) had a similarity index of 90.5 $\pm$ 4.1 ($\bar{x} \pm$ s.d.) and there were no significant differences ($P < 0.05$) between estimated and actual species' means (Arnold and Algar, unpubl. data).

6.2.2.1 Plant cuticle reference collection preparation

Preparation of plant cuticle reference collections and faecal material followed the method of Fitzgerald (1976) with certain modifications. Macropodid species have been observed to select leaf in preference to other plant parts (Griffiths and Barker, 1966; Ellis *et al.* 1977; Taylor, 1983). Reference cuticles were prepared from 5mm squares of leaf without midrib or leaf margin to allow for easy separation of abaxial and adaxial sections. The fragments were macerated in a mixed solution of 3 parts 50% chromic acid to 2 parts 50% nitric acid in a 1:2 dilution with water.

The material was heated, at 80°C, in a water bath for ten minutes. The fragments were then transferred to water, thoroughly washed, neutralized in a 20% ammonium hydroxide solution and rewashed in water. Any adhering fibre or mesophyll tissue was removed with fine needles. The cleared fragments were then stained for 1h in 1% basic fuchsin. The abaxial and adaxial sections were then washed again, dehydrated and mounted on microscope slides using Kaiser's medium. High power (x 400) and low power (x 100) photomicrographs of both adaxial and abaxial sections, for each plant specimen, were used as the reference collection. In total 160 species were used for the collection.

6.2.2.2 Faecal collection and preparation

Fresh faeces were collected from the four study species on a seasonal basis. Successful application of techniques developed for preparing faecal material for microhistological analysis required faecal samples to be collected immediately following deposition. This ensured the hardened mucus covering had not developed and also avoided problems of species faecal identification.

Faecal samples were collected from individual animals observed during surveys across sex and age classes for the range of habitats used by each species. An attempt to collect ten faecal samples per species per season was made to account for within - species' variation however, fluctuations in certain species populations did not permit attaining predetermined sample sizes in many cases.

Faecal samples were individually frozen prior to storage. The samples were then oven-dried at 60°C for 24h and then ground through a 1mm screen wiley mill.

Individual samples were analysed rather than pooled for the population. No attempt was made to examine differences within species across sexes and age classes because of the difficulties in obtaining adequate sample sizes. Samples were prepared for analysis by soaking in water and then washing through a 212mm sieve. Grinding material through the 1mm sieve and collecting material on the 212mm sieve reduced the possible bias resulting from the inclusion of different sized particles within faecal material presented for analysis.

Approximately 0.5g of faecal material collected on the sieve was transferred to a test tube containing 10ml macerating solution and processed as for the reference cuticle fragments. When ready for analysis, the stained material was deposited on a slide, using a large tipped pipette, and covered with a slip.

6.2.2.3 Slide analysis

Faecal samples were analysed using the procedures of Sparks and Malechek (1968), a widely used faecal analysis method. Twenty systematically located fields were examined per slide for particle frequency. A field was considered to be the area of the slide delineated by a microscope using a 125-power magnification. Each species found in each location was recorded. Only fragments of epidermal tissue (other than hairs) were used as positive evidence of the presence of a particular species at a particular location. The frequency percentages for each species (number of fields that the species occurred in out of 20 fields, multiplied by five) were recorded for each slide. Five slides were analysed per faecal sample as for the majority of workers using this technique. However, Holechek and Vavra (1981) indicated a far greater number of slides are required to be evaluated if the results for minor and trace species are to be accurate. The importance of such species in this dietary study was dubious and thus did not warrant examination of additional slides.

The table developed by Fracker and Brischle (1944) and further verified by Johnson (1982) was used to convert frequency to particle density. Particle density was then expressed as the percentage of each species found on a slide in relation to the total density of all species. Percentage dry weight composition for each species was assumed to be the same as its calculated relative density (Sparks and Malechek, 1968).

6.2.3 Diet relationships of the species

Food habits were compared by the degree of diet overlap, within seasons and years, among the four macropodid species, (Morisita, 1959; as modified by Horn, 1966; Schwartz and Ellis, 1981). This is an estimate of two species alpha (α) coefficients in the competition equations of MacArthur and Levins (1967). The overlap coeffieient C_λ varies from 0, for completely distinct samples (no food categories in common), to 1, for identical samples:

$$C_\lambda = \frac{2 \sum_{i=1}^{S} X_i Y_i}{\sum_{i=1}^{S} X_i^2 + \sum_{i=1}^{S} Y_i^2}$$

where S is the total number of plant groups and x_i and y_i are the mean proportions of the total diet of herbivore species X and Y taken from plant group i.

Diet relationships for each season were also subjected to discriminant function analysis (described in detail in Section 5.2.4). All diets for each species in each season were considered a group. Group membership was therefore composed of a number of cases, each case being a diet determination for a particular animal during a particular season. Each case was described by the percentage relative density of identifiable plant fragments. Plant species of less than 1% in diet determinations across seasons and years were removed from the data set. Thus, of the 98 plant species identified in diet determinations, 56 were used as variables in the discriminant function analyses.

The SPSS programme package (Klecka, 1975) on the Cyber 180 - 825 Computer, at the Western Australian Regional Computer Centre in the University of Western Australia, was used for all computations associated with discriminant function analysis.

6.3 Results

6.3.1 Diet compositions of the study species

Diet compositions of the study species, for each season during the three years, are presented (see Tables 6.1 to 6.12). Certain plant species within genera could not be distinguished on the basis of epidermal characteristics and were therefore grouped within the genus. Diet compositions, summarized in terms of plant/forage classes (described in Section 5.2.4.1) are presented in Tables 6.13 to 6.16. In these tables all non-herbaceous dicotyledonous species are grouped, as are annual and perennial sedge species.

Seasonal diet compositions of quokkas are presented in Tables 6.1 to 6.3. The results indicate that quokkas, on the reserve, are principally browsers. The non-herbaceous dicotyledonous species accounted for between 52% to 88% of the total diet in any season across all years. Four shrub species: *Hibbertia hypericoides, Acacia saligna, Melaleuca teretifolia* and *M. nesophila* were the main dietary items in the above total. There was no significant trend with respect to feeding on these individual species, their respective percentage dry weights varying seasonally both within and across years. However, there was a decline in the percentage dry weight of non-herbaceous dicotyledonous species in total, over the three year period (see Table 6.13). The percentage dry weight of sedges in diets was greatest during autumn each year and was dominated by *Baumea articulata* in each season in all years. The introduced annual *Briza spp.* and introduced perennial *Cynodon dactylon* formed the bulk of grass species in the diet. The level of these species in the diet increased over successive years as did their frequency and abundance in the vegetation (see Section 4.3.3, Table 4.6). The percentage dry weight of annual herbaceous species was greatest in diets during spring and dominated by the introduced species *Hypochoeris spp.* The percentage dry weight of perennial herbaceous species in the diet showed no consistent trend with respect to seasons within and across years.

Seasonal diet compositions of brush wallabies are presented in Tables 6.4 to 6.6. The results indicate that this species is principally a browser. The non-herbaceous dicotyledonous species represented between 80% to 95% of the total diet in any season across all years. *Hibbertia hypericoides, Eremaea pauciflora, Casuarina fraseriana, Jacksonia furcellata* and *J. sternbergiana* were the major dietary items in the above total. The total percentage dry weight of browse species was consistently lower in the diet during spring (see Table 6.14). Several grass species were found in the diets, mainly during the seasons winter and spring. The percentage dry weight of sedge species in the diets was highest during spring and summer, *Dasypogon bromeliaefolius* being the major dietary sedge species. The percentage dry weight of annual herbaceous species was highest in spring with *Hypochoeris spp.* being of importance. The succulent *Capobrotus spp.* was the major dietary perennial herbaceous species, its percentage dry weight in diets being highest during the summer periods.

Seasonal diet compositions of euros are presented in Tables 6.7 to 6.9. The results indicate that euros are principally grazers; sedge and grass species combined constituting between 75% and 98% of the total diet in any season across all years (see Table 6.15). The introduced *Briza spp.* and native *Stipa spp.* were the main dietary grass species. *Conostylis aculeata* and *Phlebocarya ciliata* were the main dietary sedge species. Sedge species consistently formed the major proportion of the diet during summer, autumn and winter, while grasses assumed major importance during the spring. The majority of non-herbaceous dicotyledons in the diet compositions comprised legume and other nitrogen-fixing species. The importance of these species in the diet was lowest in spring. Introduced capeweed (*Arctotheca calendula*) was the major dietary annual herbaceous species, its importance increasing over successive years. The percentage dry weight composition of perennial herbaceous species in diets was generally highest during the seasons summer and autumn, the succulent *Capobrotus spp.* being the major dietary item in this plant category.

Diet compositions of western grey kangaroos are presented in Tables 6.10 to 6.12. The results indicate that western grey kangaroos are pricipally grazers; sedge and grass species combined forming greater than 92% of the total diet in any season across all years (see Table 6.16). The introduced *Briza spp.* and the native *Stipa spp.* were the main dietary grass species. The percentage dry weight composition the native species: *Stipa spp.* and *Danthonia occidentalis* increased in the diet over successive years at the expense of introduced annual species. The main dietary sedge species included: *Lyginia barbata, Conostylis aculeata* and *Phlebocarya ciliata; Lyginia barbata* being a particularly important dietary species during the summer. As with the diets of euros, sedge species consistently formed the major proportion of western grey kangaroo diets during the seasons of summer, autumn and winter, while grasses assumed importance during the spring. The percentage dry weight composition of non-herbaceous dicotyledons in the diet showed little variation throughout the year, the leguminous *Jacksonia* species and nitrogen-fixing *Casuarina fraseriana* being of importance. *Hypochoeris spp.* was the main dietary annual herbaceous species, while *Capobrotus spp.* was the main dietary perennial herbaceous species.

Legend for Tables 6.1 to 6.12

* indicates the % dry weight of that species was less than 1.0%.

► symbol prefix indicates introduced species.

Table 6.1 Quokka diet composition ($\bar{x} \pm$ s.e.) 1982

	Summer (%) n=9	Autumn (%) n=9	Winter (%) n=10	Spring (%) n=5
Grass species (G)				
► *Briza spp.*	*		6.8 ± 2.0	11.6 ± 3.0
► *Cynodon dactylon*	1.0 ± 0.3	*	2.7 ± 0.9	10.6 ± 4.2
► *Polypogon monspeliensis*		*	*	1.0 ± 0.5
► *Vulpia spp.*			*	1.8 ± 1.1
Perennial Sedge species (PS)				
Baumea articulata	3.1 ± 1.5	10.6 ± 2.6	12.9 ± 3.6	7.0 ± 4.0
B. juncea	*	*	*	1.0 ± 0.6
Phlebocarya ciliata	*	3.1 ± 1.4	*	1.0 ± 0.6
Patersonia occidentalis	2.0 ± 1.4	*	*	
Tree species (T)				
Casuarina fraseriana	3.1 ± 1.1	2.7 ± 1.4	*	*
Melaleuca rhapiophylla	1.8 ± 1.1	*	3.1 ± 1.5	*
Viminaria juncea	1.2 ± 0.6	*		
Shrub species (S)				
Exocarpos sparteus	*	3.8 ± 3.3	*	*
Acacia saligna	4.6 ± 1.5	1.0 ± 0.7	16.1 ± 5.4	2.6 ± 2.6
Hibbertia hypericoides	44.1 ± 7.3	35.3 ± 6.4	31.3 ± 8.9	25.6 ± 11.6
Hypocalymma angustifolium	3.1 ± 1.6	4.1 ± 1.8	*	
Kunzea ericifolia	*	*	1.0 ± 0.4	1.2 ± 0.3
Melaleuca nesophila	11.9 ± 2.7	7.3 ± 3.4	4.1 ± 1.6	8.6 ± 3.5
M. teretifolia	13.9 ± 3.6	12.9 ± 2.6	12.4 ± 2.4	14.4 ± 4.4
Leucopogon spp.	*	*	*	1.6 ± 0.9
Perennial Herb species (PH)				
► *Capobrotus spp.*	6.4 ± 2.5	12.6 ± 6.6	1.8 ± 0.8	*
Centella cordifolia	*	1.1 ± 0.4	3.4 ± 1.1	3.8 ± 1.4
Annual Herb species (AH)				
► *Hypochoeris spp.*			*	3.8 ± 1.0
Species type A	*			
Species type B			*	
Species type C				*
Species type D	*	*	*	
Species type E		*	*	*
Species type F	*	*	*	*
Species type G			*	*
Species type H	*	*		

Species type A *Xanthorrhoea preissii (PS), Acacia cochlearis (S), Conospermum stoechadis (S), Comesperma spp. (PH).*

Table 6.1 cont. Quokka diet composition ($\bar{x} \pm$ s.e.) 1982

Species type B:- *Danthonia occidentalis (G)*, *Burchardia umbellata (PS)*, *Tricoryne elatior (PS)*, *Conostylis aculeata (PS)*.

Species type C:- *Amphipogon turbinatus (G)*, ▶*Bromus spp. (G)*, *Caladenia spp. (PS)*, ▶*Erodium botyrs (PH)*, ▶*Verbascum virgatum (AH)*, ▶*Gnaphalium luteoalbum (AH)*.

Species type D:- *Hibbertia racemosa (S)*.

Species type E:- *Stipa spp. (G)*, *Astartea fascicularis (S)*, ▶*Cardus pycnocephalus (AH)*.

Species type F:- *Dasypogon bromeliaefolius (PS)*, *Jacksonia sternbergiana (T)*, *Acacia pulchella (S)*.

Species type G:- ▶*Aira spp. (G)*, ▶*Avena barbata (G)*, ▶*Ehrharta longiflora (G)*,

Species type H:- *Jacksonia furcellata (T)*.

Table 6.2 Quokka diet composition ($\bar{x} \pm$ s.e.) 1983

	Summer (%) n=6	Autumn (%) n=9	Winter (%) n=4	Spring (%) n=8
Grass species (G)				
► *Briza spp.*	*		5.5 ± 2.3	6.1 ± 1.4
► *Cynodon dactylon*	*	5.8 ± 1.8	2.5 ± 0.9	5.8 ± 1.6
► *Polypogon monspeliensis*		*		1.0 ± 0.4
► *Vulpia spp.*				1.3 ± 0.5
Perennial Sedge species (PS)				
Baumea articulata	13.0 ± 4.5	18.2 ± 3.6	6.5 ± 3.6	12.4 ± 3.3
B. juncea	8.2 ± 4.1	3.8 ± 0.9	*	*
Cladium riparium				1.0 ± 0.9
Lyginia barbata		1.0 ± 0.8	*	
Dasypogon bromeliaefolius	*	*	3.0 ± 1.1	4.8 ± 2.8
Phlebocarya ciliata		1.3 ± 1.1	1.5 ± 0.5	4.4 ± 4.1
Patersonia occidentalis	*	*	2.0 ± 1.2	*
Tree species (T)				
Casuarina fraseriana	1.7 ± 0.6	3.7 ± 2.0	1.3 ± 0.8	*
Melaleuca rhapiophylla	*	*	3.3 ± 1.0	3.0 ± 0.4
Jacksonia furcellata	1.5 ± 0.8	*		
J. sternbergiana		1.3 ± 1.1	2.0 ± 1.4	*
Viminaria juncea	1.8 ± 0.8	*	1.5 ± 0.9	2.4 ± 1.6
Shrub species (S)				
Exocarpos sparteus	*	3.3 ± 1.6	4.0 ± 2.6	*
Acacia pulchella	1.8 ± 0.5	*	1.3 ± 0.6	2.4 ± 0.5
A. saligna	25.2 ± 3.9	15.6 ± 4.1	14.0 ± 6.9	17.1 ± 6.8
Hibbertia hypericoides	13.3 ± 8.0	16.3 ± 5.0	18.0 ± 4.1	10.8 ± 2.8
Astartea fascicularis			*	1.0 ± 0.4
Hypocalymma angustifolium	*	2.4 ± 1.1	3.0 ± 1.5	5.3 ± 2.2
Kunzea ericifolia	4.2 ± 1.2	1.6 ± 0.7	1.3 ± 1.3	1.4 ± 0.7
Melaleuca nesophila	3.7 ± 1.0	4.7 ± 1.9	5.8 ± 2.0	3.3 ± 1.1
M. teretifolia	9.8 ± 4.8	15.2 ± 5.2	13.3 ± 3.5	6.9 ± 2.0
Perennial Herb species (PH)				
► *Capobrotus spp.*	6.0 ± 2.9	3.9 ± 0.9	3.0 ± 2.1	2.0 ± 0.7
Comesperma spp.	1.5 ± 0.9			*
Centella cordifolia	6.2 ± 1.5	1.1 ± 0.4	4.8 ± 1.0	5.6 ± 1.0
Species type A	*			
Species type B		*		
Species type C			*	
Species type D				*
Species type E		*	*	*
Species type F	*			*
Species type G	*	*	*	*

Species type A:- *Acacia cochlearis (S), A. cyclops (S).*

Table 6.2 cont. Quokka diet composition ($\bar{x} \pm$ s.e.) 1983

Species type B:- *Amphipogon turbinatus (G), Hypolaena exsulca (PS), Conostylis aculeata (PS), Bossiaea eriocarpa (S), Dodonaea hackettiana (S), Leucopogon spp. (S).*

