Effects of Rabbits on the Vegetation of an Arid Zone National Park

by

Helen M. Armstrong

A thesis submitted for the
degree of Doctor of Philosophy
of the Australian National
University.

January 1988

Declaration

The work presented in this thesis is my own, except where due reference is made in the text.

Helen Armstrong

Helen Armstrong

Department of Environmental Biology,
Research School of Biological Sciences,
Australian National University,
Canberra, Australia.

Changes recommended by examiners.

Corrigenda

1. p7 ’Gibb (1979)’ should read ’Gibb (1977)’

2. p8 ’Parer (1982)’ should read ’Parer (1982b)’
   p11 "
   p13 "

3. p12 ’Gibb (1969)’ should read ’Gibb <u>et</u> <u>al</u>. (1969)’

4. p51 ’$y = 194.7 - 7.95x + 0.080x$’ should read
   ’$y = 194.7 - 7.95x + 0.080x^2$’

5. P78 ’$y = 302.4 - 1.050e$’ should read ’$y = 302.4e^{-0.0488x}$’
   p78 ’$y = 288.3 - 1.555e$’ should read ’$y = 288.3e^{-0.0463x}$’

6. p111 ’Cooke (1979)’ should read ’Cooke (1974)’

7. p126 Line 13 ’for x equal to the reciprocal of the distance in metres’ should read ’for x equal to the distance in metres’

8. p161 ’Fig.3.1.2=/’ should read ’Fig.3.2.1’

9. p181 Lines 4-5 should read ’Kangaroos and sheep, when they have access to free water, do not have the same dietary water requirements as rabbits.’

10. p 185 ’Short (1987)’ should read ’Short (1985)’

11. Bibliography

The following references should be included:

Belsky, A.J. (1986) Does herbivory benefit plants? A review of the evidence. Am. Nat. **127**(6), 870-892.

Carrington, Lord (1951) House of Lords Debate on gin traps, December 1951. *quoted in* Gilham. M.E. (1955) Ecology of the Pembrokeshire Islands. III. The Effect of grazing on the vegetation. J.Ecol. **43**, 172-206.

Neter, J. & Wasserman, W. (1974) Applied Linear Statistical Models. Richard Irwin Inc., Illinois.

Abstract

The aim of this study was to quantify the effect of rabbits, in both the short and long terms, on the ground layer, shrub and tree components of an area of chenopod shrubland.

Rabbit populations were monitored over three years to estimate rabbit density under different conditions. Rabbits reached maximum densities after two years of conditions suitable for breeding and declined rapidly under dry summer conditions.

Four grazing trials were carried out in order to assess dry matter offtake and selectivity by rabbits under different pasture conditions. Rabbits removed at least 100 g rabbit^{-1}d^{-1} dry matter when the pasture contained a green, non-toxic component. Offtake from a mature pasture was recorded as high as 170 g rabbit^{-1} d^{-1}. When *Sclerolaena* spp. were the only green species, offtake fell. The likely fibrous nature of these species may account for this.

Rabbits were found to prefer green, erect, non-spiney, non-toxic, and possibly non-fibrous and nitrogen-fixing plant species. A model of herbivore selectivity derived by Noble (1975) was found to adequately describe the results. The model predicts that, when grazing pressure due to rabbits is high, the proportion of the total biomass made up of palatable species will markedly decline. There will be little change in composition if the pasture contains only relatively unpalatable species.

Adult bluebushes (*Maireana pyramidata*) were eaten by rabbits only when the pasture had a high water content. Bluebushes were not highly palatable under any of the experimental conditions.

Pasture species composition was measured on eight occasions at thirty sites. An index of past grazing pressure for each site was derived using the distance to, and size of, all the surrounding warrens. Behaviour data collected by P. Fullagar and C. Davey of C.S.I.R.O. (division of Wildlife and Rangelands Management) were used to derive a relationship between grazing pressure and distance to a warren. Species richness was found to decline significantly with grazing index on seven of the eight sampling occasions. A susceptibility index was derived for each species which was based on palatability factors and seed size. Species with a high susceptibility index had a greater chance of declining with grazing index and species with a low susceptibility index had a greater chance of increasing with, or having a frequency unrelated to, the grazing index.

Tree girths within a 25 ha area were measured. There was no evidence that rabbits were directly responsible for preventing regeneration of either *Casuarina cristata* or *Heterodendrum oleifolium*. Removal of preferred food by rabbits during a dry period indicated that rabbits have an efficient searching ability at such times. Monitoring of bluebush seedlings both protected and unprotected from grazing by rabbits, showed that seedlings survived better when protected. Survival was not related to grazing index but may have been related to micro-climatic effects of cageing.

A model of pasture dynamics under rabbit and kangaroo grazing is described and major areas where information for such a model are lacking are identified. The model predicts that, for a given decline in rabbit density, rabbit control will be most beneficial to other herbivore species if the rabbit density is kept below about 10 rabbits ha^{-1}.

Acknowledgements

Many people have contributed, both directly and indirectly, to the production of this thesis. Dr.Ian Noble, as my major supervisor, has provided invaluable advice and assistance with the computer modelling throughout the study. Dr.Graeme Caughley I hold responsible for my making the 12,000 mile trip from Scotland, nearly five years ago, to study a British import in semi-arid Australia. My horizons have been duly broadened. Dr.Brian Cooke I hold responsible for giving me the motivation to persevere with the project when I came to the end of my first year and had been graced with witnessing a drought which had made scarce both rabbits and vegetation.

Each of the intrepid adventurers who kept me semi-sane during the three years of field work deserves a mention. Anne Adams was the only one of my field workers who was paid for her efforts. Despite this she was the only one who required tea to be brought to her in the morning in order to begin work. She deserved it, however, for putting up with the 40 C heat. Melinda Brouer was the only person to volunteer for two separate trips each of one month; quite an achievement. She discovered that when it rains in the arid zone it really rains. Field work was replaced with sock knitting, cake making and table tennis on the first trip. Her diligence, commitment and good company kept me enthused. Sarah Sharp became our star rabbit catcher, wielding a rabbit net with tremendous grace and skill. As an indirect result of volunteering she ended up married and with a baby. By contrast, Martin Fortescue had his rabbit catching career cut off in its prime when he fell over a rabbit net and broke his ankle. Despite this injury, Martin remained the most energetic of volunteers, and discovered wheelchair racing, much to the disgust of the nurses at Broken Hill hospital.

Alison Johnston joined me in marking out the fifty metre grid within the kangaroo fence one warm, fly ridden summer. She discovered that there are some advantages to being a small animal vet. Cass Armstrong accompanied me on some of my more adventurous cross-country motorbike rides to set rabbit traps and measure vegetation. Leo Thornton mapped the warrens within the kangaroo exclosure. Murray Hasseler assisted me with the final grazing trial and will remember Kinchega as being one of the few places where his feet could not take the pace and had to be protected against the three-cornered Jacks. Long may your feet go un-shod, Murray. Dave Beurle and Ian Watson helped me map buck heaps in a vain attempt to show that they mark territory

boundaries. They are remembered for fighting with the tame kangaroo and riding motor-bikes very fast and with no regard for conservation of vegetation. Cathy Beurle and Rob Palmer and Colette Goodwin helped with the third grazing trial. Andrew Hedley taught me about the birds of Kinchega and psychoanalysis while assisting without complaint with vegetation clipping. This despite the hazards of low flying aircraft and flat batteries. Rob Macgrath, Francis Holst and Rolph walked many kilometres with me to count active entrances. Klaus Henle helped me to count pieces of carrot and was notable for his dedication to the reptiles of Kinchega. Nick Dexter and John Hartas helped me to measure many a bluebush and map many a warren. Mark Calanan, John Elliot, Debbie Robertson, Jean-Marie Picard, Matt and Michael the vets, Liz and Toby from Canada, Peter and Jill from Armidale all assisted with the field work. All these people have my thanks for allowing me to maintain at least some of my sanity.

All the members of the Kinchega 'group' were of invaluable assistance not only during the field work but also with experimental design and writing up. I am indebted to Graham Robertson for innumerable discussions and for eventually forgiving me for denting the F-100. Jeff Short, Jo Smith, Robin Barker, Peter Bayliss, Greg Wellard, Murray Ellis and Bevan Brown all provided essential support and advice. Neil Shepherd sometimes beat me at table tennis and taught me how to dissect rabbits.

The rangers at Kinchega have all been extremely helpful and supportive, particularly John Eveleigh and Peter Morris. Peter Clarke, as resident archaeologist at Mungo national park, informed me of the region's pre-history and taught me to shoot rabbits.George Sinclair, of the Menindee service station, mended all the punctures without complaint and told me all about rabbits. Ed Slater took air photos of my field site at the expense of his lunch. Richard Burn created the steep turns necessary for the air photography and the loss of lunch.

I am grateful to the locals at Menindee pub for maintaining the bar in position.

Don Wood has provided useful discussions, information and rabbit nets throughout the project.

Peter Fullagar and Chris Davey kindly allowed me to use the behaviour data which are discussed in chapter 1 of Part 3.

Ross Cunningham both confused and educated me about many of the intricacies of statistics. Jim Yuncken helped me have many a good 'mornig' and solved many a computing problem.

Jim Beatie of C.S.I.R.O. (Soils) kindly undertook to do my soil analyses.

Many people within the department of Environmental Biology have also played a major part in keeping me as sane as ever. Notable among hese are Jill Landsberg, Bruce Welllington, Doug Abrecht and Peter Cochrane.

I am grateful for two friends; Larry Kamener and Randal Stewart, who, despite an, at best, marginal interest in rabbits and their interaction with their environment, found it in their hearts to interact with me during the long writing-up phase.

Lastly, I would like to thank my father for providing moral support from 12,000 miles away.

Contents

Part 1

Introduction

Part 2

Experimental measures of offtake and selectivity.

Part 3

Measurement of effects of rabbits in the field.

Part 4

General discussion and conclusions

Appendices

Part 1

Introduction

1. Background

In this section I intend to give a brief description of the ecology of the rabbit in Australia. I discuss its origins, its present distribution within Australia and its population dynamics. I then outline the problems which rabbits cause for land managers and give a brief description of the extent and types of rabbit control work which have been carried out. I then go on to point out that, although much time and money is spent on rabbit control, it has variable effects on rabbit populations and, since little is known about the extent of rabbit damage to different vegetation types and at different rabbit population levels, its benefits to conservation and/or production are unknown. Work which has been done on assessing rabbit effects on vegetation will be reviewed. I conclude by outlining the aims of this study and how I set out to achieve them.

1.1 The rabbit in Australia

Rabbits (*Oryctolagus cuniculus* (L.)) first started to colonize Australia around the 1860's. The first rabbits were brought from Britain by colonists who wanted them for sport. The spread of the British rabbit through Australia is documented by Rolls (1969). Rabbits spread at about 70 km y^{-1}, reaching the limits of their distribution by 1910 (Parer 1982a). The speed of their dispersal and the fact that new, isolated colonies appeared, suggests that they were aided in their spread by those who saw the rabbit as a useful food supply or animal to be hunted. Left to themselves, rabbits gradually spread outward from the periphery of existing colonies (Lloyd 1981) when they become densely populated. Lloyd, working in Britain, found that rabbits travelled no more than 1 km when they dispersed, and had a much greater risk of mortality than those which remained. Daly (1981), working in semi-arid Australia, found that dispersal was mostly by young adults. Both she and Lloyd found that dispersal occurred either at the end of the breeding season in which they were born or at the beginning of the next one. The end of breeding usually coincides with a scarcity of food and this is likely to induce dispersal. At the beginning of breeding seasons, territories are being formed and any rabbits which are not in social groups (usually young rabbits) are driven out by more dominant ones.

Rabbits are no longer increasing their range in Australia but a knowledge of their dispersal behaviour is useful when considering recolonization of areas where rabbits have become extinct through control or drought. The spread of the rabbit may have been helped by the decimation of potential native predators; dingoes, native cats and hawks and also by the presence in many areas of the burrows of bettongs (*Bettongia lesueur*), bilbies (*Macrotis lagotus*) and wombats (*Vombatus ursinus*) (Parer & Libke 1985). Both bettongs and bilbies are now extinct over most of Australia probably as a result of poisons laid for dingoes and competition for burrows from rabbits (Rolls 1969).

1.2 Present Distribution

From Victoria and South Australia, rabbits have spread so that now they inhabit most of the southern half of Australia, the Tropic of Capricorn being roughly their northern limit (Myers 1970). Cooke (1977) considered that the northern limit is brought about by the change from winter, or non-seasonal, rainfall to summer rainfall in the north of the continent. Since rabbits can only breed when there is green, growing vegetation present (Myers & Poole 1962; Poole 1960; Hughes & Rowley 1966; Stodart & Myers 1966), they would have to breed in summer in northern Australia. Cooke (1977) considered that summer temperatures are too high at this time to allow breeding since they are high enough to increase the rabbits' body temperatures sufficiently to cause resorbtion of embryos. Although Cooke found that burrows would provide little protection from hot conditions, Parer and Libke (1985) found that deep warrens can provide more equable conditions for rabbits in hot, dry conditions. The isolated populations north of the general limit may, therefore, be able to exist there because they are at a higher elevation where it is cooler, or the soils are suitable for deep, well ventilated warrens or there is some other source of shade or green feed at cooler times of the year. In arid areas where rainfall is non- seasonal, rabbits do well only when there is good winter/spring rainfall thus populations in such areas oscillate dramatically between high and low densities.

Within its range, the rabbit has colonized a wide variety of habitats which range from deserts to subalpine valleys (Myers 1970). Rabbits are most successful in areas where soils allow successful warren building and green food is plentiful. Increased clearing, cropping and pasture improvement in temperate south-eastern Australia has led to rabbits in these areas being restricted largely to roadsides, creek and river banks and uncleared areas (Cooke 1981). In pastoral areas, sandy soils support the greatest density of warrens (Myers & Parker 1965). The presence of good pastures nearby to such soil types will allow the highest rabbit densities since the warrens are needed for breeding and good pasture growth is needed for good quality food. In more arid areas, sand dunes, which provide good burrowing material and which abut inter-dunes or other run-on areas, provide the best habitat though rabbits also inhabit other land systems (Myers & Parker 1975a; 1975b). In Spain, the rabbit's country of origin, they also do best in areas where sandy soils abut run-on areas (Rogers & Myers 1979). Myers and Parker (1975a,b) and Parer and Libke (1985) suggest that, although sandy soils are preferred for warren building, warrens dug in harder soils are more stable and, since they are deeper, can maintain cooler temperatures and higher humidities during summer. For these reasons, they are used as 'refuge' warrens during drought, rabbits recolonizing other soil types when the drought ends. Such warrens seem, therefore, to help some rabbits to retain water during droughts in areas where they have no access to free water. Since rabbits will not regularly travel more than about 1 km to water (Wood pers.com.), the majority of semi-arid and arid zone rabbits have no access to free water but gain all their water from their food. 'Refuge' warrens may, therefore, be essential for the rabbit's persistence in these areas. Martin (1977) concluded, from his work on rabbit population dynamics in different land systems, that 'where sandy and limestone habitats overlap substantially, populations may have greater resilience than in apparently prime habitat of sandy country'. Since Parer and Libke (1985) found warrens in calcareous areas to be possible 'refuge' warrens, Martin's conclusion agrees with those of Parer and Libke and of Myers and Parker.

Rabbit populations near to creeks, rivers and dams can also persist longer than those further away from water hence these areas are also foci for the recolonization of other areas. In areas with predictable rainfall, rabbit populations are likely to be more stable.

1.3 Population dynamics

The important factors influencing rabbit densities vary greatly between different habitats. The factors which must be considered are;

1. Predictability and timing of new, green pasture growth;
2. Availability of suitable feed;
3. Predator densities;
4. Densities of burrows for breeding;
5. Presence of refuge warrens in arid areas;
6. Availability of water in arid areas;
7. Likelihood of myxomatosis epidemics;
8. Occurrence of high temperatures during breeding seasons;
9. Possible suppression of rates of reproduction at high rabbit densities.

These factors will first be considered separately. I will then make an assessment of how they interact, of the factors most likely to be important in different habitats and of the resultant population densities which they are likely to allow.

1.3.1 Predictability and timing of new, green pasture

Rabbits are known to require fresh, green growth for reproduction. In temperate regions, therefore, rabbits breed during the growing season from spring to autumn unless summer 'droughts' inhibit plant growth, and therefore breeding, during this time.

Photoperiod is a component in the fertility of male rabbits but its importance seems to vary between studies and may well differ in the nature of its effect on rabbits from different areas. In most circumstances, however, there will always be some males in reproductive condition (e.g. Wheeler & King 1985) and so the breeding season is determined by female fertility which is triggered largely by the vegetation although there is some evidence that photoperiod may also have some effect on females (Walter *et al.* 1968).