Species type C:- ►*Ehrharta longiflora (G),* ►*Gnaphalium luteoalbum (AH).*

Species type D:- *Danthonia occidentalis (G),* ►*Vulpia spp. (G),* ►*Trifolium dubium (AH).*

Species type E:- ►*Aira spp. (G).*

Species type F:- *Stipa spp. (G),* ►*Cardus pycnocephalus (AH).*

Species type G:- *Hibbertia racemosa (S),* ►*Hypochoeris spp. (AH).*

Table 6.3 Quokka diet composition ($\bar{x} \pm$ s.e.) 1984

	Summer (%) n=10	Autumn (%) n=10	Winter (%) n=10	Spring (%) n=10
Grass species (G)				
► *Briza spp.*	3.9 ± 0.9	*	17.9 ± 1.7	6.7 ± 1.6
► *Cynodon dactylon*	18.0 ± 3.5	6.6 ± 2.2	3.6 ± 1.3	7.1 ± 1.3
► *Polypogon monspeliensis*	1.5 ± 0.7	*	1.1 ± 0.4	*
Stipa spp.	*		*	1.5 ± 0.6
► *Vulpia spp.*	1.4 ± 0.8	*	2.7 ± 0.8	*
Perennial Sedge species (PS)				
Baumea articulata	3.7 ± 0.8	7.2 ± 1.5	3.7 ± 1.0	5.5 ± 2.8
B. juncea	*	2.7 ± 1.4		*
Dasypogon bromeliaefolius	*	2.0 ± 0.7	*	1.5 ± 0.9
Conostylis aculeata	1.3 ± 0.5	*	1.0 ± 0.5	*
Phlebocarya ciliata	3.7 ± 1.3	1.5 ± 0.8	*	3.6 ± 1.8
Patersonia occidentalis	1.0 ± 0.7	1.1 ± 0.7	*	*
Tree species (T)				
Casuarina fraseriana	1.6 ± 0.6	2.1 ± 1.2	1.5 ± 0.7	*
Melaleuca rhapiophylla	2.5 ± 1.2	3.0 ± 0.6	5.3 ± 1.1	4.6 ± 1.4
Jacksonia sternbergiana	*	2.0 ± 1.6	*	
Viminaria juncea	1.2 ± 0.4	*	*	1.8 ± 0.9
Shrub species (S)				
Acacia pulchella	2.0 ± 0.8	*	2.1 ± 0.4	1.1 ± 0.4
A. saligna	4.5 ± 2.2	6.9 ± 3.4	2.8 ± 1.2	4.5 ± 2.1
Dodonaea hackettiana			2.5 ± 1.4	
Hibbertia hypericoides	14.7 ± 3.0	29.9 ± 4.2	32.4 ± 3.3	34.8 ± 3.4
H. racemosa	*	1.7 ± 0.4	*	*
Hypocalymma angustifolium	9.5 ± 2.7	3.2 ± 0.9	1.4 ± 0.7	1.0 ± 0.5
Melaleuca nesophila	5.6 ± 1.7	3.7 ± 1.1	3.6 ± 1.1	4.6 ± 1.4
M. teretifolia	6.4 ± 1.4	5.3 ± 1.1	6.4 ± 1.1	6.8 ± 0.9
Leucopogon spp.	*	1.7 ± 0.5	*	1.3 ± 0.4
Perennial Herb species (PH)				
► *Capobrotus spp.*	8.2 ± 2.6	10.5 ± 2.9	3.2 ± 1.1	1.5 ± 0.6
Comesperma spp.	1.3 ± 0.3	*	*	*
Centella cordifolia	1.1 ± 0.9	*	7.6 ± 0.8	4.7 ± 1.0
Annual Herb species (AH)				
► *Hypochoeris spp.*	1.8 ± 0.9		*	10.5 ± 1.5
Species type A	*			
Species type B		*		
Species type C			*	
Species type D				*
Species type E			*	*
Species type F	*	*		
Species type G	*		*	*
Species type H	*	*	*	*

Table 6.3 cont. Quokka diet composition ($\bar{x} \pm$ s.e.) 1984

Species type A:- *Lyginia barbata (PS)*, ▶*Geranium molle (PH)*, ▶*Gnaphalium luteoalbum (AH)*.

Species type B:- *Hypolaena exsulca (PS)*, *Lomandra spp. (PS)*, *Acacia cyclops (S)*.

Species type C:- ▶*Bromus spp. (G)*, ▶*Lagurus ovatus (G)*, *Schoenus sublaxus (PS)*, *Xanthorrhoea preissii (PS)*, *Astartea fascicularis (S)*, ▶*Verbascum virgatum (AH)*.

Species type D:- *Caesia parviflora (PS)*, ▶*Gladiolus caryophyllaceus (AS)*, *Kennedia prostrata (PH)*, ▶*Silene gallica (AH)*, ▶*Arctotheca calendula (AH)*.

Species type E:- ▶*Avena barbata (G)*, *Danthonia occidentalis (G)*, ▶*Ehrharta longiflora (G)*, *Burchardia umbellata (PS)*, *Conospermum stoechadis (S)*, *Acacia cochlearis (S)*, ▶*Erodium botrys (PH)*.

Species type F:- *Cladium riparium (PS)*, *Loxocarya pubescens (PS)*, *Jacksonia furcellata (T)*, *Gompholobium tomentosum (S)*, *Hardenbergia comptoniana (S)*.

Species type G:- *Caladenia spp. (PS)*, ▶*Cardus pycnocephalus (AH)*.

Species type H:- ▶*Aira spp. (G)*, *Exocarpos sparteus (S)*, *Bossiaea eriocarpa (S)*, *Kunzea ericifolia (S)*.

Table 6.4 Brush wallaby diet composition ($\bar{x} \pm$ s.e.) 1982

	Summer (%) n=10	Autumn (%) n=10	Winter (%) n=9	Spring (%) n=9
Grass species (G)				
Danthonia occidentalis		*	*	1.0 ± 0.3
Stipa spp.				1.1 ± 0.4
Perennial Sedge species (PS)				
Dasypogon bromeliaefolius	5.4 ± 3.4	2.5 ± 1.5	*	5.0 ± 3.2
Tree species (T)				
Casuarina fraseriana	20.3 ± 3.0	22.3 ± 4.5	21.1 ± 6.2	10.4 ± 3.3
Nuytsia floribunda	1.8 ± 1.1	3.3 ± 1.3	2.3 ± 1.1	*
Jacksonia furcellata	5.3 ± 2.0	5.4 ± 3.4	3.8 ± 2.5	3.4 ± 2.7
J. sternbergiana	3.5 ± 1.7	3.3 ± 1.9	3.0 ± 2.3	4.1 ± 2.1
Shrub species (S)				
Adenanthos sericea	1.2 ± 1.1	*	1.0 ± 0.9	*
Stirlingia latifolia	*	1.2 ± 0.7	8.7 ± 4.0	*
Hibbertia hypericoides	32.7 ± 7.1	13.1 ± 4.6	39.9 ± 7.6	53.7 ± 6.9
Eremaea pauciflora	10.8 ± 4.4	37.1 ± 9.5	14.2 ± 5.5	8.9 ± 6.4
Melaleuca thymoides	5.5 ± 3.9	6.8 ± 3.4		
Scholtzia involucrata	1.6 ± 0.5	1.5 ± 0.7	1.1 ± 1.1	2.3 ± 1.1
Leucopogon spp.	3.8 ± 1.3	1.8 ± 0.6	1.3 ± 0.7	5.0 ± 1.8
Perennial Herb species (PH)				
► *Capobrotus spp.*	5.0 ± 2.1	*	*	*
Species type A	*			
Species type B		*		
Species type C			*	
Species type D				*
Species type E	*	*		
Species type F			*	*
Species type G	*	*	*	*

Species type A:- ►*Briza spp. (G), Acacia cochlearis (S), Dampiera linearis (PH).*

Species type B:- *Xanthorrhoea preissii (PS).*

Species type C:- ►*Bromus spp. (G), Burchardia umbellata (PS),* ►*Erodium botrys (PH),* ►*Arctotheca calendula (AH).*

Species type D:- ►*Aira spp. (G),* ►*Vulpia spp. (G), Conostylis aculeata (PS), Phlebocarya ciliata (PS), Hibbertia huegelii (S), Eryngium pinnatifidium (PH),* ►*Wahlenbergia capensis (AH).*

Species type E:- *Acacia saligna (S), Melaleuca teretifolia (S).*

Species type F:- ►*Avena barbata (G), Laxmannia spp. (PS), Sowerbaea laxiflora (PS), Thysanotus spp. (PS),* ►*Gladiolus caryophyllaceus (AS), Bossiaea eriocarpa (S), Hibbertia racemosa (S),* ►*Hypochoeris spp. (AH).*

Species type G:- *Loxocarya pubescens (PS), Conospermum stoechadis (S), Hovea trisperma (S).*

Table 6.5 Brush wallaby diet composition ($\bar{x} \pm$ s.e.) 1983

	Summer (%) n=9	Autumn (%) n=4	Winter (%) n=9	Spring (%) n=10
<u>Grass species</u> (G)				
► *Briza spp.*			1.3 ± 0.6	*
Stipa spp.		*	*	1.4 ± 0.4
<u>Perennial Sedge species</u> (PS)				
Burchardia umbellata			*	1.4 ± 0.5
Dasypogon bromeliaefolius	*	*		9.0 ± 5.4
<u>Tree species</u> (T)				
Casuarina fraseriana	20.2 ± 3.7	14.8 ± 6.8	1.7 ± 0.7	11.2 ± 4.6
Nuytsia floribunda	4.3 ± 1.7	*	5.3 ± 1.9	1.6 ± 1.2
Jacksonia furcellata	5.3 ± 2.0	2.0 ± 1.2	1.7 ± 0.7	3.3 ± 1.8
J. sternbergiana	9.2 ± 4.1	4.5 ± 2.2	5.0 ± 4.1	7.5 ± 2.4
<u>Shrub species</u> (S)				
Adenanthos sericea	8.3 ± 5.8	1.0 ± 0.7	2.4 ± 2.2	*
Conospermum stoechadis	1.3 ± 0.5	1.0 ± 0.7		
Stirlingia latifolia	1.1 ± 0.4	1.0 ± 0.7	1.3 ± 0.5	*
Exocarpos sparteus			*	1.1 ± 0.8
Bossiaea eriocarpa	1.7 ± 0.6			*
Hibbertia hypericoides	15.3 ± 3.8	67.5 ± 12.7	42.1 ± 7.2	37.4 ± 6.0
H. racemosa	*	*	1.0 ± 0.7	*
Eremaea pauciflora	15.6 ± 4.3	*	30.0 ± 8.4	5.8 ± 4.9
Melaleuca thymoides	9.7 ± 4.6	*	*	1.0 ± 1.0
Scholtzia involucrata	2.3 ± 0.6	*	2.3 ± 1.6	2.6 ± 1.1
Leucopogon spp.	1.8 ± 0.6	2.3 ± 1.0	1.7 ± 0.3	2.7 ± 1.0
<u>Perennial Herb species</u> (PH)				
► *Capobrotus spp.*	2.2 ± 0.4	2.0 ± 1.1	*	1.6 ± 0.7
<u>Annual Herb species</u> (AH)				
► *Hypochoeris spp.*			*	3.3 ± 0.8
Species type A	*			
Species type B			*	
Species type C				*
Species type D			*	*
Species type E	*	*	*	*

Species type A:- *Lyginia barbata (PS), Acacia cochlearis (S), Euchilopsis linearis (S), Hardenbergia comptoniana (S), Hypocalymma robustum (S).*

Species type B:- *Phyllanthus calycinus (S).*

Species type C:- *Laxmannia spp. (PS), Sowerbaea laxiflora (PS), Thysanotus spp. (PS), Xanthorrhoea preissii (PS), Conostylis aculeata (PS), Patersonia occidentalis (PS),* ► *Gladiolus caryophyllaceus (AS),*

Table 6.5 cont. Brush wallaby diet composition ($\bar{x} \pm$ s.e.) 1983

Acacia pulchella (S), *A. stenoptera (S)*, *Melaleuca teretifolia (S)*, *Centella cordifolia (PH)*, *Dampiera linearis (PH)*, ►*Silene gallica (AH)*, ►*Petrorhagia prolifera (AH)*, ►*Trifolium dubium (AH)*, ►*Vicia sativa (AH)*, ►*Anagallis arvensis (AH)*, ►*Wahlenbergia capensis (AH)*.

Species type D:- ►*Avena barbata (G)*, ►*Bromus spp. (G)*, *Danthonia occidentalis (G)*, ►*Ehrharta longiflora (G)*, ►*Vulpia spp. (G)*, *Schoenus sublaxus (PS)*, *Kennedia prostrata (PH)*, ►*Erodium botrys (PH)*, *Eryngium pinnatifidium (PH)*.

Species type E:- *Loxocarya pubescens (PS)*, *Hovea trisperma (S)*, *Hibbertia huegelii (S)*.

Table 6.6 Brush wallaby diet composition ($\bar{x} \pm$ s.e.) 1984

	Summer (%) n=10	Autumn (%) n=4	Winter (%) n=6	Spring (%) n=5
Grass species (G)				
► *Briza spp.*	*		3.2 ± 0.9	*
Danthonia occidentalis	*	*	*	1.0 ± 0.6
► *Ehrharta longiflora*			1.8 ± 0.4	*
Stipa spp	*		*	1.8 ± 0.4
Perennial Sedge species (PS)				
Loxocarya pubescens		1.3 ± 0.3		*
Burchardia umbellata			1.7 ± 0.2	1.6 ± 0.9
Dasypogon bromeliaefolius	*	*		2.0 ± 1.3
Laxmannia spp.	*	*		1.4 ± 0.7
Tree species (T)				
Casuarina fraseriana	16.5 ± 2.8	15.5 ± 3.9	1.0 ± 0.3	5.4 ± 4.2
Nuytsia floribunda	3.8 ± 1.9		*	*
Jacksonia furcellata	5.8 ± 2.6	1.3 ± 0.8	*	5.0 ± 2.9
J. sternbergiana	6.4 ± 2.5		*	10.8 ± 3.3
Shrub species (S)				
Adenanthos sericea	1.7 ± 1.5			8.3 ± 7.9
Stirlingia latifolia	*	*	1.5 ± 0.6	*
Hovea trisperma	2.3 ± 0.8	1.3 ± 0.6	*	1.8 ± 0.5
Hibbertia hypericoides	34.1 ± 5.8	30.8 ± 17.1	70.5 ± 7.2	47.0 ± 8.0
Eremaea pauciflora	9.1 ± 5.3	16.5 ± 13.9	7.5 ± 5.8	
Melaleuca teretifolia	1.0 ± 0.7			
M. thymoides	1.3 ± 0.5			*
Scholtzia involucrata	1.7 ± 0.8	1.3 ± 0.9	*	4.2 ± 1.5
Leucopogon spp.	1.7 ± 0.5	*	2.2 ± 0.8	3.0 ± 1.6
Perennial Herb species (PH)				
► *Capobrotus spp.*	3.1 ± 0.4	4.0 ± 1.1	1.8 ± 1.0	1.6 ± 0.9
Kennedia prostrata	*			1.4 ± 0.8
Annual Herb species (AH)				
► *Hypochoeris spp.*			1.0 ± 0.4	5.0 ± 1.2
Species type A	*			
Species type B		*		
Species type C			*	
Species type D				*
Species type E			*	*
Species type F	*	*		
Species type G	*		*	*

Species type A:- *Mesomelaena stygia (PS), Schoenus sublaxus (PS), Acacia cochlearis (S), A. stenoptera (S), Phyllanthus calycinus (S),*

Table 6.6 cont. Brush wallaby diet composition ($\bar{x} \pm$ s.e.) 1984

Kunzea ericifolia (S), ►*Solanum nigrum (PH)*.

Species type B:- *Tricoryne elatior (PS)*, *Hypocalymma robustum (S)*.

Species type C:- ►*Aira spp. (G)*, ►*Avena barbata (G)*, ►*Bromus spp. (G)*, *Baumea juncea (PS)*, *Exocarpos spateus (S)*, *Acacia pulchella (S)*, *Hardenbergia comptoniana (S)*.

Species type D:- *Anigozanthos humilis (PS)*, *Hybanthus calycinus (PH)*, *Eryngium pinnatifidium (PH)*, ►*Trifolium dubium (AH)*, ►*Cardus pycnocephalus (AH)*.

Species type E:- *Caesia parviflora (PS)*, *Sowerbaea laxiflora (PS)*, *Thysanotus spp. (PS)*, *Caladenia spp. (PS)*, ►*Silene gallica (AH)*, ►*Wahlenbergia capensis (AH)*, ►*Ursinia anthemoides (AH)*.

Species type F:- *Lomandra spp. (PS)*, *Xanthorrhoea preissii (PS)*, *Conostylis aculeata (PS)*.