In arid and semi-arid areas, the situation is very different. In such areas rainfall can either be seasonal or non-seasonal. In Australia, semi-arid areas in the south tend to have higher rainfall in winter. This becomes more non-seasonal further north such that at Broken Hill the rainfall shows no tendency to be higher in any season (Robertson *et al.* 1987). North of Alice Springs the rainfall again becomes seasonal but this time it falls largely in summer. The total quantity of rainfall also has a tendency to decrease towards the centre of Australia thus there is a transition from a semi-arid to an arid zone from the south towards the centre and from the north towards the centre. Unpredictability also increases with low rainfall.

In summer, temperatures are often too high for successful rabbit reproduction even if green growth appears (see Part 1, section 1.2). At other times of year, rabbit reproduction is initiated when green, growing pasture is available. In the arid and semi-arid areas, temperatures, even in winter, are rarely low enough to completely prevent plant growth. In these areas, therefore, rabbit reproduction occurs whenever effective rainfall occurs at times other than in mid-summer. Since such rainfall is often very unpredictable in amount and timing, rabbit reproduction is equally unpredictable in duration and timing.

Female rabbits can reach sexual maturity as early as four months from birth (Cooke, pers. com.). A breeding female will produce between four and eight kittens in a litter and can produce a litter every 30 days or so while conditions are suitable for breeding (Cooke 1977). Rabbits, therefore, have the potential for very fast increases in number.

1.3.2 Availability of suitable feed

Cooke (1974) concluded from a literature review and his own field studies that rabbits require a diet of less than 40% fibre. From results for caged rabbits, Cooke (1982) also concluded that rabbits require a diet of at least 55% water. Wood and Lee (1985), also studying caged rabbits, found that 50% water content was sufficient. They proposed that the rabbits in their study required less water than those of Cooke because their rabbits had had time (50 days) to adjust to a low water diet.

In arid areas, many plants, particularly chenopod shrubs, have high salt contents and, despite their high water contents, cannot be eaten unless rabbits have access to free water since rabbits are not adapted to excreting large quantities of salt when water is restricted (Wood & Lee 1985). In sub-alpine areas, salt can often be in short supply and Myers (1970) believes that salt deprivation in summer will reduce rates of reproduction. Usually, however, a pasture which contains a green component will be sufficient for rabbits' needs.

The times when suitable feed can be lacking, and rabbits lose condition and die, are when insufficient rain has fallen or when rabbits and/or other grazers have removed all suitable feed. The two cases, of course, interact since grazers have more effect when there is little pasture biomass. In temperate regions, severe overgrazing can cause a lack of feed. Under such conditions, rabbits have the ability to find food for longer than stock since they can eat small plants and can dig up roots. Before such extreme conditions occur, however, the quality of the feed is likely to have declined since rabbits are selective feeders and this will affect both rabbit and stock condition . This will be discussed in more detail in later chapters of this thesis.

In arid and semi-arid areas, a lack of suitable feed occurs often and can be caused by drought alone, grazing pressure alone, or a combination the two. Under conditions of low grazing pressure, vegetation becomes too dry to supply rabbits with their water needs after several months of no effective rainfall. The time that this takes depends, of course, on the season and on the vegetation type. It is possible that before Europeans arrived, and grazing pressure was low, there were more species of plant which could survive periods of low rainfall and remain green. Sheep and/or cattle, rabbits and increased numbers of kangaroos have since had ample opportunity to deplete the numbers of any such species. Areas where grazing pressure has been low may have a more drought resistant flora but, to the best of my knowledge, this has never been investigated.

Where grazing pressure from all herbivores is high, grazing can cause food shortages when the pasture is no longer growing. Cooke (1974) estimated that removal of biomass by herbivores (including insect plagues) causes a crash in rabbit populations about one year in five on a grazing property in semi-arid South Australia. Unlike in temperate areas, in the semi-arid and arid zones it is the rabbits which die before the larger herbivores when conditions dry out since most rabbits have no access to water so cannot eat dry feed. The more mobile sheep and kangaroos, in contrast, regularly move to and from water points (Stafford Smith 1984, Pridell 1983). A very small number of rabbits do seem to survive the longest droughts in most places but it is not known what they eat during this time.

Even where selectivity by herbivores has depleted the quality of the pasture, rabbits seem to be able to maintain condition if the water, fibre and non-toxic requirements are upheld. Seventeen rabbits shot as part of this study on Mungo National Park, in December 1982 (well into the 1982/83 drought) had good supplies of kidney fat (7.3 ± 1.0 g wet weight per kidney), indicating that they were in good condition despite the lack of growth and continuous grazing that the pasture would have received, over the previous year. They were all shot in an area where there was no free water available. The vegetation consisted of scattered *Casuarina cristata* and *Heterodendrum oleifolium* growing among *Maireana pyramidata* and *M.sedifolia.* These results suggest that the rabbits were able to maintain condition despite having to eat a diet which was becoming less palatable with time. Myers and Poole (1963) also found that rabbits could breed and grow normally on a pasture which would have been classed as unpalatable to stock.

1.3.3 Predator densities

The major predators of rabbits in Australia are European foxes and feral cats (Myers 1970). Other predators include birds of prey, such as Wedge-Tailed eagles, and occasionally snakes. Although predation can account for 80% mortality of young rabbits (Myers 1970), it seems that predators alone can limit the growth of rabbit populations only under some circumstances. They can, however, reduce the rate of increase of a population (Newsome pers.com.) and may be able to increase its rate of decline once breeding has ceased (Gibb 1979). Numbers of foxes and cats, however, can be extremely variable from one area to another and from one time to another. In many areas, foxes and cats are shot. Long droughts can also reduce numbers unless there is an alternative food supply. If no such alternative prey exists then predator numbers will follow those of the rabbits and they are unlikely to be able to reduce the rate of increase of a rabbit population after a drought. In such conditions, however, they will have a large effect on the rate of decline since they will be forced to hunt even small populations of rabbits. Although foxes and cats are likely to have this effect on rabbit populations in many areas, they have the undesirable drawback of turning to native mammals, lizards and birds when rabbit numbers are low. These, however, are unlikely to support them through a long drought. To survive this there would have to be a supply of dead kangaroos or sheep. Their survival would thus depend on the time between small prey no longer being available and larger herbivores beginning to die. This time will vary considerably with location. Gibb *et al.* (1969) concluded that a sparse population of rabbits in New Zealand was kept low by cat predation but this is the only report of such an occurrence. Elsewhere it seems that conditions do not allow this type of population control.

1.3.4. Densities of burrows for breeding

Warren densities and sizes vary considerably between areas but the highest densities occur on sandy soils. Although such warrens are not suitable for occupation during droughts (see Part 1, section 1.2), these soil types can support the highest densities of rabbits after a succession of good years. Rabbits can live successfully above ground (Wheeler and King 1983; Gibb *et al.* 1969) particularly where there is bush or scrub cover. They usually need burrows for breeding. Parer (1982) found that the number of active entrances in an area correlated well with real rabbit densities. This measure of density is only likely to be accurate during breeding seasons and when there are still some burrows to be occupied. When all the warrens are in full use, rabbits will live above ground although they will be unable to breed. Parer (1982b) suggests that maximum densities for an area can be calculated assuming that all entrances are active at maximum densities. He suggests doubling the equivalent rabbit densities obtained from assuming this to take account of the ground living rabbits.

Density of warrens can, therefore, have an effect on maximum densities and rates of increase once all burrows are occupied. Outside the breeding season, territories break down and warrens are less used. Population estimates from active entrance counts become less reliable.

1.3.5 Presence of refuge warrens

Myers and Parker (1975a;b) first proposed that, in arid areas, some warrens are better suited to harbouring rabbits during droughts than others. These warrens are on hard, often calcareous, soils. These are more stable and go deeper than those on sandy soils and so may provide a more mesic environment. They may also be close to run-on areas or other areas where vegetation can stay green for longer. Where water is available, deep warrens may not be essential for rabbit survival during drought. The presence and density of such 'refuge' areas and warrens will be of great importance in determining the size of populations surviving droughts.

1.3.6 Availability of water in arid areas

As mentioned above, where water is available, rabbits can live longer into a drought. Populations from such areas can then form the foci of rabbit spread at the end of a drought, as can those from 'refuge' warrens.

1.3.7 Liklihood of myxomatosis epidemics

When myxomatosis first spread in Australia in 1951 it caused a mortality rate of greater than 90% among infected populations (Fenner *et al.* 1953). Since then mortality rates have fallen (Fenner 1983) although few recent studies have been done on its effectiveness. Where rabbit breeding is regular, the disease vector is the rabbit flea but in arid areas these fleas die out when there is a prolonged period of no breeding since the flea's breeding cycle is tied in with that of the rabbit. In these areas mosquitoes are the vectors so outbreaks of myxomatosis occur only after summer rainfall when mosquitoes appear. Even then, an epidemic may not occur. The effects of myxomatosis are, thus, unpredictable in timing and extent although it is undoubtedly often a factor in depressing population growth rates, particularly after summer rainfall in arid areas.

1.3.8 Occurrence of high temperatures during the breeding season

It has already been noted that high summer temperatures prevent breeding, hence also the spread of rabbits, in northern Australia. As has been mentioned above, decreased fertility at high temperatures is also likely to depress rates of increase in summer in other areas, within the rabbit's range, where summer temperatures are high.

1.3.9 Suppression of reproduction at high rabbit densities

Myers (1970) found that rabbits living in high density populations often resorb embryos, thereby reducing breeding rates. He concluded, however, that in natural populations, densities sufficient to cause this would not be reached.

1.3.10 Importance of different population factors

Social factors are probably of minor importance in rabbit population dynamics. High temperatures probably have a large effect on breeding rates only near the edges of the rabbit's distribution. In arid areas, after a summer rainfall, high temperatures probably cause lower breeding rates than might otherwise be expected. Myxomatosis can have dramatic effects on population densities but its occurrence is unpredictable. Predation is likely to slow down rates of increase and speed up rates of decline of populations but, in most cases, it will not affect maximum potential densities. Breeding occurs when pastures are green and growing and ceases when the growing season ends or temperatures become too high. During this time, rates of increase could potentially be as high as five kittens per adult female per month. Kitten mortality, however, will in most cases reduce this figure by about 80%. In a long breeding season i.e. greater than 3 months, the first-born females can themselves give birth before it ends (Wheeler & King 1985). If a myxomatosis epidemic occurs, mortality rates of about 70% could be expected. Maximum potential densities can be estimated from burrow densities. At the end of a breeding season, populations decline through predation and/or myxomatosis until very few rabbits remain or food quality becomes limiting. If rabbits cannot obtain a non-toxic diet of >50-55% water and <40% fibre, then they will lose condition and die. Plants with leaves which contain high salt or oxalate concentrations are here classed as toxic since their use for food by rabbits requires an increased water intake. The vegetation may reach this low quality due to heavy grazing by rabbits and/or other herbivores or from natural desiccation in arid areas. Anything green, and non-toxic, will normally be of high enough quality to maintain a rabbit in good condition. Rabbits also require about 100 g dry weight of food per rabbit per day to maintain condition hence standing biomass will be important under conditions where pasture quality is not limiting. Since, however, rabbits have the ability to dig up roots and to eat very small plants (pers. obs.), biomass will probably not become limiting until it is extremely low.

If food does not become limiting, then the population density at the start of the next breeding season is determined by the levels of mortality due mostly to predation and myxomatosis. Dunsmore (1974) found that the average age of rabbits over a five year study was 1.7 and 1.9 years for males and females respectively. Myers (1970) found that the proportion of rabbits over two years of age at five sites throughout Australia varied from about 5 % to 28 %. The population in arid New South Wales consisted of about 15 % of animals over two years of age. King (1984) estimated an 80% probability of an adult surviving from one month to the next in south western Western Australia. Thus, since few rabbits are likely to die of old age, and age past maturity will have little effect on mortality rates, age structure is of little significance to mortality rates.

1.4 The rabbit problem

Since its first occurrence in plague proportions in the late 19th century, the rabbit has been seen as the enemy of the pastoralist. The pastoralists saw the presence of rabbits in terms of the sheep which they displaced. Little research was done but the prevailing view was that rabbits were serious competitors with livestock. In areas with a perennial grass cover, rabbits could dig up grass roots and impair their potential to resprout and hold the soil. No-one compared this effect with that of the hooves of sheep and cattle or measured its prevalence. In arid country, rabbit plagues could denude the country of valuable stock feed and ring-bark trees and shrubs (Rolls 1969). No-one could say for certain just how much damage was done, when it was likely to be worst, or indeed whether rabbits were competing directly with stock or ate different components of the vegetation. Recently, some work has begun to be done to measure the effect of rabbits on vegetation and how they compete with stock and native grazers (e.g Cooke 1974; Foran *et al.* 1985; Friedel 1985; Lange & Graham 1983). It is only recently that ecologists have begun to ask questions about the role of rabbits in Australia in terms of conservation as well as economics.

For the past century, large sums of money have been spent on rabbit control and research has been directed towards increasing the efficiency of such measures. The major ways of controlling rabbits now are by poisoning with sodium fluoracetate (1080) and by ripping warrens. Both these measures have short-lived effects and are costly. Their effects can only be assessed in terms of numbers of rabbits killed and not in terms of money saved or conservation value since insufficient is known about how rabbits interact with their environment.

1.5 Rabbits and vegetation

The effect of rabbits is dependent on rabbit numbers. I have described the various factors which contribute to the wide variations which can be seen in rabbit populations, both spatially and temporally, throughout Australia. From this knowledge, and real measures of abundance at different times and in different areas, predictions can be made about likely rabbit densities in any place at any time. Real measures of abundance can be made by mark and recapture techniques (Dunnet 1957) or, during breeding seasons, using Parer's (1982) correlation between number of active entrances and rabbit numbers. Indices of abundance can be gained from spotlight counts, late afternoon sightings or density of faecal pellets (Gibb 1969). Cooke (unpubl.) estimated rabbit densities at a semi-arid site in South Australia as potentially varying between 100 and 3,500 rabbits km^{-2}. He concluded from his work that 'plagues' would occur after two consecutive years of prolonged pasture growth.

Knowing how many rabbits are likely to be present in any area at any time, is the first step towards answering questions about their effect on vegetation and how they compete with other grazers. The next steps require a knowledge of how rabbits' grazing is spatially distributed, how much they eat and the nature and extent of their selectivity. Such information can then be combined with plant ecological knowledge to predict effects on vegetation and with information on the grazing habits of other herbivores to predict the effect of competition. Such predictions have rarely been made but some empirical studies have been carried out which give information on rabbit effect and competition at particular sites under particular conditions.

I will now review the work which has been done in the areas listed above then draw some tentative conclusions and point out some of the gaps in our knowledge.

1.5.1 Spatial distribution of grazing

The distribution of rabbits in Australia has already been discussed. Grazing pressure, however, is not necessarily uniform even within any one land system which has an apparently even distribution of rabbits.

Most rabbits live in warrens, and burrows are used as an escape from predators. The area round warrens, therefore, tends to be heavily grazed; the grazing pressure decreasing with distance from the warren. Rabbits also have limits to their range and normally do not move more than 200 m away from the warren (Gibb 1979; Cooke 1974), although this may increase in times of food or water shortage (Gibb 1979; Fullagar 1981). Areas more than about 200 m away from a warren may, therefore, never be affected by rabbits, unless there is a large population living above ground as Wheeler and King (1983) found. This is likely to happen where there is shrub cover and all the warrens are being used or the soil is unsuitable for burrowing. Little has been done to study this spatial unevenness in grazing pressure although behaviour studies have measured time spent in different areas (Fullagar and Davey, unpubl.). These data are discussed in Part 3, section 1.2, as they relate to grazing pressure relative to distance from warrens.

Grazing pressure may also be related to warren size, since large warrens have the potential to accommodate large numbers of rabbits. A variety of sizes of warrens will, therefore, also lead to varied grazing pressures within any area when rabbit numbers are high. Since maximum numbers of rabbit occupants can be estimated from the number of entrances (Parer 1982), this can be taken into account when assessing grazing pressure.

Another source of uneven grazing pressure may be caused by rabbits' food preferences. Within their range, rabbits may tend to concentrate their grazing in preferred areas and some evidence for this is discussed in Part 3, section 1.2. Little is known, however, about this possible effect.

1.5.2 Biomass Removal

Few measurements have been made of rabbit offtake in the field. Cooke (1974) estimated offtake for a 1.75 kg rabbit as approximately 100 g rabbit^{-1} day^{-1}. Short (1985) measured rabbit offtake in a grazing trial in semi-arid New South Wales. He found maximum offtake to be 80 g rabbit^{-1} day^{-1}. The rabbits which Short used were smaller than 1.75 kg which may, partly, account for the lower offtake. Offtake declined during the trial as pasture biomass, and quality, declined. Short (1985) did not distinguish between the effects of declining biomass and quality but it appears unlikely that biomass could have limited offtake since, even at the end of the trial, there remained vegetation which was classed as 'available'. It is more likely that offtake declined due to a decline in pasture quality since Cooke (1974) found that intake declined as fibre content increased. Cooke (1974; 1982) concluded from field studies that rabbits need a diet of <40% fibre and >55% water. He stated (unpubld.) that almost any green plant, even if wilted, will fulfill these criteria. Thus, if such a diet is available then offtake can be estimated as 100 g adult rabbit $^{-1}$ day $^{-1}$ although this may be lower in arid areas where rabbits are, on average, smaller (Myers 1970).