Species type G:- ►*Vulpia spp. (G)*, *Loxocarya pubescens (PS)*, *Dasypogon bromeliaefolius (PS)*, ►*Gladiolus caryophyllaceus (AS)*, *Conospermum stoechadis (S)*, *Bossiaea eriocarpa (S)*, *Euchilopsis linearis (S)*, *Gompholobium tomentosum (S)*, *Hibbertia huegelii (S)*, *H. racemosa (S)*, ►*Petrorhagia prolifera (AH)*.

Table 6.7 Euro diet composition ($\bar{x} \pm$ s.e.) 1982.

	Summer (%) n=10	Autumn (%) n=8	Winter (%) n=9	Spring (%) n=7
Grass species (G)				
►*Aira spp.*	1.0 ± 0.4	*	*	*
►*Avena barbata*	*		*	2.3 ± 0.6
►*Briza spp.*	5.1 ± 1.4	*	11.2 ± 4.6	7.3 ± 1.6
►*Cynodon dactylon*	3.6 ± 1.0	*	*	1.7 ± 0.6
Danthonia occidentalis	*	*	*	7.1 ± 2.3
►*Ehrharta longiflora*			2.3 ± 0.6	3.6 ± 0.8
Stipa spp.	19.0 ± 4.5	1.1 ± 0.5	3.0 ± 1.0	47.9 ± 4.4
►*Vulpia spp.*	2.9 ± 0.9	*	2.6 ± 1.1	5.3 ± 0.9
Perennial Sedge species (PS)				
Baumea articulata	3.8 ± 1.3	6.1 ± 1.2		
B. juncea	3.4 ± 0.8	2.0 ± 0.8	2.1 ± 1.3	*
Lepidosperma costale	*	*	2.3 ± 0.7	
Schoenus sublaxus	*		7.7 ± 2.0	*
Hypolaena exsulca	*	1.4 ± 1.1	*	
Loxocarya pubescens	3.2 ± 1.3	7.8 ± 2.4	1.4 ± 0.8	
Lyginia barbata	2.3 ± 0.9	5.1 ± 3.6	3.4 ± 1.5	
Burchardia umbellata			1.0 ± 0.3	*
Dasypogon bromeliaefolius	6.0 ± 3.1	2.0 ± 1.4	6.6 ± 3.6	*
Conostylis aculeata	28.5 ± 5.3	28.4 ± 3.5	26.3 ± 3.9	18.4 ± 4.6
Phlebocarya ciliata	10.4 ± 1.4	34.5 ± 5.4	18.6 ± 4.6	*
Annual Sedge species (AS)				
►*Gladiolus caryophyllaceus*			1.7 ± 0.5	*
Tree species (T)				
Casuarina fraseriana	*	*	2.1 ± 0.9	
Jacksonia furcellata	1.4 ± 0.6	2.9 ± 1.7	*	*
J. sternbergiana	3.2 ± 1.1	3.0 ± 2.0	2.0 ± 1.0	*
Shrub species (S)				
Hibbertia hypericoides		*	1.0 ± 0.4	*
Perennial Herb species (PH)				
►*Capobrotus spp.*	3.4 ± 0.8	1.5 ± 0.6	*	*
Centella cordifolia	*	*	1.6 ± 0.9	*
Species type A	*			
Species type B		*		
Species type C			*	
Species type D		*	*	
Species type E			*	*
Species type F	*	*		
Species type G	*	*	*	

Species type A:- *Polypogon monspeliensis (G), Exocarpos sparteus (S).*

Table 6.7 cont. Euro diet composition ($\bar{x} \pm$ s.e.) 1982.

Species type B:- *Acacia cochlearis (S), Scholtzia involucrata (S), Leucopogon spp. (S).*

Species type C:- *Caesia parviflora (PS), Caladenia spp. (PS),* ►*Petrorhagia prolifera (AH),* ►*Trifolium dubium (AH),* ►*Verbascum virgatum (AH),* ►*Vicia sativa (AH),* ►*Arctotheca calendula (AH),* ►*Cardus pycnocephalus (AH),* ►*Erigeron bonariensis (AH),* ►*Hypochoeris spp. (AH).*

Species type D:- *Mesomelaena stygia (PS), Xanthorrhoea preissii (PS), Patersonia occidentalis (PS), Acacia pulchella (S).*

Species type E:- *Amphipogon turbinatus (G),* ►*Bromus spp. (G).*

Species type F:- *Cladium riparium (PS), Lomandra spp. (PS).*

Species type G:- *Tricoryne elatior (PS), Acacia saligna (S).*

Table 6.8 Euro diet composition ($\bar{x} \pm$ s.e.) 1983.

	Summer (%) n=5	Autumn (%) n=5	Winter (%) n=7	Spring (%) n=5
<u>Grass species</u> (G)				
▶ *Aira spp.*	1.6 ± 0.5			
Amphipogon turbinatus	1.8 ± 0.8			
▶ *Avena barbata*			1.7 ± 1.2	2.4 ± 0.4
▶ *Briza spp.*		1.0 ± 0.4	11.0 ± 3.9	7.0 ± 1.0
▶ *Cynodon dactylon*	6.2 ± 2.6	5.0 ± 1.6	*	*
Danthonia occidentalis	2.4 ± 1.6	*	*	7.6 ± 1.2
▶ *Ehrharta longiflora*			2.7 ± 0.8	5.2 ± 0.9
Stipa spp.	5.6 ± 4.0	1.2 ± 0.7	17.0 ± 4.0	39.2 ± 2.4
▶ *Vulpia spp.*	1.6 ± 1.2	2.4 ± 1.4	1.7 ± 0.5	1.0 ± 0.3
<u>Perennial Sedge species</u> (PS)				
Baumea articulata	7.2 ± 3.2	5.6 ± 2.3	2.0 ± 1.1	
B. juncea	6.6 ± 2.4	4.6 ± 1.1	1.4 ± 0.5	*
Lepidosperma costale	*	1.2 ± 0.6	2.6 ± 0.7	*
Schoenus sublaxus		1.8 ± 1.1	5.6 ± 2.8	
Hypolaena exsulca	*	1.4 ± 0.7		
Loxocarya pubescens	7.8 ± 4.4	2.8 ± 1.2	*	
Lyginia barbata		1.4 ± 0.6	1.3 ± 0.8	
Burchardia umbellata			*	2.4 ± 0.5
Dasypogon bromeliaefolius	14.6 ± 8.5	5.8 ± 1.7	7.0 ± 3.7	*
Xanthorrhoea preissii	*	*	1.9 ± 0.4	
Conostylis aculeata	5.4 ± 3.3	25.0 ± 2.1	29.6 ± 7.9	19.6 ± 2.0
Phlebocarya ciliata	14.0 ± 4.9	13.6 ± 3.6	7.3 ± 2.0	8.6 ± 1.4
Patersonia occidentalis		1.0 ± 0.6	*	
<u>Annual Sedge species</u> (AS)				
▶ *Gladiolus caryophyllaceus*			1.6 ± 0.9	2.8 ± 0.4
<u>Tree species</u> (T)				
Casuarina fraseriana	5.6 ± 3.1	1.2 ± 0.6	1.0 ± 0.4	
Jacksonia furcellata	*	5.6 ± 2.0		
J. sternbergiana		4.0 ± 1.3	2.3 ± 1.1	*
Viminaria juncea	1.2 ± 0.7			
<u>Shrub species</u> (S)				
Conospermum stoechadis	1.4 ± 0.8			
Exocarpos sparteus	2.2 ± 2.0	*	*	
Acacia saligna	8.6 ± 3.1	5.4 ± 2.4	1.3 ± 0.7	1.2 ± 0.6
Melaleuca teretifolia	1.6 ± 1.2	*	*	
<u>Perennial Herb species</u> (PH)				
▶ *Capobrotus spp.*	3.2 ± 1.5	5.4 ± 1.1	1.7 ± 1.0	*
Centella cordifolia	*	1.2 ± 0.6	*	*
<u>Annual Herb species</u> (AH)				
▶ *Arctotheca calendula*			3.1 ± 2.2	

Table 6.8 cont. Euro diet composition ($\bar{x} \pm$ s.e.) 1983

	Summer (%) n=5	Autumn (%) n=5	Winter (%) n=7	Spring (%) n=5
Species type A	*			
Species type B			*	
Species type C		*	*	
Species type D	*	*		

Species type A:- *Tricoryne elatior (PS), Bossiaea eriocarpa (S).*

Species type B:- ►*Bromus spp. (G), Lomandra spp. (PS), Leucopogon spp. (S), Comesperma spp. (PH),* ►*Petrorhagia prolifera (AH),* ►*Cardus pycnocephalus (AH),* ►*Hypochoeris spp. (AH).*

Species type C:- *Hibbertia hypericoides (S).*

Species type D:- *Acacia pulchella (S).*

Table 6.9 Euro diet composition ($\bar{x} \pm$ s.e.) 1984.

	Summer (%) n=4	Autumn (%) n=4	Winter (%) n=3	Spring (%) n=3
Grass species (G)				
▶ *Avena barbata*			5.0 ± 3.1	1.0 ± 0.6
▶ *Briza spp.*	4.5 ± 0.7	1.0 ± 0.4	12.0 ± 2.5	6.7 ± 0.9
▶ *Cynodon dactylon*		2.8 ± 1.4	1.7 ± 0.9	*
Danthonia occidentalis	3.0 ± 1.2	*	*	6.3 ± 2.0
▶ *Ehrharta longiflora*			4.7 ± 2.0	7.3 ± 0.9
Stipa spp.	9.8 ± 2.9	2.3 ± 1.3	12.0 ± 2.9	39.3 ± 0.9
▶ *Vulpia spp.*	*	1.8 ± 1.2	3.7 ± 1.2	1.7 ± 0.9
Perennial Sedge species (PS)				
Baumea articulata	1.3 ± 0.3	3.5 ± 1.0	*	
B. juncea	14.8 ± 2.3	4.0 ± 2.2		1.3 ± 0.9
Lepidosperma costale	2.3 ± 0.3		3.3 ± 2.4	1.0 ± 0.6
Schoenus sublaxus	1.8 ± 0.3	1.5 ± 1.0	1.3 ± 0.9	
Hypolaena exsulca		1.5 ± 0.9	*	
Loxocarya pubescens	10.0 ± 4.1	6.5 ± 1.7	3.3 ± 1.9	1.3 ± 0.3
Lyginia barbata	*	2.0 ± 0.8	1.0 ± 0.6	
Burchardia umbellata			1.7 ± 1.2	2.3 ± 0.3
Dasypogon bromeliaefolius	1.8 ± 1.4	6.8 ± 1.8		
Lomandra spp.		*	1.3 ± 0.8	
Tricoryne elatior	*	2.5 ± 1.5		
Xanthorrhoea preissii		1.0 ± 0.7	3.0 ± 2.1	
Conostylis aculeata	33.0 ± 7.3	29.8 ± 2.3	16.3 ± 4.2	9.7 ± 2.7
Phlebocarya ciliata	9.8 ± 2.4	18.8 ± 4.4	12.3 ± 2.4	12.0 ± 2.1
Annual Sedge species (AS)				
▶ *Gladiolus caryophyllaceus*			*	1.3 ± 0.9
Tree species (T)				
Casuarina fraseriana		*	1.7 ± 1.2	*
Jacksonia furcellata	2.0 ± 0.4	2.0 ± 0.8		
J. sternbergiana	2.0 ± 0.8	1.5 ± 0.5	*	
Shrub species (S)				
Acacia pulchella			*	1.0 ± 0.6
Hibbertia hypericoides		1.8 ± 1.8		
Perennial Herb species (PH)				
▶ *Capobrotus spp.*	3.5 ± 2.1	4.3 ± 0.9	3.0 ± 1.2	2.0 ± 1.2
Comesperma spp.	*			1.3 ± 0.9
Centella cordifolia	1.8 ± 1.0	2.0 ± 0.8	1.0 ± 0.6	2.0 ± 0.6
Annual Herb species (AH)				
▶ *Arctotheca calendula*			11.3 ± 9.4	

Table 6.9 cont. Euro diet composition ($\bar{x} \pm$ s.e.) 1984.

	Summer (%) n=4	Autumn (%) n=4	Winter (%) n=3	Spring (%) n=3
Species type A	*			
Species type B			*	
Species type C				*
Species type D			*	*
Species type E		*	*	*

Species type A:- *Cladium riparium (PS), Dianella revoluta (PS), Conospermum stoechadis (S), Hardenbergia comptoniana (S), Melaleuca nesophila (S), M. teretifolia (S).*

Species type B:- *Thysanotus spp. (PS), Exocarpos sparteus (S).*

Species type C:- *Acacia saligna (S), Kennedia prostrata (PH), Ursinia anthemoides (AH).*

Species type D:- *Amphipogon turbinatus (G),* ▶*Bromus spp. (G).*

Species type E:- ▶*Aira spp. (G), Mesomelaena stygia (PS).*

Table 6.10 Western grey kangaroo diet composition ($\bar{x} \pm$ s.e.) 1982.

	Summer (%) n=10	Autumn (%) n=10	Winter (%) n=10	Spring (%) n=10
<u>Grass species</u> (G)				
► *Aira spp.*	*		*	1.5 ± 0.3
► *Briza spp.*	1.1 ± 0.5		4.8 ± 1.6	4.4 ± 0.5
Danthonia occidentalis	*		*	1.4 ± 0.7
► *Ehrharta longiflora*			*	1.0 ± 0.3
Stipa spp.	5.3 ± 1.9	1.1 ± 0.5	1.8 ± 0.7	17.6 ± 3.6
► *Vulpia spp.*	1.5 ± 0.7	*	*	2.6 ± 0.7
<u>Perennial Sedge species</u> (PS)				
Baumea juncea		5.9 ± 2.4	1.9 ± 1.7	*
Lepidosperma costale	2.0 ± 0.8	1.6 ± 0.5	2.9 ± 0.6	*
Mesomelaena stygia	4.6 ± 2.1	*	11.6 ± 5.4	*
Schoenus sublaxus	1.4 ± 0.5	1.5 ± 0.7	3.6 ± 0.8	2.6 ± 0.8
Hypolaena exsulca	2.2 ± 1.0	2.7 ± 1.3	1.6 ± 0.8	*
Loxocarya pubescens	3.2 ± 0.6	3.6 ± 1.1	3.2 ± 0.8	5.0 ± 1.3
Lyginia barbata	21.1 ± 6.7	11.7 ± 3.7	6.0 ± 1.9	4.8 ± 1.8
Dasypogon bromeliaefolius	8.0 ± 2.8	2.9 ± 0.7	9.0 ± 3.5	9.1 ± 2.2
Lomandra spp.	2.8 ± 0.4	1.6 ± 0.5	3.1 ± 1.1	1.0 ± 0.4
Conostylis aculeata	23.1 ± 3.8	35.1 ± 4.1	15.1 ± 4.5	27.9 ± 5.5
Phlebocarya ciliata	17.7 ± 2.9	23.3 ± 3.8	27.3 ± 5.7	10.9 ± 2.2
<u>Annual Sedge species</u> (AS)				
► *Gladiolus caryophyllaceus*			*	1.1 ± 0.6
<u>Tree species</u> (T)				
Casuarina fraseriana	1.1 ± 0.6	*	*	1.7 ± 0.8
Jacksonia furcellata	2.7 ± 1.3	4.0 ± 1.5	*	*
J. sternbergiana	*	2.0 ± 0.7	2.1 ± 0.6	1.5 ± 0.5
<u>Perennial Herb species</u> (PH)				
► *Capobrotus spp.*	2.0 ± 0.5	1.9 ± 0.7	*	*
<u>Annual Herb species</u>				
► *Hypochoeris spp.*			1.3 ± 0.4	1.4 ± 0.6
Species type A	*			
Species type B		*		
Species type C			*	
Species type D				*
Species type E			*	*
Species type F	*	*		
Species type G		*	*	
Species type H	*		*	*
Species type I		*	*	*

Species type A:- *Stirlingia latifolia (S), Gompholobium tomentosum (S).*

Table 6.10 cont. Western grey kangaroo diet composition ($\bar{x} \pm$ s.e.) 1982.

Species type B:- *Hibbertia racemosa (S).*

Species type C:- *Tricoryne elatior (PS), Patersonia occidentalis (PS),* ►*Petrorhagia prolifera (AH),* ►*Trifolium dubium (AH).*

Species type D:- *Burchardia umbellata (PS), Eryngium pinnatifidum (PH).*

Species type E:- ►*Avena barbata (G),* ►*Bromus spp. (G).*

Species type F:- *Acacia saligna (S).*

Species type G:- *Baumea articulata (PS), Xanthorrhoea preissii (PS), Conospermum stoechadis (S), Acacia cochlearis (S).*

Species type H:- *Laxmannia spp. (PS), Scholtzia involucrata (S).*

Species type I:- *Adenanthos sericea (S), Hibbertia hypericoides (S).*

Table 6.11 Western grey kangaroo diet composition ($\bar{x} \pm$ s.e.) 1983.