1.5.3 Effect on pasture biomass

Foran et al. (1985), working in Central Australia, found that grazing by rabbits at about 300 rabbits km^{-2} (3 rabbits ha^{-1}) in one year, decreased pasture biomass in the following year by about 300 kg ha^{-1}. The mechanism for this decrease is not discussed. Johnston (1969) found that in an area of white cypress pine (*Callitris* *columellaris*) woodland which was protected from sheep and rabbit grazing for 16 years, there was a 'marked build-up of ground cover'. A similar unprotected area was frequently bare. In an area fenced to allow grazing by rabbits but not sheep, the ground cover fluctuated considerably with the 'ground commonly being as bare as in the unprotected plot'. This shows that in this area both rabbits and sheep could have a very definite effect on pasture biomass. Such a build up of ground cover is likely to influence future biomass simply by its presence since soil moisture relations, insolation and competition will all be different where there is ground cover.

Myers and Poole (1963), working in New South Wales, found that 20 rabbits per acre could decrease the grass crop by 25%. Some of this decrease was due to changes in species composition which will be discussed below. The rest was due to biomass removal and, possibly, effects on growth rate. Southern (1955) quotes Phillips (1953) as finding that the yield of herbage on a sown pasture in England was from 2 to 8 times higher without rabbits than if rabbits were present. The size of the difference depended on season.

It is evident that little is known about the effect of rabbits on biomass in either the short or long term and how it can vary with vegetation type and rabbit numbers. Furthering this area of our knowledge will require an integration of plant and animal ecology.

1.5.4 Rabbit selectivity

There is ample evidence that rabbits are selective feeders and enough information is available to formulate some selection criteria.

Rabbits tend to select erect rather than prostrate plants (Campbell 1978; Myers & Poole 1963; Gillham 1955; Farrow 1917). There is some evidence that they select for leguminous plants (Cochrane & McDonald 1966). Gillham (1955) defined palatable species as being tall, delicate of texture and having a high water content. She defined unpalatable species as being coarse (i.e. having a high proportion of woody tissue), spiny, stinging, very tall or hairy. Myers and Poole (1963) found that all species except aromatic and bitter herbs were eaten. Under dry conditions, rabbits select for plants with a high water content (Myers & Poole 1963; Foran *et al.* 1985; Cooke 1974; Westoby 1980 (for *Lepus californicus* in Utah)). Their preference for grasses over forbs or vice versa varies with site and situation.

1.5.5 Effect on vegetation species composition

The changes which result from rabbits' selective grazing depend on the nature of the vegetation and the intensity of grazing. In general, with increasing grazing pressure by rabbits, vegetation tends to decrease in stature, decrease in the proportion of perennial species in the pasture, become more exotic, become more 'weedy' and become more fibrous or otherwise unpalatable. Myers and Poole (1963) found that dwarf or fibrous grasses and weeds were resistant to grazing hence able to increase under heavy grazing pressure. Gillham (1955) defined rabbit resistant species as those with meristems at, or below, ground level or with a growth habit that can change from erect to rosette. Decreasing stature results from rabbits' preference for easily accessible plants. Very tall species, however, are above rabbit height hence are less susceptible. Rabbits are liable, however, to 'fell' seed heads of grasses (Myers & Poole 1963) . The rabbit's preference for erect plants, as well as its selection for green plants in dry times, makes many shrub and tree seedlings particularly susceptible to rabbit grazing (Foran et al. 1985; Farrow 1917; Johnston 1969; Lange & Graham 1983). This can lead to a decline of tree and shrub populations in rabbit inhabited areas or to the prevention of invasion of trees and shrubs into open areas. Johnston (1969), working in south west Queensland, found that white cypress pine (*Callitris collumellaris*) seedlings died in rabbit-grazed areas but that this was due more to a change in microclimate than rabbit grazing itself. Without rabbit grazing, vegetation cover built up and provided necessary shade for the seedlings.

A decline in the proportion of perennial species in the pasture results if the perennial species are preferred by rabbits and are intolerant to rabbit grazing. This is the case, unless the perennial is particularly unpalatable, as is the highly fibrous Snow grass (*Poa* spp.)(Wimbush pers. com.) in the Snowy mountains. Since perennials are consistently grazed, their cover is often decreased, leaving room for more ephemeral species to invade, if there is a seed source. These species are usually described as 'weedy' and, in Australia, are often exotic. In arid areas, perennials which stay green in dry times and are non-toxic are particularly susceptible (Cooke 1974). Annual and ephemeral species are not immune, however, since rabbits have the ability to remove seed heads thus reducing numbers of seeds (Myers 1961) or preventing seeding. Grayson and Hassal (1985) found a higher density of flowering stems on ungrazed than on grazed turf and Farrow (1917) found that many species were prevented from flowering. Gillham (1955), however, found an increase in seeding in some grass species due to grazing. The effect, therefore, depends on the individual plant's response to being grazed.

Ungrazed species, and resistant species, which possess the characteristics listed above, tend to increase under grazing. These species are often less palatable, and of lower nutritional value, to other grazers as well as to rabbits. Myers and Poole (1963) recorded a change in a pasture under heavy rabbit grazing pressure from a reseeded grass-clover pasture to one which consisted of dwarf, fibrous grasses and 'weeds'. Despite this, the rabbits were able to reproduce and grow without hindrance even when most of the sward consisted of species usually thought of as unpalatable to stock.

The effect on species richness depends on the vegetation type. Where grazing opens up a dense, perennial sward to allow more ephemeral species in, species richness increases with grazing (Gillham 1955). Where grazing selectively removes susceptible species and no new species invade, species richness decreases with grazing (Stanley & Milthorpe 1977; Cochrane & MacDonald 1966).

Two studies (Gillham 1955; Farrow 1917) have looked at changes in vegetation with distance from rabbit warrens. The changes were taken to be due to decreasing rabbit grazing pressure with distance from warren. In both of these, the changes can be explained in terms of the rabbit preferences described above. These two studies, however, were undertaken in temperate areas in the U.K. Until recently, no-one had looked for similar vegetation gradients in more arid areas. Lange and Graham (1983), working in arid South Australia, found that cut myall (*Acacia papyrocarpa*) shoots were removed more quickly close to warrens than further away. Farrow (1917) found that trees could only regenerate in wetter, low-lying areas where growth was faster than on dunes and where the seedlings could 'escape' from rabbit grazing. Leigh and Wood (pers. com.) have found gradients in rabbit effect with distance from an isolated rabbit warren at Yathong nature reserve in semi-arid New South Wales.

1.6 Competition with other herbivores

Only two studies have measured the effect on other grazers of competition with rabbits. Myers and Poole (1963) found that the more rabbits there were, the poorer the condition of sheep on the same pasture. Thompson (1951), found that the live weight gain of sheep over 7 months was 800 lb (364 kg) on rabbit-free plots and 650 lb (295 kg) on rabbit-grazed plots. There is, thus, some evidence that rabbits can decrease condition and/or growth of other herbivores on the same pasture. No studies have been carried out on competition between rabbits and kangaroos.

The degree of competition will depend mainly on the effect of rabbit selectivity on pasture quality, on the needs of the other grazing species and, of course, on the grazing pressure of both. It will also vary with pasture type. Given this, it is impossible to make predictions about degree of competition purely from the densities of the two species at a site. Various comparisons have been made between the effect of rabbits and that of a single sheep or cow. Campbell (1978) stated that eight rabbits were equivalent to one sheep. Myers and Poole (1963) equated the effect of one sheep with that of seven to ten rabbits and Carrington (1951) (quoted in Gillham (1955)) thought that nine rabbits were equivalent to two sheep. Foran *et al.* (1985) estimated the effect of 180 rabbits to be equal to that of one 1,450 kg cow. Although these comparisons are often made, it is misleading to calculate possible increases in stocking density, were rabbits removed, purely on the basis of remaining biomass since competition is not usually for biomass *per se* but is for the best quality parts of the pasture.

In some cases, if tall, rank vegetation is removed by other grazers, rabbits may benefit from the presence of the other grazers.

No studies have been done to look at the effect on other herbivores of long term changes in vegetation composition due to rabbit grazing. This is probably because any changes due to rabbits are often confounded by those due to the other grazing species itself, hence any such studies would have to use long-term rabbit exclosures and few of these exist.