	Summer (%) n=10	Autumn (%) n=10	Winter (%) n=10	Spring (%) n=10
<u>Grass species</u> (G)				
▶ *Aira spp.*	*		*	1.3 ± 0.4
▶ *Briza spp.*	1.4 ± 0.4	1.5 ± 0.4	5.2 ± 1.4	5.0 ± 0.9
Danthonia occidentalis	*	*	*	3.9 ± 0.8
▶ *Ehrharta longiflora*			1.1 ± 0.4	2.2 ± 0.6
Stipa spp.	4.0 ± 1.6	2.0 ± 0.7	4.2 ± 1.1	28.2 ± 5.2
▶ *Vulpia spp.*	2.0 ± 0.7	*	*	2.3 ± 0.7
<u>Perennial Sedge species</u> (PS)				
Baumea articulata		*	4.6 ± 2.4	*
B. juncea		*	3.8 ± 2.8	1.0 ± 0.4
Lepidosperma costale	2.2 ± 0.9	2.3 ± 0.7	3.2 ± 0.8	*
Mesomelaena stygia	6.3 ± 4.3	2.2 ± 2.2	1.3 ± 0.6	3.4 ± 1.2
Schoenus sublaxus	1.0 ± 0.4	6.9 ± 2.5	2.3 ± 1.0	4.1 ± 1.4
Hypolaena exsulca	2.5 ± 0.6	4.0 ± 1.9	1.0 ± 0.4	*
Loxocarya pubescens	5.1 ± 1.3	2.9 ± 0.9	2.3 ± 0.8	3.4 ± 1.3
Lyginia barbata	38.1 ± 7.0	2.5 ± 0.8	1.1 ± 0.5	3.2 ± 0.8
Burchardia umbellata			1.5 ± 0.6	1.2 ± 0.5
Dasypogon bromeliaefolius	4.4 ± 1.9	18.7 ± 6.8	17.3 ± 5.1	2.2 ± 0.7
Lomandra spp.	1.8 ± 0.5	2.8 ± 1.1	2.5 ± 1.1	5.1 ± 1.2
Conostylis aculeata	18.3 ± 3.9	28.9 ± 7.5	16.3 ± 4.7	22.4 ± 4.7
Phlebocarya ciliata	4.7 ± 1.6	8.7 ± 1.9	30.6 ± 6.2	7.4 ± 3.0
Patersonia occidentalis		1.4 ± 0.5		
<u>Annual Sedge species</u> (AS)				
▶ *Gladiolus caryophyllaceus*			2.4 ± 0.5	*
<u>Tree species</u> (T)				
Casuarina fraseriana	1.2 ± 0.5	1.9 ± 0.8	*	*
Jacksonia sternbergiana	1.1 ± 0.4	1.2 ± 0.5	1.2 ± 0.4	*
<u>Shrub species</u> (S)				
Adenanthos sericea	1.3 ± 0.9	1.7 ± 1.7		*
<u>Perennial Herb species</u> (PH)				
▶ *Capobrotus spp.*	1.1 ± 0.5	2.5 ± 0.8	1.4 ± 0.4	*
<u>Annual Herb species</u> (AH)				
▶ *Hypochoeris spp.*			*	2.2 ± 0.6

Species type A	*			
Species type B		*		
Species type C			*	
Species type D				*
Species type E	*	*		
Species type F	*	*	*	*

Table 6.11 cont. Western grey kangaroo diet composition ($\bar{x} \pm$ s.e.) 1983.

Species type A:- *Melaleuca teretifolia (S),* ►*Wahlenbergia capensis (AH).*

Species type B:- *Schoenus grandiflorus (PS), Dodonaea hackettiana (S), Melaleuca nesophila (S).*

Species type C:- ►*Avena barbata (G), Acacia pulchella (S), Bossiaea eriocarpa (S), Centella cordifolia (PH), Eryngium pinnatifidum (PH),* ►*Trifolium dubium (AH).*

Species type D:- ►*Bromus spp. (G), Leucopogon spp. (S),* ►*Silene gallica (AH).*

Species type E:- *Hibbertia hypericoides (S), H. racemosa (S), Scholtzia involucrata (S).*

Species type F:- *Laxmannia spp. (PS), Xanthorrhoea preissii (PS), Jacksonia furcellata (T).*

Table 6.12 Western grey kangaroo diet composition ($\bar{x} \pm$ s.e.) 1984.

	Summer (%) n=10	Autumn (%) n=10	Winter (%) n=10	Spring (%) n=10
<u>Grass species</u> (G)				
▶ *Briza spp.*	1.5 $\pm$ 0.5	*	5.4 $\pm$ 0.4	1.5 $\pm$ 0.6
Danthonia occidentalis	*	*	1.2 $\pm$ 0.4	5.1 $\pm$ 0.6
▶ *Ehrharta longiflora*			1.6 $\pm$ 0.4	*
Stipa spp.	4.6 $\pm$ 0.9	1.1 $\pm$ 0.4	6.8 $\pm$ 0.9	29.6 $\pm$ 4.5
▶ *Vulpia spp.*	1.3 $\pm$ 0.3	1.2 $\pm$ 0.5	1.8 $\pm$ 0.6	*
<u>Perennial Sedge species</u> (PS)				
Baumea articulata	*	1.6 $\pm$ 0.7	*	*
B. juncea	*	3.0 $\pm$ 1.1	*	
Lepidosperma costale	3.1 $\pm$ 0.8	4.7 $\pm$ 1.2	4.7 $\pm$ 0.8	*
Mesomelaena stygia	8.8 $\pm$ 2.7	5.6 $\pm$ 2.2	*	1.6 $\pm$ 0.6
Schoenus sublaxus	7.4 $\pm$ 1.5	3.0 $\pm$ 0.5	5.1 $\pm$ 2.3	5.1 $\pm$ 2.1
Hypolaena exsulca	1.6 $\pm$ 0.9	*	*	1.1 $\pm$ 0.5
Loxocarya pubescens	5.7 $\pm$ 1.0	5.8 $\pm$ 0.6	3.4 $\pm$ 1.4	2.8 $\pm$ 0.9
Lyginia barbata	22.4 $\pm$ 5.3	16.6 $\pm$ 5.5	2.0 $\pm$ 0.7	6.4 $\pm$ 2.6
Burchardia umbellata			2.1 $\pm$ 0.6	*
Dasypogon bromeliaefolius	*	8.0 $\pm$ 2.0	15.3 $\pm$ 4.7	*
Lomandra spp.	4.3 $\pm$ 0.7	6.2 $\pm$ 0.9	8.3 $\pm$ 1.3	4.4 $\pm$ 1.2
Xanthorrhoea preissii	*	1.8 $\pm$ 1.0	*	
Conostylis aculeata	23.6 $\pm$ 3.6	25.0 $\pm$ 2.6	21.1 $\pm$ 5.3	20.1 $\pm$ 3.0
Phlebocarya ciliata	5.4 $\pm$ 1.5	2.9 $\pm$ 1.0	17.4 $\pm$ 3.3	10.3 $\pm$ 1.9
Patersonia occidentalis		*	1.1 $\pm$ 0.4	*
<u>Tree species</u> (T)				
Casuarina fraseriana	*	1.6 $\pm$ 0.5	1.7 $\pm$ 0.5	3.7 $\pm$ 1.7
Jacksonia sternbergiana	*	*	1.2 $\pm$ 0.3	1.6 $\pm$ 0.5
<u>Shrub species</u> (S)				
Adenanthos sericea	1.8 $\pm$ 0.8	*	*	*
<u>Perennial Herb species</u> (PH)				
▶ *Capobrotus spp.*	1.9 $\pm$ 0.6	6.6 $\pm$ 2.5	*	*
<u>Annual Herb species</u> (AH)				
▶ *Hypochoeris spp.*			*	3.0 $\pm$ 0.5
Species type A	*			
Species type B		*		
Species type C			*	
Species type D				*
Species type E			*	*
Species type F	*	*		
Species type G	*		*	*
Species type H	*	*	*	*

Species type A:- *Bossiaea eriocarpa (S), Daviesia juncea (S), Gompholobium tomentosum (S), Hardenbergia comptoniana (S),*

Table 6.12 cont. Western grey kangaroo diet composition ($\bar{x} \pm$ s.e.) 1984.

Melaleuca teretifolia (S), *Dampiera linearis* (PH).

Species type B:- ►*Aira* spp. (G), *Amphipogon turbinatus* (G), *Schoenus curvifolius* (PS), *Nuytsia floribunda* (T), *Exocarpos sparteus* (S), *Hibbertia racemosa* (S).

Species type C:- *Sowerbaea laxiflora* (PS), *Acacia saligna* (S), *Hybanthus calycinus* (PH), *Centella cordifolia* (PH), ►*Ursinia anthemoides* (AH).

Species type D:- *Caesia parviflora* (PS), *Kennedia prostrata* (PH).

Species type E:- ►*Avena barbata* (G), ►*Bromus* spp. (G), *Schoenus grandiflorus* (PS), *Caladenia* spp. (PS), *Erynigium pinnatifidum* (PH), ►*Wahlenbergia capensis* (AH).

Species type F:- *Dianella revoluta* (PS), *Thysanotus* spp. (PS), *Tricoryne elatior* (PS), *Stirlingia latifolia* (S), *Acacia cochlearis* (S), *Euchilopsis linearis* (S), *Scholtzia involucrata* (S).

Species type G:- *Laxmannia* spp. (PS), ►*Gladiolus caryophyllaceus* (AS), *Leucopogon* spp. (S).

Species type H:- *Jacksonia furcellata* (T), *Conospermum stoechadis* (S), *Hovea trisperma* (S).

Table 6.13 Quokka diet composition ($\bar{x} \pm$ s.e.) summarized in terms of plant classes.

PLANT CLASSES	1982				1983				1984			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Grass species	1.1±0.3	0.4±0.2	10.7±2.2	26.8±7.5	1.3±0.6	6.1±1.8	9.5±1.2	14.9±3.4	26.1±5.1	9.6±2.7	27.1±2.4	15.6±3.0
Sedge species	6.0±1.8	15.0±3.6	14.4±3.8	10.8±4.1	21.7±4.5	25.0±5.2	14.0±3.6	23.3±5.4	11.8±2.6	15.3±2.7	6.3±1.2	11.5±2.7
Non-herb. dicots.	88.1±3.1	72.7±5.4	70.8±3.8	56.6±12.3	66.5±3.8	67.0±5.9	69.5±5.6	55.8±8.2	52.1±5.8	66.9±3.6	59.0±3.3	59.6±4.5
Perennial herbs	6.8±2.4	13.7±6.5	5.1±1.1	4.6±1.6	13.7±3.5	5.2±0.6	5.5±0.9	7.9±1.2	10.7±3.6	11.5±2.9	11.1±1.6	6.9±1.4
Annual herbs	0.1±0.1		0.6±0.2	4.8±0.8	0.8±0.4		0.8±0.5	1.0±0.4	3.2±1.1		0.8±0.3	10.5±1.4

Table 6.14 Brush wallaby diet composition ($\bar{X} \pm$ s.e.) summarized in terms of plant classes.

PLANT CLASSES	1982				1983				1984			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Grass species	0.1±0.1	0.1±0.1	0.9±0.4	3.1±1.0		0.8±0.3	2.6±0.6	3.4±0.9	1.7±0.5	1.0±0.6	8.0±2.0	4.6±0.8
Sedge species	4.3±3.6	2.6±1.5	1.7±0.7	6.2±3.4	1.6±0.6	1.0±0.0	0.8±0.3	12.2±5.9	3.8±1.5	4.0±2.1	3.2±0.6	7.6±1.8
Non-herb. dicots.	89.9±4.1	96.8±1.7	96.7±1.1	89.7±3.6	97.2±0.7	97.8±1.1	95.0±0.9	79.1±6.3	91.1±2.0	91.3±2.1	85.3±2.0	80.2±1.1
Perennial herbs	5.1±2.1	0.7±0.2	0.6±0.2	0.3±0.2	2.2±0.4	0.8±0.5	1.2±0.3	2.4±0.8	3.2±0.4	4.0±1.1	2.5±1.0	3.0±0.4
Annual herbs			0.6±0.2	1.1±0.7	0.2±0.2		0.8±0.4	4.7±0.7	0.8±0.5		1.5±0.7	6.2±1.2

Table 6.15 Euro diet composition ($\bar{x} \pm$ s.e.) summarized in terms of plant classes.

PLANT CLASSES	1982				1983				1984			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Grass species	34.3±7.0	3.3±1.1	20.9±6.2	77.7±5.1	19.2±8.8	10.4±2.0	30.4±6.6	63.2±1.5	16.5±3.6	9.3±5.0	39.3±5.8	64.3±3.2
Sedge species	59.1±6.7	91.4±2.3	72.9±5.4	20.7±4.8	57.4±11.2	65.0±3.3	61.7±6.5	35.4±0.5	79.3±4.4	79.0±4.8	45.3±12.5	29.0±0.6
Non-herb. dicots.	5.5±1.9	6.8±2.3	5.7±1.6	1.0±0.4	21.8±2.8	17.8±2.2	6.3±1.6	2.4±1.0	5.3±1.6	5.8±1.5	3.0±1.5	1.3±0.7
Perennial herbs	3.6±0.8	2.1±0.6	2.0±1.0	1.0±0.6	3.4±1.4	6.6±1.4	2.6±1.2	1.6±0.7	5.5±3.0	6.3±1.7	4.0±1.5	5.7±0.7
Annual herbs			1.9±0.8	0.1±0.1			4.0±2.1		0.3±0.3		11.3±9.4	4.3±2.9

Table 6.16 Western grey kangaroo diet composition ($\bar{x} \pm$ s.e.) summarized in terms of plant classes.

PLANT CLASSES	1982				1983				1984			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Grass species	8.4±2.8	1.6±0.6	8.4±2.1	29.0±4.4	8.4±2.8	4.2±1.2	12.0±2.4	42.4±5.7	8.6±1.6	3.4±1.0	16.0±1.6	37.5±5.1
Sedge species	86.8±2.9	91.5±1.7	88.0±2.3	67.8±4.5	86.7±2.6	88.7±1.8	85.1±2.5	55.4±5.6	85.1±2.3	87.8±3.2	82.1±1.8	55.6±5.2
Non-herb. dicots.	5.6±1.6	7.8±1.7	3.5±1.0	4.2±0.9	5.3±1.5	6.1±1.9	2.7±0.5	1.4±0.5	5.5±2.2	5.6±0.8	4.2±0.8	6.6±1.8
Perennial herbs	2.0±0.5	1.9±0.7	0.9±0.5	0.3±0.2	1.1±0.5	2.5±0.8	1.7±0.3	0.8±0.4	2.2±0.7	6.6±2.6	1.1±0.4	1.1±0.3
Annual herbs			1.7±0.5	1.5±0.7	0.1±0.1		0.3±0.2	2.1±0.7	0.2±0.2		0.7±0.3	3.0±0.4

There was no consistent trend with respect to the number of plant species in diet compositions, between seasons or over successive years, for any of the macropodid species.

6.3.2 Species dietary overlap

Seasonal dietary overlap between the macropodid species for each year is presented in Table 6.17. The magnitude of dietary overlap was greatest between western grey kangaroos and euros and then, in decreasing order, between quokkas and brush wallabies, and between euros and quokkas. The degree of dietary overlap between brush wallabies and western grey kangaroos, quokkas and western grey kangaroos, and brush wallabies and euros was negligable. There was no consistent trend in the degree of species' dietary overlap between seasons within and across years.

6.3.3 Discriminant function analysis of species' feeding patterns

Reduced species' population sizes, particularly changes in quokka and euro numbers, and thus limited faecal collections for these species did not permit useful discriminant function analyses to be conducted seasonally for each year. Rather, it was necessary to pool data across years for each season.

Discriminant function analyses were conducted on data for individual seasons, across all seasons and various combinations of seasons. Use of the classification option in the programme DISCRIMINANT enabled comparisons of predicted group membership with actual group membership. Thus, it was possible to measure the success of discrimination, for each analysis, by observing the proportion of correct classifications. Comparisons of predicted and actual group membership showed greatest correspondance for individual seasonal analysis, rather than for seasonal combinations. As such, further discussion of discriminant function analysis of species' feeding patterns will be restricted to a seasonal basis.

Table 6.17 Dietary overlap coefficients (C_λ) among the four macropodid species.

	Quokka			Brush wallaby			Euro		
	1982	1983	1984	1982	1983	1984	1982	1983	1984
Brush wallaby									
Summer	0.75	0.21	0.45						
Autumn	0.27	0.39	0.74						
Winter	0.62	0.43	0.71						
Spring	0.62	0.36	0.82						
Euro									
Summer	0.02	0.40	0.10	0.04	0.12	0.02			
Autumn	0.10	0.25	0.15	0.01	0.02	0.06			
Winter	0.08	0.12	0.21	0.05	0.01	0.02			
Spring	0.06	0.07	0.09	0.02	0.03	0.04			
Western grey kangaroo									
Summer	0.01	0.01	0.07	0.06	0.03	0.01	0.74	0.22	0.65
Autumn	0.05	0.03	0.10	0.02	0.01	0.04	0.93	0.83	0.76
Winter	0.02	0.13	0.09	0.00	0.01	0.01	0.83	0.65	0.72
Spring	0.05	0.07	0.08	0.04	0.04	0.05	0.68	0.93	0.88

Discriminant functions were extracted until at least 90% of the among-species variance was accounted for. In all cases, the first two discriminant functions accounted for more than 90% of the variance extracted. The distribution of species' centroids (niche centres) and discriminant score plots for each individual diet composition are plotted for the first two discriminant functions for each season (see Figures 6.1 to 6.4). The distances between the species' centroids and their locations, relative to the two axes, indicate the extent and nature of species separation. The discriminant score plots for individual diet compositions indicate the degree of overlap between species' feeding niches. Variable patterns (standardized weights), communalities and the extracted percentage of among-species variance are presented for the discriminant functions (see Tables 6.18 to 6.21).