The effects of one herbivore on another may perhaps best be deduced from a knowledge of the selectivity of the species concerned and the plant ecology of the pasture species.

1.7 Effects of rabbits on vegetation in arid Australia

As has been discussed, we know that rabbits, and probably also sheep, have the potential to severely limit tree, and shrub, regeneration, either by changing the microclimate for regeneration or directly killing seedlings. It is also widely reported that rabbits can defoliate shrubs and ring bark trees. Much of this anecdotal evidence was recorded in the last century, or early this century, when the vegetation is likely to have been changing in response to grazing as it may still be now. Cooke (unpubl.), however, recorded rabbits eating bark and climbing into trees during a time of severe food shortage. The effect of this on the shrubs and trees was not recorded.

Less is known about the effect of grazing on the ground layer species in arid areas. It is often stated that rainfall drives arid systems (Noy-Meir 1973; Noble 1977; Noble & Crisp 1980). This is undeniably true and, by comparison, the effect of grazing on arid vegetation at times of peak productivity is probably small. For example, Robertson (1987) working at Kinchega National Park in western New South Wales measured peak pasture biomass levels to be around 1,000 kg ha^{-1}. At peak densities, herbivores would remove only 75 kg ha^{-1} month^{-1} (Caughley et al. 1987). This would be readily replaced if the pasture were growing. This does not mean, however, that grazing is a process which can be ignored. At times when pasture production is low, such as after a small rainfall, or when high quality food is scarce, such as during a drought, there can be severe competition for food not only within, but also between, herbivore species (Cooke 1974). The long term effects of grazing in the arid zone have not been well documented. In such areas, documenting changes is particularly difficult since the ground flora changes dramatically in biomass and species composition in response to environmental conditions. A grazing effect is, therefore, not always obvious; the vegetation is always seen to 'come back' as soon as there is a good rainfall.

It might be thought that ephemeral species, by virtue of their abundance after rain and short time to flowering and seed set, would be immune to grazing. A highly selective herbivore, however, may be able to reduce the seed production of selected species even if biomass is high. There are also many perennial, facultatively perennial and semi-perennial species which grow in arid pastures; largely grasses and chenopods. These can remain green when other species dry out and are, thus, susceptible to grazing by rabbits. Foran *et al.* (1985) found a decrease in abundance of *Enneapogon* spp. with decreasing grazing pressure. He reports that these grasses can stay green 'long after the forage in surrounding areas has dried off'. It is, therefore, highly likely that rabbits can change the species composition of the ephemeral flora and reduce the perenniality of the ground layer flora in general. This will lead to a change in the response of the flora to small rainfalls since there are fewer perennials to resprout and less protection from insolation for new germinants. The study of Cochrane and McDonald (1966) in the Victorian mallee provides evidence that rabbits alone are capable of causing these changes. This, however, is only one study carried out in one particular area where rabbit densities were not known. In order to be able to make predictions about the effects of rabbits, it is necessary to quantify the processes involved and not merely record the effect of exclosure after a given time.

2. This study

2.1 The questions this study was designed to answer

In this study, I set out to find out what effect rabbits have on the vegetation of an area of chenopod shrubland in western New South Wales. The aims were to quantify the effect of rabbits at different densities and under different pasture conditions, in both the long and short terms.

The answers to these questions would provide information which would help park managers to assess the conservation value of rabbit control. They would also provide enough information to speculate about the effects of rabbit control on kangaroo condition and/or growth rates and total numbers. The information would also be useful in predicting the answers to similar questions in other areas.

I chose to answer these questions by studying both the processes involved in the impact of rabbits on vegetation and the effects of rabbit grazing in the field. The latter were partly used to test predictions made from the results of the process studies. Rabbit numbers were never high enough for me to measure a short term effect of rabbits on vegetation but I was able to measure a long term effect and compare this with predictions. Throughout the study I monitored rabbit densities in order to gain accurate information on the dynamics of rabbits in the study area. Since the process studies gave information about the effect of individual rabbits, and the total effect of rabbits is determined by the number of rabbits, an understanding of the population dynamics of rabbits is essential when making predictions about effects.

Kinchega National Park was chosen as the study area. I will hereafter refer to this area as Kinchega. This area was chosen because of the other research which was being carried out there by C.S.I.R.O. (Wildlife and Rangelands Management) and by the National Parks and Wildlife Service of New South Wales. Their work took the form of a five year study. It was set up with the aim of gaining sufficient information to be able to model kangaroo population dynamics from rainfall data. To do this, the relationship between rainfall and vegetation growth and species composition was studied as was the effect of kangaroos on pasture biomass. My study commenced two years after the start of this broader one and was to provide complementary information on the effect of rabbits on pastures.

Ideally, I would have studied the dynamics of the pasture as well as those of the rabbits since the effect of grazers is dependent on the quantity and quality of the vegetation. Time limitations, however, allowed me to carry out only limited and qualitative vegetation studies but I have been able to draw on the results of the Kinchega project to obtain realistic static estimates of pasture biomass and species composition. I have also been able to use their estimates of kangaroo densities to make predictions about the extent of competition between kangaroos and rabbits. These are discussed in Part 4.

Time limitations did not allow me to study the short term effects of digging up of roots by rabbits on vegetation although the effects of this process will be reflected in the long term effects. I was also unable to study the effect of ringbarking of trees and shrubs largely because this was not in evidence within my study area during the period of study.

2.2 Description of the study area

2.2.1 Location, climate and grazing history

Kinchega National Park is 110 km south east of Broken Hill and west of Menindee (32 25'S; 142 25'E, elevation: 61 m) (Fig.1.2.1).

Kinchega lies toward the arid end of the semi-arid zone having a mean annual rainfall of 236 mm. Its rainfall is non-seasonal (Robertson et al. 1987)and is extremely variable from year to year. The distribution of rainfall within years is also extremely variable. Thus, although spring and autumn rains produce the greatest vegetation response, these rainfalls cannot be relied upon.

Temperatures are consistent from year to year. They range roughly between 40 °C during the day and 20 °C at night in summer and 20 °C during the day and 0 °C at night in winter. Broken Hill receives about ten frosts each year.

The climate can be summarized as low, non-seasonal and unpredictable rainfall together with extreme changes in temperature on a daily and seasonal basis.

Kinchega was grazed by sheep from 1860 until 1967 when it was declared a

National Park. From this time on sheep have been fenced out and kangaroos fenced in. Rabbits reached this area around the end of the nineteenth century.

2.2.2 Soils and vegetation

Throughout this thesis I have used systematic names of plants as they are cited in Cunningham et al. (1981).

The Soil Conservation Service of New South Wales (National Parks and Wildlife Service of New South Wales internal report) recognises nine land systems within Kinchega national park. These are: rivers, creeks, swamps, swamps and dunes, scalds and dunes, sandplains, sandplains and low dunes, dunefields and lake systems. Of these, the first four and the last occur only in the vicinity of lakes or rivers although floodplains (included in the rivers land system) can extend some kilometres from rivers. My studies have been concerned with the sandplains and low dunes system where rabbits can reach high numbers. They are able to build warrens in the sandy soils of these areas, whereas, in the floodplain areas, where the soil is more clayey, warren building is likely to be unsuccessful. The sandplains and dune system is represented over large areas of semi-arid Australia.

The soils within the sandplains and dune system range from almost pure sands to sandy loams. They are derived from the wind-blown sands of an ancient sea bed (Bowler 1982). They often contain calcium carbonate nodules usually below the surface but sometimes appearing above ground. They usually have a shallow or non-existent litter layer and an A-horizon which can be as deep as two metres.

The Soil Conservation Service of New South Wales (unpublished report) further divides this land system into four types according to vegetation. These are: sparse, dense or very dense bluebush and clumps of dense timber. My studies covered areas of all four vegetation types. The major trees in the area are *Casuarina cristata* and *Heterodendrum oleifolium* which can grow in either single species, or mixed species, clumps. Both trees can regenerate by means of suckering as well as from seed.

The major shrub in the area is the chenopod, black bluebush (*Maireana pyramidata*). Pearl bluebush (*Maireana sedifolia*) grows in a few, small areas. This species is reputed to be more palatable than *Maireana pyramidata* hence may have been more prolific before sheep were introduced.

The ground layer vegetation is a mixture of ephemeral, facultatively perennial and semi-perennial forbs and grasses consisting of over eighty species. The dominant species differs considerably from time to time. (See Appendix 2 for species lists and biomasses measured at different times during the study).

2.3 Structure of the project

The project can be divided into three main sections;

1. Estimation of offtake and selectivity by rabbits under different conditions.
2. Monitoring of plant and rabbit populations every two months for three years.
3. The search for a permanent gradient of vegetation species composition which could be related to the decrease in grazing pressure with distance from warrens.