Differences in group centroids were tested for statistical significance by calculating an F ratio for the Mahalonobis distance between each pair of groups. Results indicated all pairs of centroids were significantly different ($p < 0.01$).

Analysis of the discriminant function coefficients revealed the most valuable plant species for discriminating between the diet compositions of the various macropodid species. It was therefore possible to name the discriminant functions on this basis. The significance of variables to species' separation differed with the species seasonal changes in dietary preferences. Thus, interpretation of the discriminant function analyses is best approached from examination of the variable patterns in terms of broad forage classes and site vegetation floristics. On this basis, the results indicate a general pattern in niche separation of species' feeding patterns across seasons.

The primary dimensions may be interpreted as a gradient from diets variably dominated by sedge and grass species to diets dominated by perennial non-herbaceous dicotyledons and perennial herbaceous species. This gradient separates the feeding niches of western grey kangaroos and euros, predominately grazing species, from quokkas and brush wallabies, predominately browsing species. The variable *Cynodon dactylon,* a perennial grass species, is the one exception to this general trend. The species is present only in the *Astartea fascicularis/Hypocalymma angustifolium* vegetation association where it forms an important dietary component for quokkas.

The secondary dimensions separate the feeding niches of the two browsing species; the feeding niches of western grey kangaroos and euros being intermediate. Separation between quokkas and brush wallabies is achieved by certain dietary variables associated with particular vegetation associations. On these dimensions the quokka feeding niche is associated with shrub and perennial herbaceous dietary species found in the *Astartea fascicularis/ Hypocalymma angustifolium* vegetation association. The brush wallaby feeding feeding niche is associated with dietary species found in the drier woodland sites. The percentage of among-species variance extracted on the secondary dimensions during autumn and winter is particularly low. Thus, the degree of separation and variable patterns associated should be treated with caution.

Figure 6.1 Species' feeding patterns in summer - a two dimensional plot of discriminant scores and group centroides (letters) on each discriminant function.

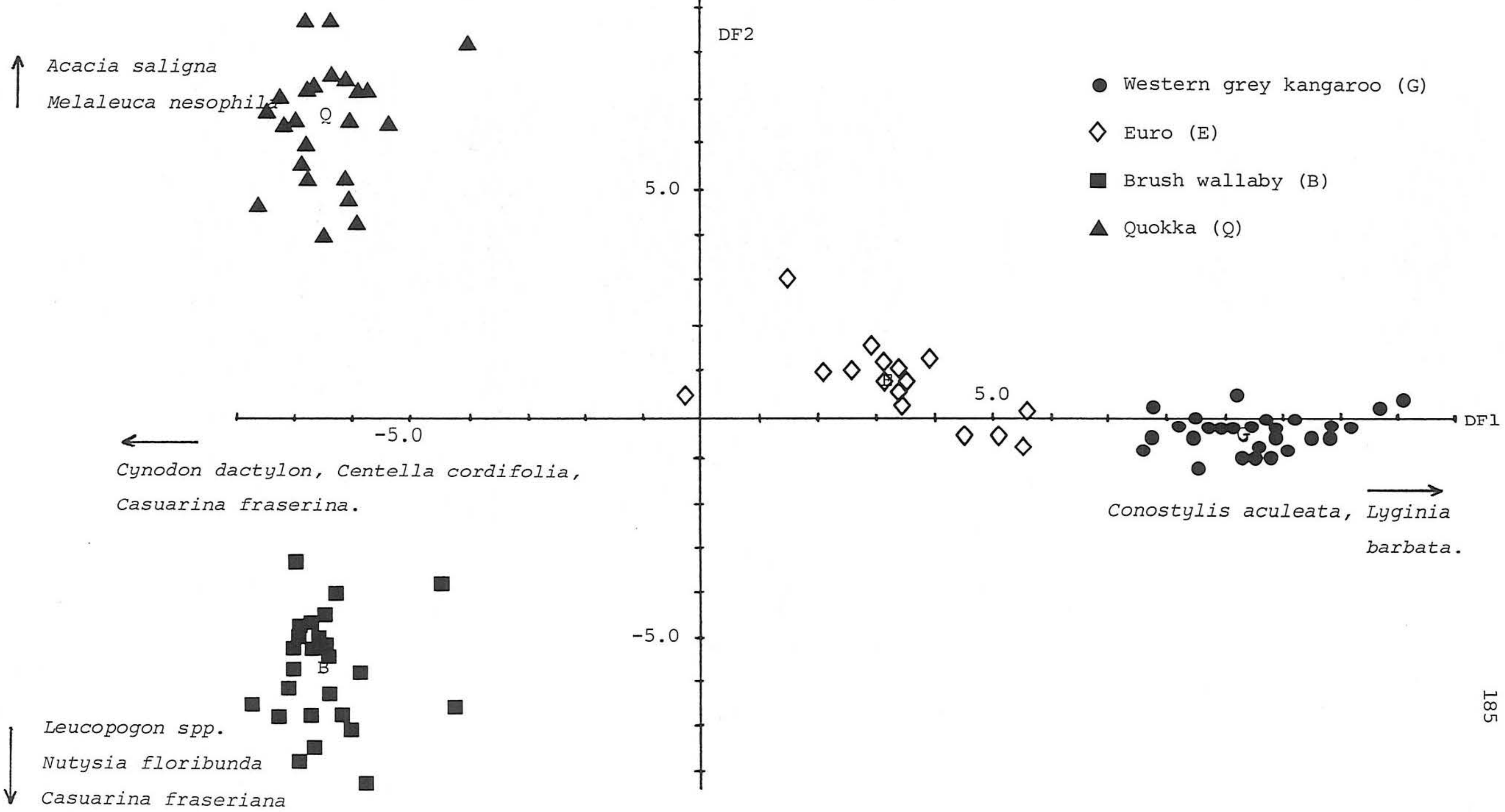


Table 6.18 Standardized discriminant function coefficients and communalities for summer diet variables.

VARIABLES	DF1	DF2	COMMUNALITIES
GRASS SPECIES			
Stipa spp.	0.2241	0.1928	0.0874
Cynodon dactylon	-0.5637	1.2734	1.9393
Vulpia spp.	0.8008	0.0439	0.6432
Danthonia occidentalis	0.4255	-0.1189	0.1952
Ehrharta longiflora	0.0778	0.2567	0.0719
SEDGE SPECIES			
Baumea articulata	0.3366	0.2643	0.1832
B. juncea	0.1097	0.2346	0.0671
Mesomelaena stygia	1.0570	0.2414	1.1755
Schoenus sublaxus	0.4354	-0.0473	0.1918
Hypolaena exsulca	0.4130	0.1788	0.2025
Loxocarya pubescens	0.3993	-0.3240	0.2644
Lyginia barbata	1.9289	0.3713	3.8585
Dasypogon bromeliaefolius	0.5197	-0.1204	0.2846
Lomandra spp.	0.4463	0.3132	0.2973
Tricoryne elatior	-0.3829	0.2290	0.1991
Conostylis aculeata	1.1761	0.3545	1.5089
Phlebocarya ciliata	1.0566	0.1902	1.1526
Gladiolus caryophyllaceus	-0.3072	-0.2890	0.1779
NON- HERB. DICOTS.			
Casuarina fraseriana	-0.3093	-0.5804	0.4325
Conospermum stoechadis	0.3828	0.2402	0.2042
Exocarpos sparteus	-0.1484	0.5201	0.2925
Nuytsia floribunda	-0.1757	-0.4680	0.2499
Acacia saligna	-0.3246	1.5327	2.4545
Viminaria juncea	0.2955	0.6299	0.4841
Leucopogon spp.	-0.2706	-0.4962	0.3194
Hibbertia hypericoides	-0.0991	0.3989	0.1689
Hypocalymma angustifolium	-0.0814	0.4352	0.1960
Kunzea ericifolia	-0.3354	1.0346	1.1828
Melaleuca nesophila	-0.3238	1.4060	2.0817
M. teretifolia	-0.1524	0.9598	0.9444
M. thymoides	-0.2782	-0.0786	0.0836

Table 6.18 cont. Standardized discriminant function coefficients and communalities for summer diet variables.

VARIABLE			
PERENNIAL HERB SPECIES			
Centella cordifloia	-0.4494	0.9673	1.1376
Comesperma spp.	-0.1956	-0.2283	0.0904
% among-species variance extracted	67.1	26.4	

Figure 6.2 Species' feeding patterns in autumn - A two dimensional plot of discriminant scores and group centroides (letters) on each discriminant function.

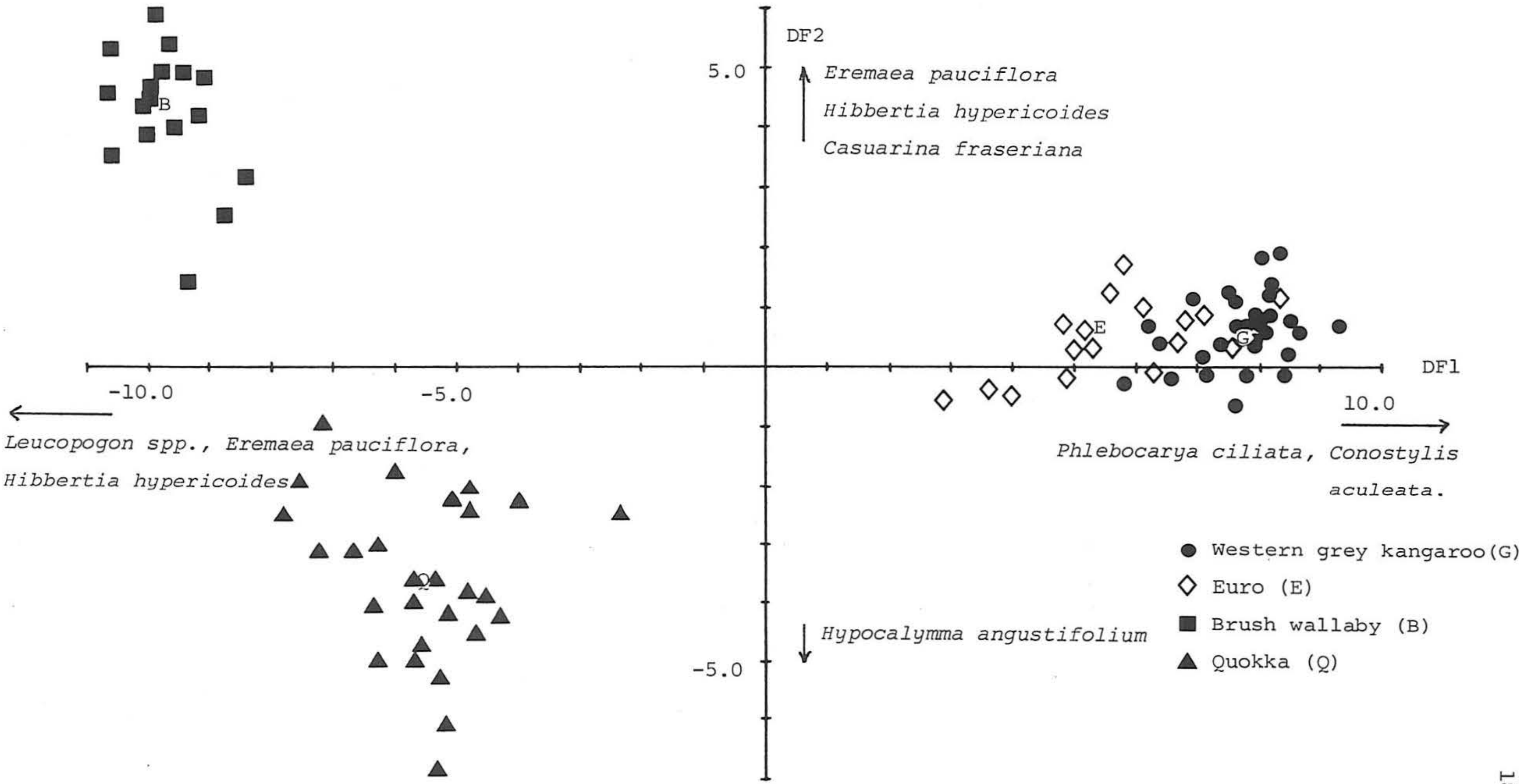


Table 6.19 Standardized discriminant function coefficients and communalities for autumn diet variables

VARIABLES	DF1	DF2	COMMUNALITIES
GRASS SPECIES			
Briza spp.	0.8253	0.2957	0.7686
Vulpia spp.	0.1204	0.0970	0.0239
Danthonia occidentalis	0.0314	0.2340	0.0557
SEDGE SPECIES			
Baumea juncea	1.0070	0.3120	1.1114
Lepidosperma costale	0.4469	0.2276	0.2515
Mesomelaena stygia	0.3617	0.1774	0.1623
Schoenus sublaxus	0.2153	0.2023	0.0873
Hypolaena exsulca	0.4272	0.1118	0.1950
Loxocarya pubescens	0.3679	0.3905	0.2878
Lyginia barbata	1.1935	0.6401	1.8342
Dasypogon bromeliaefolius	1.2151	0.5923	1.8273
Laxmannia spp.	-0.1991	0.1552	0.0637
Lomandra spp.	0.4513	0.3252	0.3094
Conostylis aculeata	1.7463	0.8267	3.7330
Phlebocarya ciliata	1.2971	0.8301	2.3715
Patersonia occidentalis	0.3309	-0.3341	0.2211
NON-HERB. DICOTS.			
Casuarina fraseriana	-0.1469	1.2324	1.5404
Adenanthos sericea	0.2753	0.2650	0.1460
Acacia saligna	0.1042	0.4408	0.2052
Bossiaea eriocarpa	0.0216	-0.0606	0.0041
Jacksonia furcellata	0.0325	0.4980	0.2491
J. sternbergiana	-0.0406	0.8142	0.6646
Leucopogon spp.	-0.6522	0.3516	0.5490
Hibbertia hypericoides	-0.3604	1.5785	2.6126
H. racemosa	0.0247	-0.3253	0.1064
Eremaea pauciflora	-0.4406	1.5819	2.6965
Hypocalymma angustifolium	0.0955	-0.3521	0.1331
Melaleuca thymoides	-0.0371	0.5698	0.3260
PERENNIAL HERB SPECIES			
Capobrotus spp.	0.3190	0.5155	0.3676
Centella cordifolia	0.1798	0.2226	0.0819
% among-species variance extracted	83.9	12.2	

Figure 6.3 Species' feeding patterns in winter - a two dimensional plot of discriminant scores and group centroids (letters) on each discriminant function.

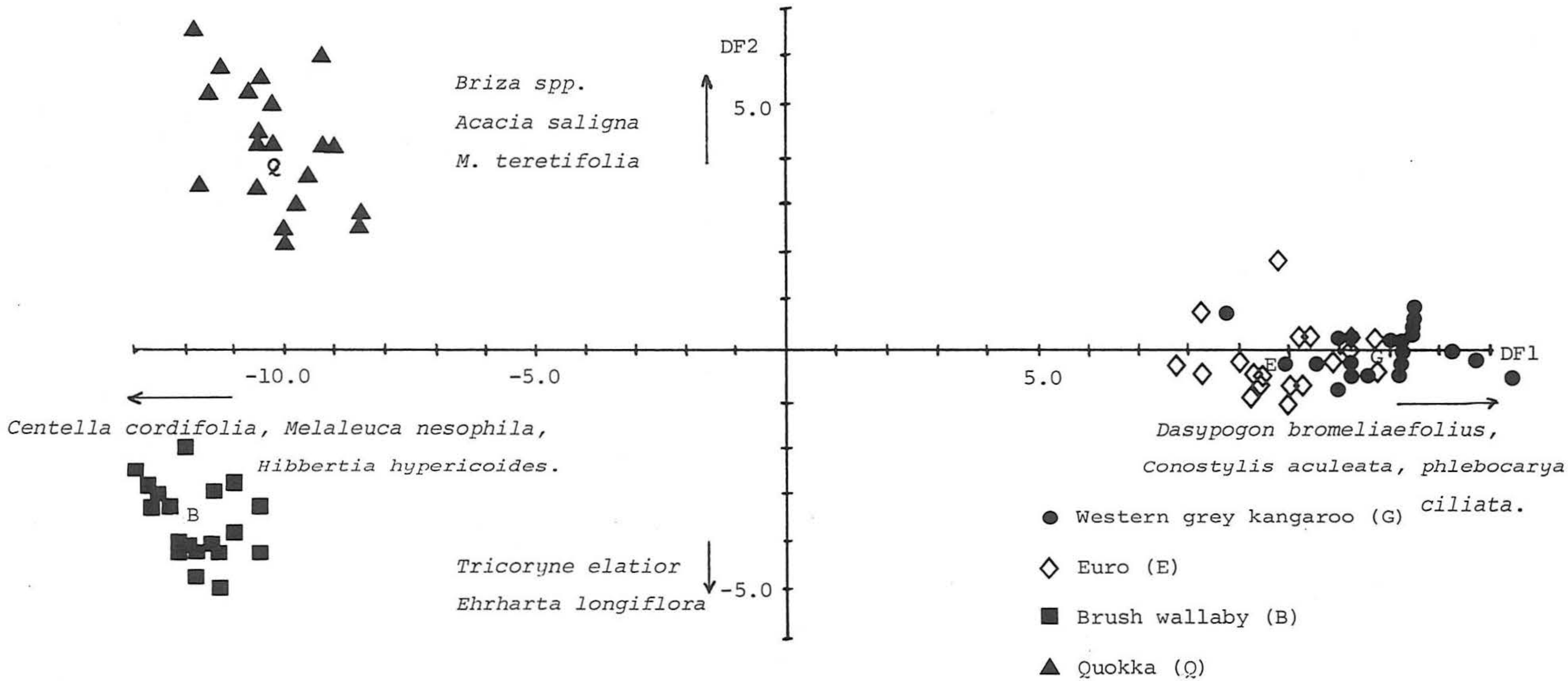


Table 6.20 Standardized discriminant function coefficients and communalities for winter diet variables.

VARIABLES	DF1	DF2	COMMUNALITIES
GRASS SPECIES			
Stipa spp.	1.0519	0.0895	1.1145
Briza spp.	1.6880	0.8461	3.5652
Cynodon dactylon	-0.2929	0.0314	0.3096
Ehrharta longiflora	0.4589	-0.3146	0.3096
SEDGE SPECIES			
Baumea articulata	0.6347	0.0134	0.4030
B. juncea	0.4668	0.0807	0.2244
Lepidosperma costale	0.4273	0.2565	0.2484
Mesomelaena stygia	1.5735	0.3557	2.6024
Schoenus sublaxus	0.5711	0.2484	0.3879
Hypolaena exsulca	0.7015	0.0129	0.4923
Loxocarya pubescens	0.7784	0.1983	0.6452
Lyginia barbata	0.3125	0.0433	0.0995
Dasypogon bromeliaefolius	1.9699	0.4472	4.0805
Lomandra spp.	0.8797	0.0495	0.7763
Tricoryne elatior	0.3427	-0.1843	0.1514
Conostylis aculeata	2.6661	0.4883	7.3465
Phlebocarya ciliata	2.7249	0.6372	7.8311
NON-HERB. DICOTS.			
Acacia pulchella	0.4868	0.1819	0.2701
A. saligna	0.2715	0.7298	0.6063
Hibbertia hypericoides	-0.3760	0.5280	0.4202
H. racemosa	0.0188	-0.2855	0.0819
Melaleuca nesophila	-0.3593	0.5488	0.4303
M. teretifolia	-0.0603	0.6785	0.4640
M. rhapiophylla	-0.0531	0.4582	0.2128
PERENNIAL HERB SPECIES			
Centella cordifolia	-0.8302	0.4395	0.8824
Comesperma spp.	-0.1491	0.4020	0.1838
ANNUAL HERB SPECIES			
Arctotheca calendula	0.9120	0.2872	0.9142
% among-species variance extracted	93.0	5.4	

Figure 6.4 Species' feeding patterns in spring - a two dimensional plot of discriminant scores and group centroids (letters) on each discriminant function.

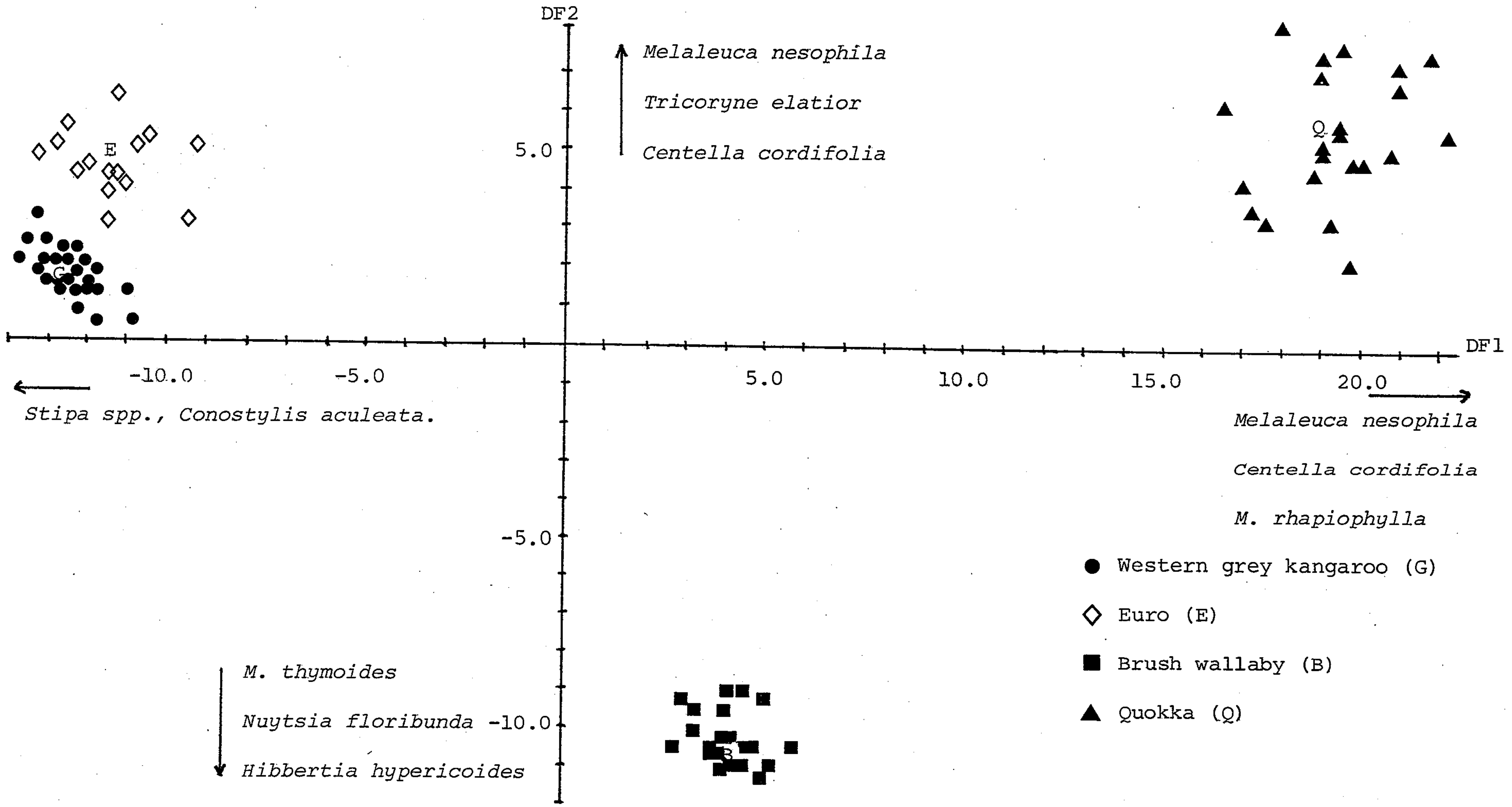


Table 6.21 Standardized discriminant function coefficients and communalities for spring diet variables.

VARIABLES	DF1	DF2	COMMUNALITIES
GRASS SPECIES			
Stipa spp.	-1.0696	1.0037	2.1514
Cynodon dactylon	1.5219	1.0008	3.3178
Vulpia spp.	-0.4134	0.4432	0.3673
Ehrharta longiflora	-0.4003	0.5872	0.5050
SEDGE SPECIES			
Baumea articulata	0.8976	0.1184	0.8197
B. juncea	-0.5420	-0.2955	0.3811
Lepidosperma costale	0.3312	-0.1833	0.1433
Schoenus sublaxus	-0.5244	0.3523	0.3991
Loxocarya pubescens	-0.4216	0.3435	0.2957
Lyginia barbata	-0.4806	0.4200	0.4074
Laxmannia spp.	0.4096	-0.3323	0.2782
Lomandra spp.	-0.3586	0.2129	0.1739
Tricoryne elatior	-0.7626	1.4024	2.5483
Conostylis aculeata	-0.7952	0.7365	1.1748
Phlebocarya ciliata	-0.5794	0.4572	0.5447
Gladiolus caryophyllaceus	-0.2413	0.3270	0.1652
Patersonia occidentalis	-0.4061	0.0838	0.1719
NON-HERB. DICOTS.			
Casuarina fraseriana	0.4447	-0.2960	0.2854
Nuytsia floribunda	0.3959	-0.5610	0.4715
Acacia pulchella	0.9520	0.4394	1.0994
Jacksonia furcellata	0.4332	-0.4506	0.3907
J. sternbergiana	0.4108	-0.4941	0.4129
Hibbertia hypericoides	1.5192	-0.6734	2.7614
H. racemosa	-0.1868	0.3399	0.1504
Eremaea pauciflora	0.6051	-0.2767	0.4427
Hypocalymma angustifolium	0.7634	-0.0029	0.5828
Kunzea ericifolia	0.2759	0.1375	0.0950
Melaleuca nesophila	2.1878	1.6243	7.4248
M. teretifolia	0.4010	0.4280	0.3440
M. thymoides	1.0239	-0.5258	1.3248
M. rhapiophylla	1.5783	0.9860	3.4632

Table 6.21 cont. Standardized discriminant function coefficients and communalities for spring diet variables.

VARIABLES	DF1	DF2	COMMUNALITIES
PERENNIAL HERB SPECIES			
Centella cordifolia	1.8837	1.2685	5.1574
Comesperma spp.	0.8708	-0.2747	0.8338
ANNUAL HERB SPECIES			
Arctotheca calendula	0.7854	0.7288	1.1480
% among-species variance extracted	79.8	18.7	

6.4 Discussion

Food selection is governed by a complex mixture of factors which are reviewed by Van Dyne *et al.* (1980). A conceptual framework for understanding the nutritional basis for food selection and food resource partitioning in herbivore comminities has been outlined by Hanley (1982). The framework consists of four morphological parameters: (1) body size, (2) type of digestive system, (3) rumino-reticular volume to bodyweight ratio and (4) mouth size.

Bodyweight and type of digestive system determine the metabolic rate and overall time-energy constraints within which the herbivore must secure its food. The rumino-reticular volume to bodyweight ratio of a herbivore, and thus the rate of passage, determines the type of food the animal is most efficient at processing. High rumino-reticular volume to bodyweight ratio is an adaption to a high cellulose content diet, typically a diet consisting primarily of grasses and sedges. Low rumino-reticular volume to bodyweight ratio is an adaption to a high cellular content and/or high lignin diet, typically a diet consisting primarily of young grasses, forbs and browse (Hofmann and Stewart, 1972; Hanley, 1982). Mouth size determines the ability of the herbivore to harvest selectively plant parts or individuals.

Classification of herbivore species into feeder categories was conducted by Hofmann (1973). On the basis of diet compositions and stomach morphologies, he classified a number of African ungulates into three major groups:

1. Bulk or roughage feeders - Species with large rumens , these animals feed principally on diets composed of grass and sedge species.
2. Concentrate feeders - Species with small rumens, these animals have a high proportion of forb and browse species in

their diets.

3. Mixed feeders - Species with an intermediate sized rumen whose diets comprised grass, forbs and browse.

Small species tend to be concentrate or mixed feeders, that is having diets of high nutritive value, while the larger species tend to be bulk or roughage feeders, that is having diets of lower nutritive value. While this general trend may be true in most cases, notable exceptions to the rule demonstrate that body size and rumen volume are not necessarily dependent on one another. Rather, the relationship is dependent on the nutritional characteristics of the forage resource that is exploited (Hanley, 1982). Optimum combinations of the above morphological parameters also depend on the constraints of climate, predation and potential modification by social organization factors (*Op. cit.*).

Results of discriminant function analyses in this study indicated a gradient of forage selectivity associated with differences in diet compositions. Species' seasonal feeding niches were separated, on the primary dimensions, along a gradient of forage type preference. The larger macropodid species, western grey kangaroos and euros, dietary preferences consisted of sedge and grass species. The smaller macropodid species, brush wallabies and quokkas, dietary preferences comprised principally of browse species. Despite similarities in the forage types selected by these two groups of species, the highly significant differences between species' seasonal centroid locations indicates dissimilarities in the plant species compositions of their diets.

Using the classification system of Hofmann (1973), western grey kangaroos and euros may be considered bulk or roughage feeders, quokkas mixed / concentrate feeders and brush wallabies to be concentrate feeders. These feeding classifications are in agreement with those of Main (1986). Although ratios of rumino-reticular volume to bodyweight were not recorded for the study species, dietary preferences would appear to indicate correlation of the two parameters in this group of macropodid species.

Herbivores select food items from a chemically heterogenous spectrum and what constitutes an individual food item is often not evident. Chemical descriptions of a food item is a difficult task. Each plant is highly variable, depending on plant part, plant vigour, habitat, phenology and intraspecific variation (Hanley, 1982). Different species of plants also differ greatly in their content of specific nutrients, toxins and plant secondary compounds. Thus, at a finer grain of resolution than the above morphological constraints, herbivores must select diets within the constraints of obtaining minimum levels of specific plant nutrients (Westoby, 1974) while not exceeding maximal levels of specific plant secondary compounds (Freeland and Janzen (1974).

Within the above constraints, species will select the most nutritious items available at a given time of year. The forage quality of a plant (or plant parts) varies as a function of phenology; and phenological changes occur at different times of year for different species. Thus, the optimal diet for a herbivore, determined on the basis of the relative quality and availability of forage species, varies seasonally as a consequence of seasonal changes in both these parameters.

Results of this study indicated seasonal changes in the dietary items of the species. However, changes in the utilization of many dietary items was not consistent over years and thus allowed no interpretation of the relationship between dietary species and seasonal incidence of nutritional stress. Over successive years, increases occurred in what is believed the more palatable plant species, due to the reduction in the locally overabundant macropodid populations. General increases in the percentage dry weight composition of the native grass species *Danthonia occidentalis* and *Stipa spp.* were recorded in the diets of western grey kangaroos and to a lesser and more variable extent in euro diets over successive years. The percentage dry weight composition of many leguminous species increased in all study species' diets over successive years. All the above plant species showed general increases in occurrence over the reserve in successive years. Thus, it is suggested that the increased availability of certain more palatable species enabled animals to select more preferred dietary items at the expense of less preferred species. These shifts in dietary items were therefore responsible for the inconsistent seasonal utilization of many plant species; particularly the common species of dietary plants.

Contemporary competition theory suggests that diet overlap should be greater among similar sized animals however, the actual relationship between niche overlap and competition is not clear. The more abundant the resource, the less likely it is that competition will result from its common use. Rather, it is the ratio of demand to supply or the degree of saturation, of the environmental resource that is of vital importance in the relationship between niche overlap and competition (Pianka, 1981; Giller, 1984).

Results of this study indicate overlap was greatest between similar sized species however, there was no consistent trend in the degree of species' dietary overlap between seasons within and across years. Inconsistent changes in the seasonal utilization of many plant species discussed above, confounded the measures of overlap.

As stated above, dietary overlap is not sufficient evidence for exploitative competition (Colwell and Futuyuma, 1971; Pianka, 1981). Under light or moderate grazing there are often compensatory growth responses by the grazed plants resulting in a prolongation of the time period of active leaf growth (Crawley, 1983). Clipping experiments with shrubs that are regularly browsed by ungulates frequently show increases in productivity (Ellison, 1960). Defoliation of grasses results in the production of new leaves either from the same tiller or through the development of new tillers.

Examination of the relationships between species' feeding patterns and spatial distributions will be used in Chapter 7 in the interpretation of the overall niche differentiation among the coexisting study species on the reserve.

CHAPTER 7

GENERAL DISCUSSION

7 GENERAL DISCUSSION

Results of this study suggest that the ecological relationships between the study species on the reserve may be discussed in terms of their spatial distributions and feeding patterns. A broad summary of the ecological niches of the study species is given below. Seasonal changes in spatial distributions and feeding patterns are discussed in the relevant chapters. Changes in the species' ecological niches following manipulation of the community niche are discussed later.

Habitat variables important to euro spatial distributions suggest that this species prefers open, grass-dominated areas of the reserve. Euros were classified as bulk or roughage feeders, their diets being dominated by sedge and grass species.

Habitat variables indicating woodland sites of high shrub abundance were of importance to brush wallaby and western grey kangaroo spatial distributions. Diets of brush wallabies were composed principally of browse species. *Hibbertia hypericoides*, one of the dominant shrub species in the woodland vegetation associations, was a particularly common dietary item. On the other hand, western grey kangaroo diets were similar to those of the euro, with the bulk of the diet consisting of sedge and grass species.

The dietary species of euros and western grey kangaroos were generally widespread and abundant throughout the reserve. The variable shrub cover in western grey kangaroo spatial distributions reflected its importance as structural cover rather than a forage category. Niche separation between western grey kangaroos and brush wallabies was based on broad forage-type divisions of preferred dietary resources within the similar spatial distributions.