The location of the study sites is shown in Fig.1.2.2.

I will now give a broad description of the aims of each of these sections and the methods used for them.

2.3.1 Vegetation and rabbit monitoring

The aim of this monitoring was to provide information on the responses of the vegetation, and of rabbit populations, to changing environmental conditions. Although much information is available on rabbit population dynamics, information for Kinchega provided confirmation for any predictions of likely rabbit densities. The population monitoring was done in two ways. One was by regular spotlight counts along roads in different parts of the park and the other was by mapping warrens at the study area and counting active entrances every two months (Part 3, section 1.1).

The information on vegetation changes was intended to highlight plant species which might be particularly at risk by, say, remaining green longer than other species into a drought. The monitoring was done by the use of 0.7 m by 1.0 m photoquadrats set up in three herbivore proof exclosures and in the open. Each exclosure was 50 m by 50 m. One excluded kangaroos, one kangaroos but not rabbits and one rabbits but not kangaroos. The exclosures were set up by Graham Robertson, of the National Parks and Wildlife Service of New South Wales, as part of the study mentioned above. Sixteen, regularly spaced, permanent quadrats were marked out in each of the exclosures and in an adjacent open area. Horizontal photographs were taken approximately every two months from March 1982 to March 1985. Initially, I had hoped that the photoquadrats might be used to study the fate of individuals of different species subjected to the different grazing conditions, however, herbivore densities were too low during the study for a grazing impact to be observed using this method.

2.3.2 The vegetation gradient

Initially, a search was made for a vegetation gradient with distance from the nearest warren. Any gradient would reflect a long term effect of differential rabbit grazing pressures. Since there was a drought during the first year of the study, I decided to look for a gradient in bluebush (*Maireana pyramidata*) population parameters and in seed banks. I carried out pilot studies to find out the magnitude of any effect such that feasibility of further sampling could be assessed. For the seed bank study, I took soil samples at four distances of up to 120 m out in one direction from one warren. I collected soil from 20 cm by 2 cm rectangular quadrats which were 2 cm deep. At each distance I used 16 such quadrats in groups of four. The quadrats in each group of four were placed contiguously with the 2 cm edges adjacent to each other. This was done so that I could gain information on the spatial distribution of seeds. The soil was then taken back to Canberra and each soil sample was spread out in a 10 cm by 5 cm tub on top of greenhouse soil. The soil samples were then placed in a greenhouse in a random arrangement and kept moist by watering from below until germination had ceased. The numbers of each species of germinant were recorded for each soil sample. A previous experiment using simulated summer and winter growth conditions had shown that the composition of species which germinated was not affected by temperature although the speed of germination and growth were. Greenhouse temperatures were, therefore, considered adequate for such comparative studies.

The results showed as high a variance in numbers of germinants of most species between contiguous soil samples as between non-contiguous soil samples from each distance. Although there were differences between total numbers of different species between distances, there were no trends in numbers of any species which corresponded to distance from the warren. I concluded that, if a gradient in seed bank composition did exist, it would require a more intensive sampling technique than I had used for it to be detected. Since this would have been impossible for reasons of time and greenhouse space, and in view of the negative results of the pilot study, I abandoned this approach.

The bluebush 'gradient' was measured by sampling various population parameters in sample quadrats set out regularly over a 500 m by 1 km area. The rabbit warrens were then mapped and a relationship sought between bluebush population parameters and distance to the nearest warren. No significant correlations were found. There are several possible reasons for this to be so. The first is that rabbits do, in fact, have no impact on bluebushes. The lack of significant damage to adult bluebushes at a time when damage would be expected to be at its highest i.e. at the start of a drought, suggests that rabbits do not, generally, have much impact on bluebushes. I estimated rabbit removal to be about 2 kg ha^{-1} of the total bluebush foliage biomass during the three months of the drought when they were 'trimming' bluebushes. This is equivalent to between 0.1 % and 2 % of total bluebush biomass (Robertson pers. com.). This estimate was gained by removing, drying and weighing all the fresh bluebush litter from six 25 m by 5 m quadrats at my study site. This species also has the capacity to resprout after almost complete defoliation and can be extremely long-lived. Thus, even if rabbits can affect regeneration from seed, this may not yet have manifested itself in the population structure. Soil changes may also have affected the result, as might the fact that size of the nearest warren was not considered, merely the distance to it.

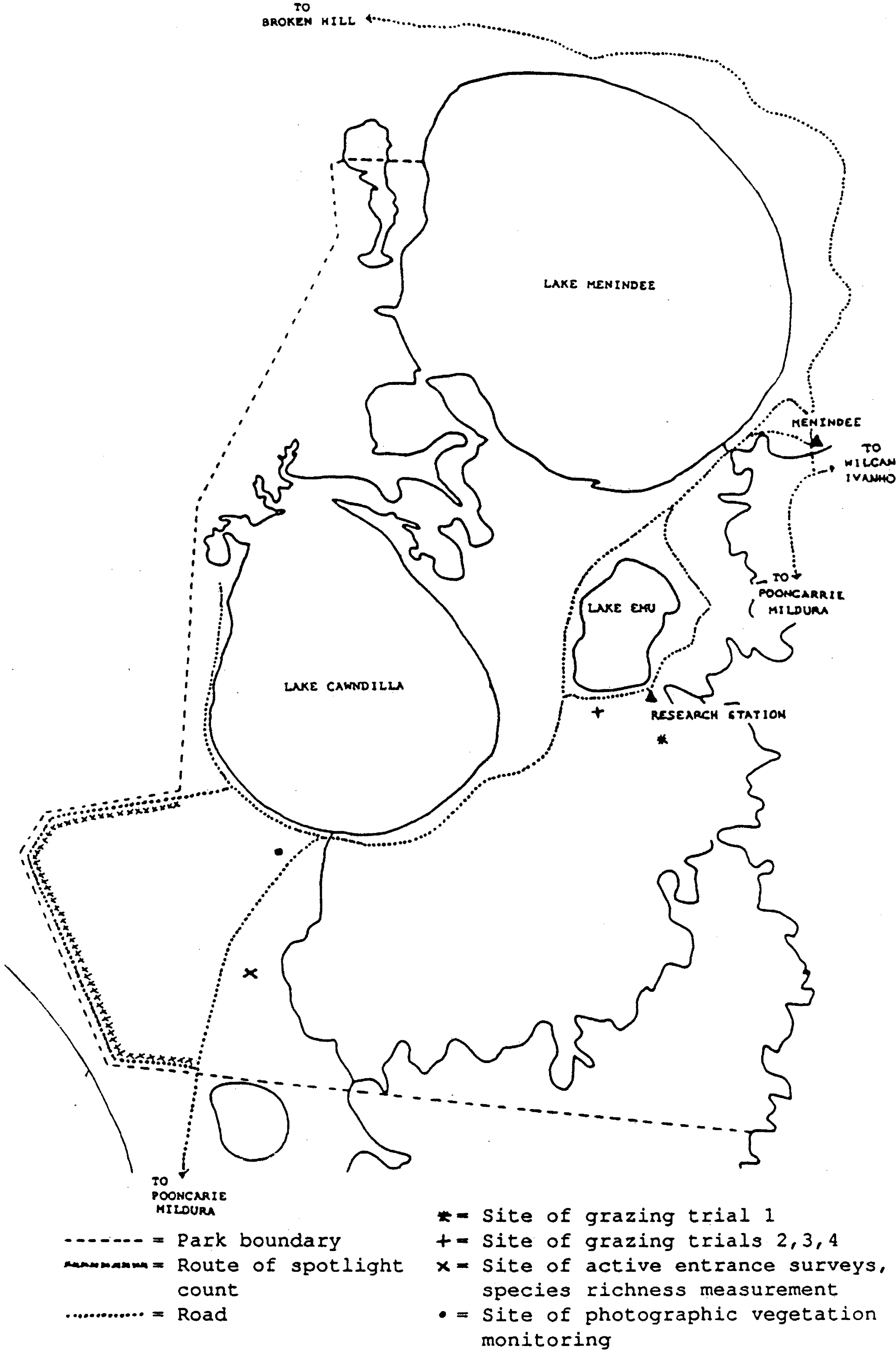
Given the results of the pilot studies, I decided to look for a gradient in a different way. A 100 ha kangaroo exclosure was set up. Within that, vegetation species richness was measured inside and outside rabbit-proof cages placed in a regular pattern within the area. The warrens were mapped both inside, and surrounding, the area and numbers of entrances of each warren recorded. Initially, I looked for a correlation between distance to the nearest warren and species richness. None existed. One possible explanation for this was that distance to the nearest warren did not accurately enough reflect past grazing pressure. I decided to make the measure of past grazing pressure more realistic. To do this, I calculated a 'grazing index' for each vegetation sampling site. The grazing index was dependent on size of, and distance to, all surrounding warrens. This was then compared with species richness at different times. This method yielded more fruitful results which are reported in Part 3 section 2.