Quokka spatial distributions were restricted to a specific site type, reflecting the importance of the vegetation structural components; horizontal density and canopy cover. Quokka habitat preferences were restricted to areas in close proximity to the dense thickets of *Baumea articulata* surrounding Banganup Lake. These thickets provided the only area of dense continuous cover on the reserve. Analyses of quokka diets suggest this species is a mixed/concentrate feeder. Quokkas fed on browse species and to a lesser extent on grass and sedge species. Quokka dietary items were mainly restricted to plant species within the lake area vegetation association. However, the level of *Hibbertia hypericoides* in quokka diets indicates limited movement outside their preferred habitat, this shrub being the dominant understorey species in areas immediately adjacent to the lake.

Niche theory provided an appropriate framework for examination of the ecological relationships between the study species. It also provides a sound basis for examination of the effectiveness of past management practices and direction for future management policies.

The original management plan for the reserve proposed to exploit the species' different feeding patterns and habitat preferences, so that the resources of the reserve would be partitioned according to their behavioural and physiological differences. Ecological separation between species, observed in this study, suggest that this policy may have been appropriate in theory but not in practice.

The system of stratified grazing did not necessarily ensure grazing the range of shrubs, herbs and grasses present to facilitate vegetation management for maintenance of the quokka colony. Quokkas were restricated to the limited area of dense continuous cover surrounding Banganup Lake. Feeding activity by the other species was minimal in this area and was generally restricted to autumn when certain dietary items were in common usage. Thus, there was little stratified grazing in this area.

The active management policies pursued did not consider factors of population regulation. Erection of the boundary fence had prevented dispersal as a regulator of population density. Control of predators had also enabled populations of certain species to increase significantly. Populations of western grey kangaroos, brush wallabies and rabbits, species present within the area prior to fencing, had become locally overabundant. As a result of sustained population increases, excessive overgrazing had occurred and plant species richness and diversity had decreased. Wildfires within the reserve had exacerbated the problem of overgrazing. The locally overabundant species' populations had created a system of habitat instability and restricted resource availability, which eventually resulted in the population crashes observed in this study.

Manipulation of the community niche by: (a) reduction of species' population levels to reduce overall grazing pressure and (b) the use of fire to simulate conditions of natural vegetation regeneration, were designed to increase the resources available to the species' populations. Within the limited study time following the manipulations, results indicated increased niche separation in species' spatial distributions and changes in dietary item preferences over consecutive years. Thus, within the broadly defined species' habitat preferences, increased resource availability enabled the reduced population levels to be more selective for specific components of the habitat types. The increased availability of certain more palatable dietary items enabled animals to be more selective in their diet choice. As such, possible problems associated with interspecific and intraspecific competition were reduced.

The initial vegetation surveys indicated a number of leguminous species, preferred grasses such as *Cynodon dactylon*, *Danthonia occidentalis* and *Stipa spp.* and various sedges which when present were observed to be heavily browsed/grazed or inaccessible. During later surveys, when macropodid populations were reduced, species' richness and occurrence of these palatable forms increased. These increases occurred despite their increased dietary importance.

Examination of the impact of fire and subsequent grazing pressure on plant species composition and occurrence suggested a number of important considerations if fire is to be used as an effective environmental management technique.

The hot autumn burn was shown to be important in nutrient recycling, widespread germination of leguminous species, invasion of palatable grasses and the rejuvenation of fire-resistant shrubs through vigorous resprouting from rootstocks and lignotubers. However, the post-burn regenerating vegetation was subjected to intensive grazing pressure, particularly from western grey kangaroos, a mobile species that sheltered in unburnt areas and grazed on the post-burn vegetation.

On reserves of limited size only small area burns are practical. Large scale burns would reduce the total area available for shelter and food resources prior to germination. Such factors would limit the well-being and survival of herbivores present. The area should be fenced to permit plant species' germination and establishment, which would otherwise be the subject of intense grazing pressure. The length of time an area needs to be exclosed and the frequency of fire require examination.

Management programmes must provide a balance between the feeding requirements of herbivore species and the requirements of plant species for fire and the relative freedom from grazing. Results of this study emphasize the importance of regulating herbivore population levels to maintain existing vegetation species' richness and diversity.

The importance of dense continuous cover to quokka habitat preferences deserves special attention if a breeding colony is to be established successfully. It is believed that this type of cover minimizes aggressive encounters between adult males and thus promotes stability for social organization factors to operate within the family group. Secondly, the habitat preferences reflect feeding sites adjacent to shelter where community factors may operate.

The area of dense continuous cover on the reserve is limited. During years of heavy rainfall, this area is further reduced due to water level rises in Banganup Lake. Therefore, the dramatic population declines observed in quokkas may be in part due to inadequate cover. Provision of dense thickets, with species such as *Acacia rostellifera*, in sites distant from the lake area would provide an appropriate solution. These thickets are common in areas near to the reserve and would provide both cover and a palatable food source. Provision of palatable grass species such as *Cynodon dactylon* adjacent to these areas would provide an additional nutritional resource. Similar species of grasses growing at the edge of salt lakes on Rottnest Island maintain high numbers of quokkas during the autumn months when nutritional stress is at its peak.

The reserve management practices derived from this study are considered to have wide application to small reserves where macropodid species are present. In such reserves, detailed monitoring programmes, herbivore population regulation and fire are considered key management practices. These management practices are essential if the vegetation/habitat heterogeneity, in terms of patches, patch size, post-fire regeneration and associated ecotones

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APPENDIX 1

CLIMATIC DATA FOR THE RESERVE.

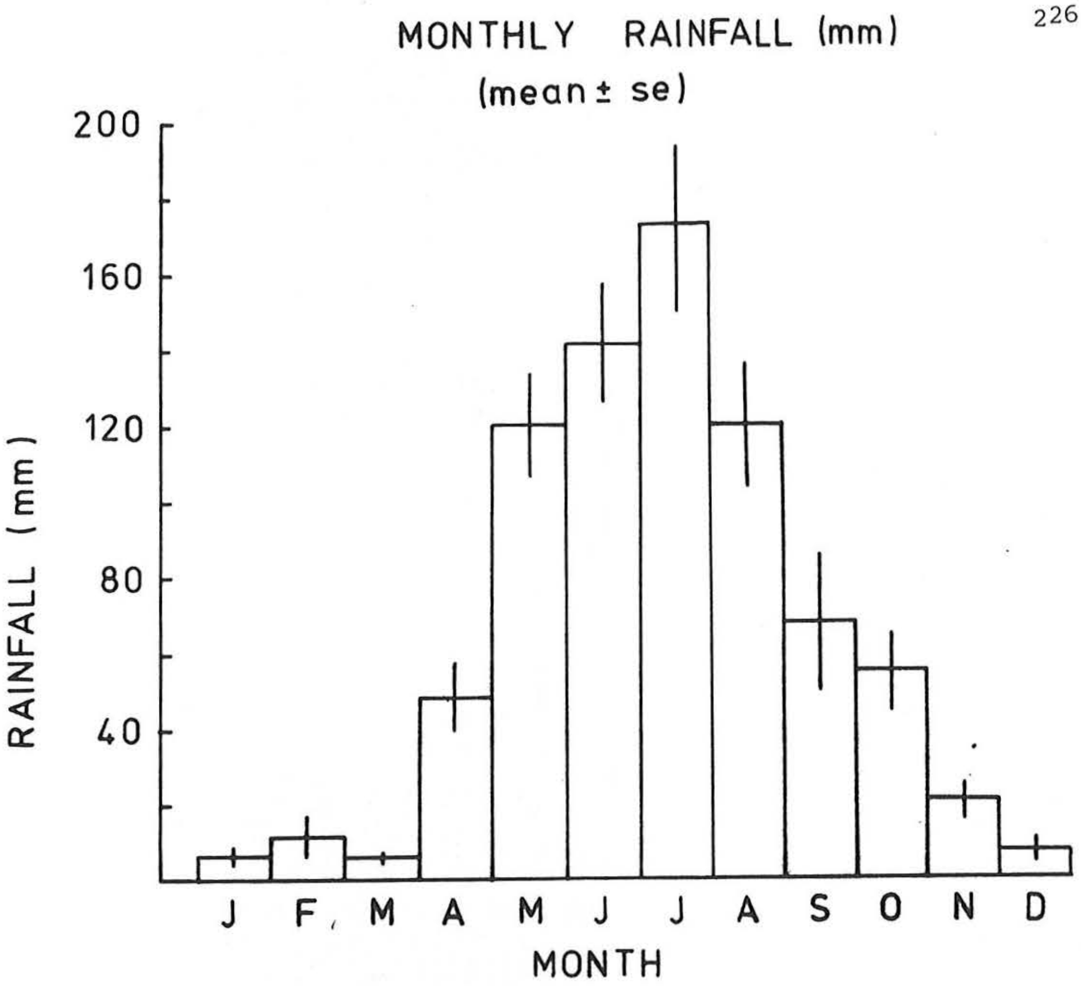

Figure 1.1 Average monthly rainfall (mm), years 1973 to 1980.

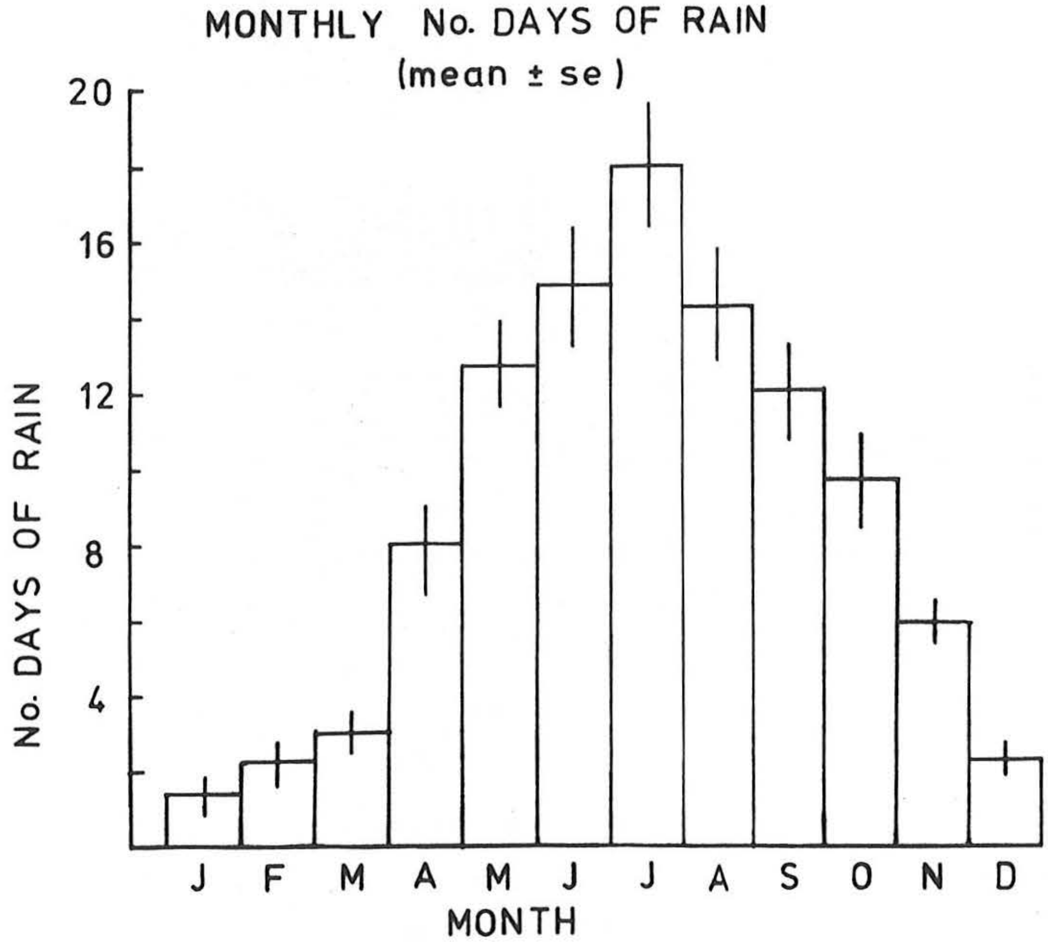

Figure 1.2 Average monthly No. days of rain, years 1973 to 1980.

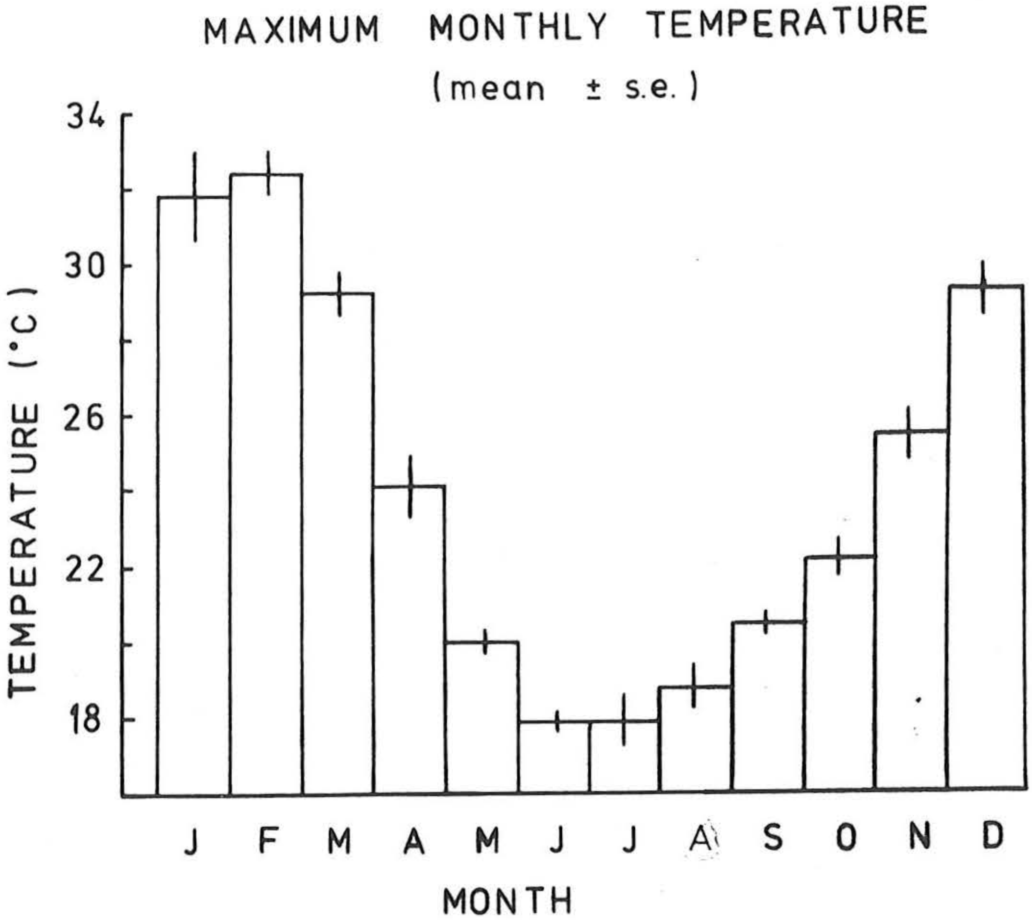

Figure 1.3 Average maximum monthly temperatures, years 1973 to 1980.

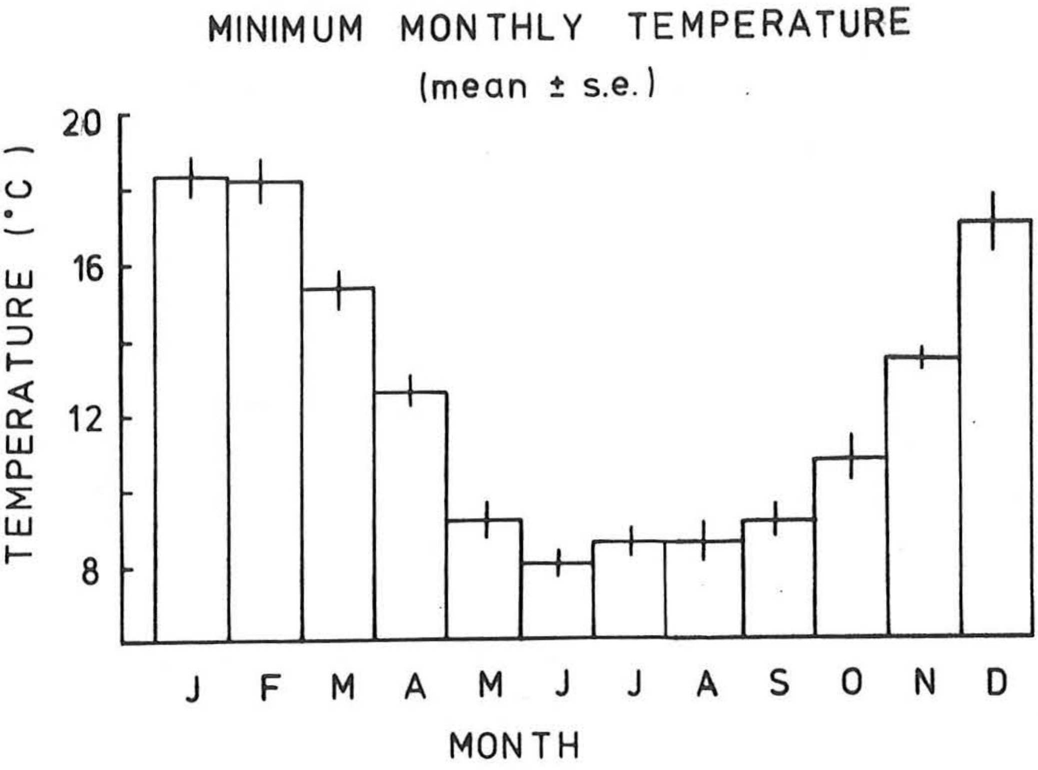

Figure 1.4 Average minimum monthly temperatures, years 1973 to 1980.

Figure 1.5 Monthly rainfall (mm) during the study period.

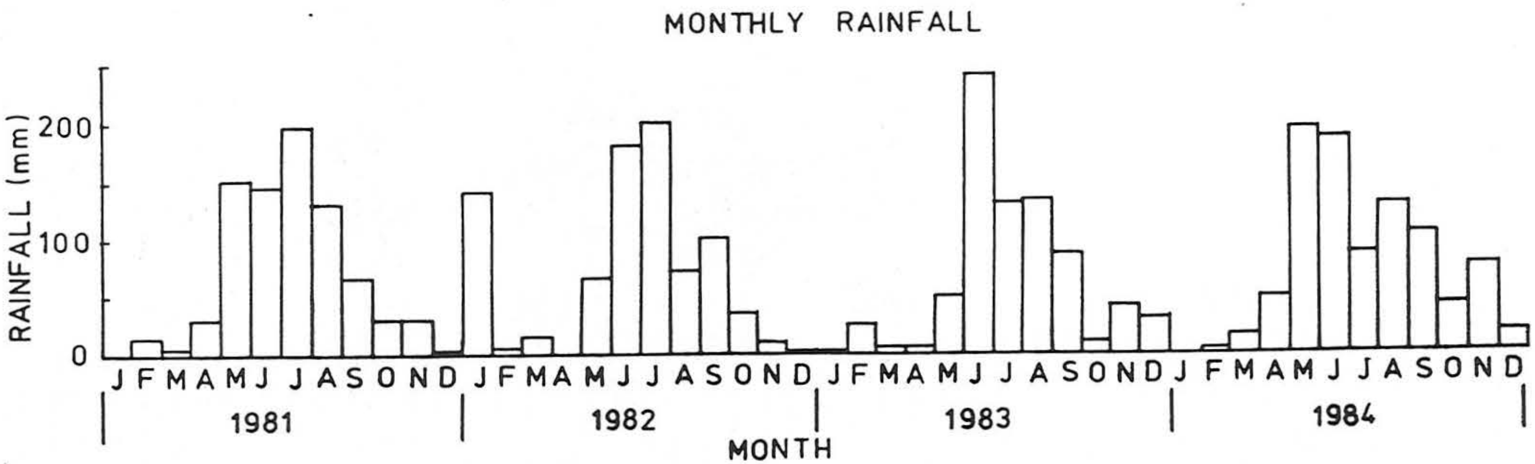

Figure 1.6 Monthly No. days of rain during the study period.

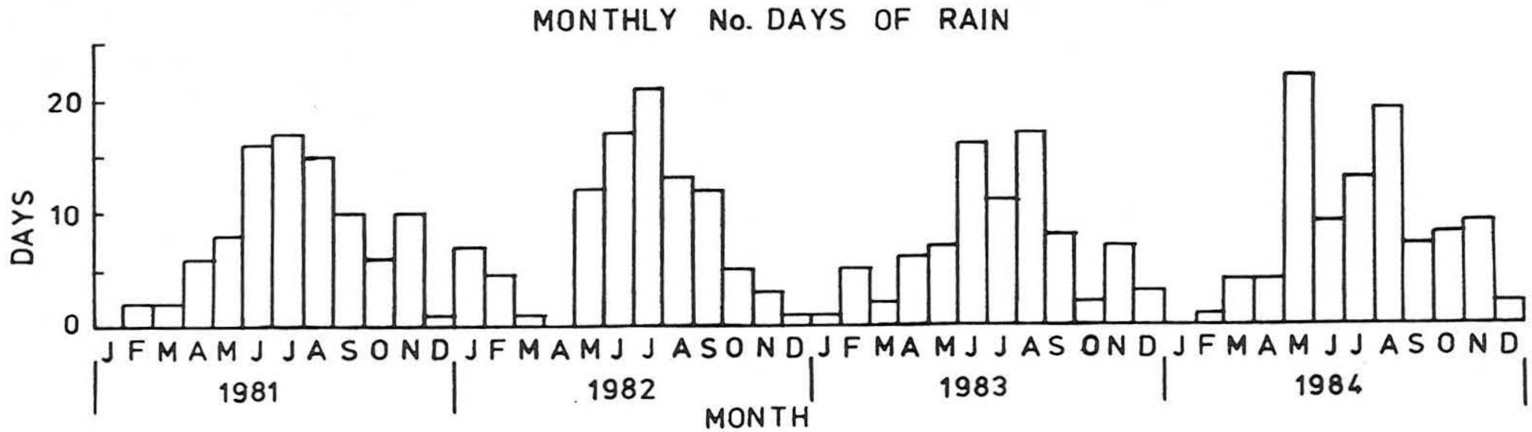

Figure 1.7 Maximum temperatures (^{0}C) during the study period.

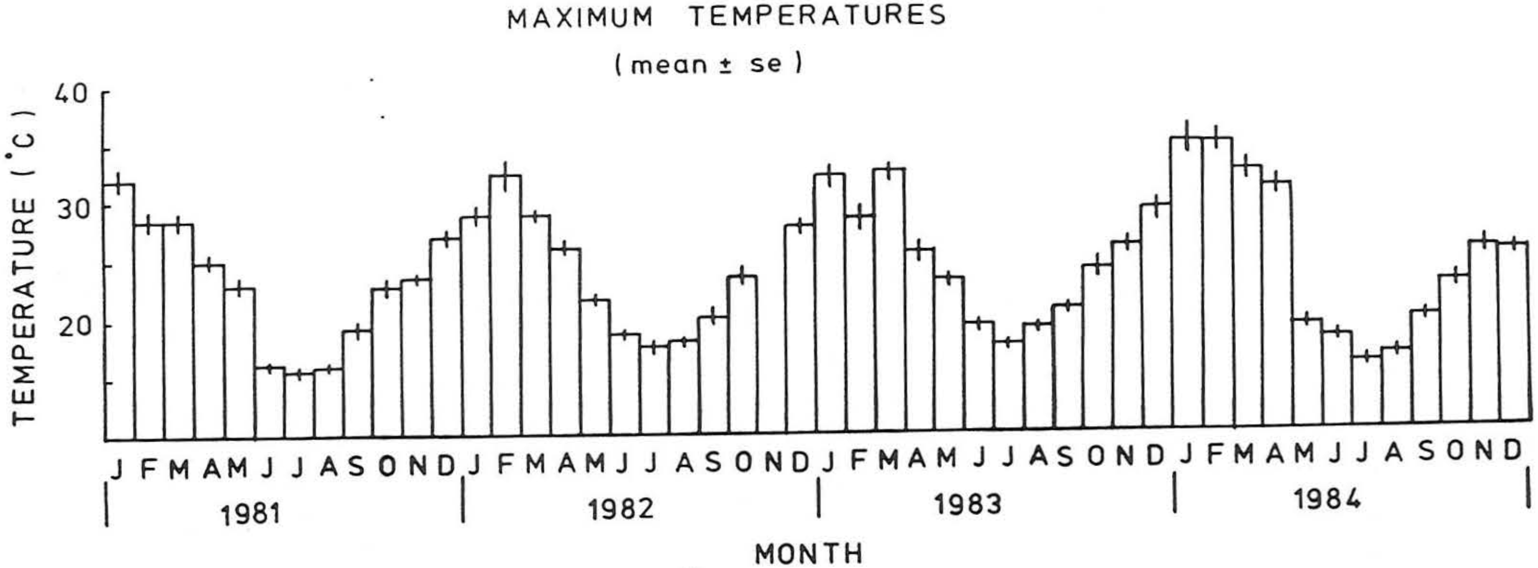

Figure 1.8 Minimum temperatures (^{0}C) during the study period.

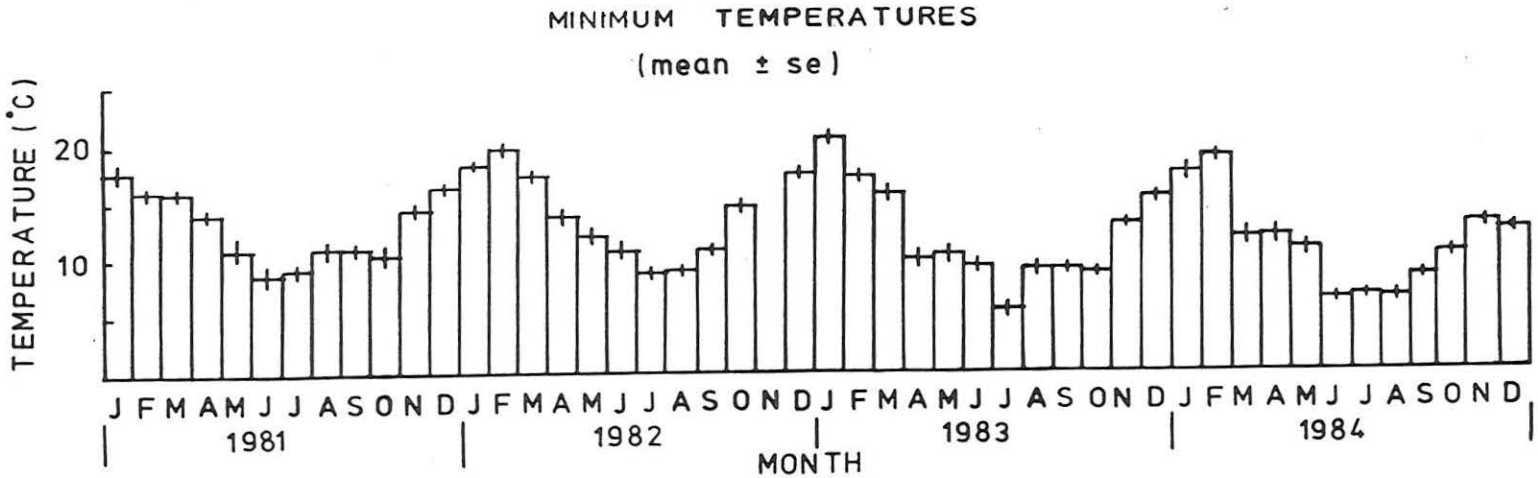

Table 1.1 Monthly Water Levels (m) : Reduced Level R.L. wrt Australian Height Datum A.H.D.

YEAR	JAN.	FEB.	MARCH	APRIL	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
1975		13.542	13.479	13.154	13.134	13.329	13.479	13.667	13.734	13.759	13.701	
1976			12.969	12.884	12.709	12.814	13.239	13.429	13.454	13.444	13.304	
1977				12.472	12.517	12.735	12.939		13.004	12.842	12.641	
1978		11.783	11.713	11.705	11.903	12.348	13.128	13.173	13.383	13.233	12.733	12.403
1979	12.233	12.113	12.013	12.023	12.093	12.253	12.533	12.708	12.808	12.633	12.473	12.193
1980	12.023	11.993	11.843	11.923	12.003		12.908		12.973	12.783	12.703	12.333
1981	12.143	12.013	11.823	11.743	11.683	11.843	12.633	13.263	13.163	12.933	12.803	12.503
1982	12.540	12.240	12.070	12.030	12.000	12.343	12.875	12.828	12.925	12.630	12.270	11.978
1983	11.750	11.730	11.677	11.613	11.700	12.260	12.584			12.352	12.150	
1984	11.770	11.590	11.570	11.714	12.040	12.560		12.510		12.770	12.500	12.025

Reference R.L. of the Well = 13.783m , A.H.D. = 0.000m.

APPENDIX 2

PLANT SPECIES LIST

Legend for Appendix 2

*   indicates introduced plant species.

... indicates plant species found in macropodid diets but not in vegetation surveys.

GRASS SPECIES

POACEAE

* *Aira spp.*	
A. caryophylla L.	annual
A. cupaniana Guss.	"
A. praecox L.	"
Amphipogon turbinatus R.Br.	"
* *Avena barbata* Brot.	"
* *Briza maxima* L.	"
* *B. minor* L.	"
* *Bromus spp.*	
B. gussonii (Parl.) Nevski.	"
B. madritensis Brot.	"
* *Cynodon dactylon* (L) Pers.	perennial
Danthonia occidentalis J. Vickery	"
* *Ehrharta longiflora* Sm.	annual
* *Holcus setiger* Nees	"
... * *Lagurus ovatus* L.	"
* *Polypogon monspeliensis* (L.) Desf.	"
Stipa spp.	
S. compressa R.Br.	"
S. eremophila Reader.	perennial
S. semibarbata R.Br.	"
S. variabilis Hughes	"
* *Vulpia spp.*	
V. bromoides (L.) S. Gray	annual
V. myurus (L.) Gmel.	"

PERENNIAL SEDGE SPECIES

CYPERACEAE

Baumea articulata R.Br.

B. juncea R.Br.

Cladium riparium (Nees) Benth.

Lepidosperma costale Nees

L. scabrum Nees

Mesomelaena stygia (R.Br.) Nees

Schoenus curvifolius (R.Br.) Benth.

S. grandiflorus (Nees) F. Muell.

S. sublaxus Kukenth

RESTIONACEAE

Hypolaena exsulca R.Br.

Loxocarya pubescens (R.Br.) Benth.

Lyginia barbata R.Br.

JUNCACEAE

Luzula meridionalis Nordensk.

LILIACEAE

Burchardia umbellata R.Br.

Caesia parviflora R.Br. tuber

Dasypogon bromeliaefolius R.Br.

Dianella revoluta R.Br.

Laxmannia spp.

L. ramosa Lindl.

L. squarrosa Lindl.

Lomandra spp.

L. endlicheri (F. Muell.) Ewart

L. micrantha (Lindl.) Ewart

L. saveolens (Endl.) Ewart

Sowerbaea laxiflora Lindl.	
Thysanotus spp.	
T. patersonii R.Br.	tuber
T. sparteus R.Br.	"
T. triandrus (Labill.) R.Br.	"
Tricoryne elatior R.Br.	rhizome
Xanthorrhoea preissii Endl.	
HAEMODORACEAE	
Anigozanthos humilis Lindl.	rhizome
A. manglesii D. Don	"
Conostylis aculeata R.Br.	
C. setigera R.Br.	
Phlebocarya ciliata R.Br.	
IRIDACEAE	
Patersonia occidentalis R.Br.	
ORCHIDACEAE	
Caladenia spp.	
C. deformis R.Br.	rhizome/tuber
C. discoidea Lindl.	"
C. filamentosa R.Br.	"
C. flava R.Br.	"
C. gemmata Lindl.	"
C. huegelii Reichb.f.	"
C. latifolia R.Br.	"
C. patersonii R.Br.	"

ANNUAL SEDGE SPECIES

CYPERACEAE

Scirpus spp.

S. antarcticus L.

S. congruus (Nees) S.T. Blake

CENTROLEPIDACEAE

Centrolepsis spp.

C. aristata (R.Br.) Roem. & Schultz

C. drummondii (Nees) Hieron.

IRIDACEAE

* *Gladiolus caryophyllaceus* (Burm.f.) Poir

TREE SPECIES

CASUARINACEAE

Casuarina fraseriana Miq.

PROTEACEAE

Banksia attenuata R.Br.

B. ilicifolia R.Br.

B. littoralis R.Br.

B. menziesii R.Br.

LORANTHACEAE

Nuytsia floribunda (Labill.) R.Br.

MYRTACEAE

Eucalyptus marginata Sm.

E. rudis Endl.

Melaleuca rhapiophylla

FABACEAE

Jacksonia furcellata (Bonpl.) DC

J. sternbergiana Hueg.

Viminaria juncea (Schrad.) Hoffmgg.

SHRUB SPECIES

PROTEACEAE

Adenanthos sericea Labill.

Conospermum stoechadis Endl.

Dryandra nivea R.Br.

Petrophile linearis R.Br.

Stirlingia latifolia (R.Br.) Steud.

SANTALACEAE

Exocarpos sparteus R.Br.

MIMOSACEAE

Acacia cochlearis Labill.

... *A. cyclops* Cunn.

A. pulchella R.Br.

... *A. saligna* (Labill.) Wendl.

A. stenoptera Benth.

FABACEAE

Bossiaea eriocarpa Benth.

... *Daviesia juncea* Sm.

Euchilopsis linearis (Benth.) F. Muell.

Gompholobium tomentosum Labill.

Hardenbergia comptoniana Benth.

Hovea trisperma Benth.

Sphaerolobium spp.

EUPHORBIACEAE

Phyllanthus calycinus Labill.

SAPINDACEAE

Dodonaea hackettiana A. Cunn.

DILLENIACEAE

Hibbertia huegelii (Endl.) F. Muell.

H. hypericoides (DC) Benth.

H. racemosa (Endl.) Gilg.

H. subvaginata (Steud.) F. Muell.

MYRTACEAE

Astartea fascicularis (Labill.) DC

Calytrix flavescens A. Cunn.