2.3.3 Offtake and selectivity

To provide information about total biomass removal, and nature and degree of rabbit selectivity, four grazing trials were carried out under different pasture conditions. These are described in Part 2. Biomass of each species, and species richness, were also measured inside and outside rabbit-proof cages set up close to warrens for which the rabbit populations were estimated by mark and recapture methods (Part 3, section 3). Rate of removal of carrots from the sampling sites within the kangaroo fence was also measured, as was survival of bluebush seedlings inside and outside cages (Part 3, section 4). I had hoped to be able to measure rabbit offtake within the kangaroo exclosure described in Part 3, section 2.1 but rabbit numbers were at no time high enough to detect offtake anywhere but close to warrens.

Fig.1.2.1 Location of study area.

Fig.1.2.2 Kinchega National Park showing location of study sites.



Part 2

Experimental Measures of Offtake and Selectivity

1. Introduction

The aim of these trials was to gain sufficient knowledge about the nature and extent of rabbit grazing to be able to predict the effects of different levels of rabbit grazing on different pasture types both in the long and short terms. The aim was to predict effects on both total pasture biomass and species composition.

In order to predict the effects on pasture biomass, it is necessary to know how much rabbits eat under different pasture conditions. Offtake per rabbit can be measured directly under field conditions, measured in contrived experimental situations which simulate different field conditions or estimated from theoretical considerations of metabolic requirements and experiments with rabbits in metabolism cages. Cooke (1974) used theoretical considerations to conclude that an average sized rabbit, weighing 1.75 kg, would eat approximately 100 g d^{-1} dry weight of vegetation. This is equivalent to 57 g kg^{-1} d^{-1}. Short (1985) used the second method to estimate rabbit offtake under good conditions as 62 g kg^{-1} d^{-1}. I aimed to use the first and second methods to test this conclusion under different pasture conditions. The field studies were set up along with the field test of rabbit effect on species richness discussed in Part 3, section 2 of this thesis. Rabbit numbers, however, were too low during the study to measure the effect of rabbit offtake on biomass except in areas directly adjacent to two warrens. These results will be discussed in Part 3, section 3.

The second method is the subject of this section. In an attempt to answer the questions outlined above I ran four grazing trials. Grazing trials usually involve putting an abnormally high density of animals in an enclosure with natural vegetation and measuring the effect on the pasture over time.

There are many assumptions associated with using the results of grazing trials for prediction of real effects in the field. One of these is that the animals graze in the same way in pens as they do in the field. This is less likely to be a problem with domestic animals but feral and wild animals can show behavioural abnormalities as a result of capture and cageing. Shepherd (1983) showed that capture of kangaroos by a stunning method similar to that used for rabbits in the present study, resulted in severely distorted behaviour in many of the animals captured as well as causing physical damage. Rabbits, being smaller and more easily caught, might be expected be less stressed during capture. For a highly social animal, such as the rabbit, being placed in a pen in close proximity with strange animals may be another cause of behavioural abnormalities as might be the absence of a warren. There is no way of knowing if the rabbits were, indeed, behaving in a normal way. In the trials where time allowed, however, the rabbits were put in a holding pen for a number of days before the trial so would have had a chance to become accustomed to each other. In the fourth trial, the rabbits in one pen dug themselves a burrow. The possible effects of this will be discussed in the relevant section. A low offtake on the first day of the trials or a weight loss under good pasture conditions would be indications of stress. Where either of these occurred in any of the trials, their possible effects are discussed in the relevant chapter.

Another assumption that might be made when extrapolating from grazing trials to the situation in the field is that offtake is purely a function of biomass. Short(1985) ran grazing trials at Kinchega in 1981 with sheep, kangaroos and rabbits. He found a decline in offtake with time and biomass. Short did not speculate about the possible reasons for the decline in offtake during his trial although he draws relationships between biomass remaining in the pen and offtake. Since declining biomass will be linked to declining quality if the rabbits are selecting then it is impossible to separate the two potential causes unless there is some good reason to discount one. Short does not discuss the likely relative importance of these two factors. He did, however, find that, at the end of the trial, there was vegetation left which he judged to be accessible to rabbits. If this was so then biomass *per se* could not have been limiting offtake. For biomass to limit offtake it must be either unavailable by virtue of its small size such that a rabbit cannot physically eat it or it must be unavailable because the rabbits cannot search the whole pen in the time available between sampling. The first of these seems unlikely since rabbits have been known to eat new germinants (Myers and Poole 1963; Part 2, section 5) and Short found 'available' vegetation left at the end of the trial and the second is unlikely considering the size of the pens and the rabbit's excellent searching ability in short vegetation (Lange and Graham,1983; Part 3, section 5). I therefore conclude that a decline in offtake in rabbit grazing trials such as that of Short and those described here, is more likely to be due to a decline in quality of the pasture rather than to biomass *per se*.

A decline in offtake with biomass on offer is often assumed to indicate that the herbivore would remove a reduced amount when a similar amount of vegetation was on offer in the field. This, of course, ignores the fact that the quality of the pasture may be different in the two situations. If the herbivore was limited in its intake by the quality of the vegetation e.g. its fibre content, then a difference in pasture quality could have a large impact on offtake. In the field there is also the factor of the rabbits' searching ability which may cause a reduction in offtake but this is not measured in grazing trials. To extrapolate from grazing trials to the field, it must be assumed that the rabbits are never limited by this factor.

A decline in pasture quality could cause a decline in offtake in two ways. Firstly, some low quality plant species may be avoided because the rabbits have some sense of their low or negative food value. Secondly, a reduced quality of intake may cause the rabbits to retain their food in the gut for longer, thereby reducing gut space available for fresh intake. Predicting offtake under different conditions in the field therefore requires a knowledge of the nature of the limitations to intake and a knowledge of the levels of the important components in the pasture in question. In these trials the biomass of individual species was recorded not only to gain information about rabbit selectivity (see below) but also to enable a better extrapolation of total offtake data from the trial to the field.

Even if pasture quality can be taken into account when extrapolating to the field situation, any predictions rely on another assumption that rabbits are unable to adjust to a gradual decrease in pasture quality. In a grazing trial the change in biomass, and pasture quality, happens in a few days. In the field, similar changes might be expected to happen over a number of months. Thus there would be time for the herbivore to adjust physiologically and/or physically and/or behaviourally. In rabbits, it is unknown if this type of adjustment can occur. Wood and Lee (1985), however, found that after 46 days of water intake restriction, the weights of experimental rabbits in metabolism cages started to increase after decreasing until that time. It is possible that this increase in weight was due to an adjustment to the low water conditions. A similar ability to adjust cannot, therefore, be excluded for rabbits in the field.

Selectivity, as used in this dissertation, can be defined as the tendency of a herbivore to eat a greater, or lesser, quantity of a plant species than it would were it grazing in a random manner. Information was therefore gathered in this trial about individual species decline as well as total offtake. In order to make predictions about selectivity in a pasture other than the ones in which it has been studied, it is necessary to know the criteria behind the selectivity. The innate tendency of a particular plant species in a particular form to be selected is here termed the palatability of that species. Palatability is a property of the species and does not vary with the composition of the pasture although it may vary with the condition of the species. Herbivore preference is here defined as the degree to which a particular plant species is selected for in a particular pasture. This will be a function of both the amounts of all species in the sward and their palatabilities.

The grazing trials which are described in the following sections therefore had three aims:

1) To verify previous estimates of rabbit offtake

2) To measure changes in rabbit offtake and attempt to find reasons for these changes in terms of changing palatability of the sward

3) To measure rabbit selectivity, relate this to palatability of individual species and, if possible, form hypotheses about the reasons for differences in palatability.

The results will be used to make predictions about the long, and short, term effects of rabbits at different densities on different types of pasture.

1.1 General methods

Two 7 m by 7 m rabbit-proof pens were set up in the study area. They were chosen so as to have vegetation as similar as possible. Each pen was chosen so as to contain at least one black bluebush (*Maireana pyramidata*). An electric wire was set up round the top of the 1 m high fence to keep ground predators out. Chicken wire, 0.5 m wide, was stapled to the ground inside the fence. A 0.5 m chicken wire overhang was attached to the top of the fence to prevent the rabbits from climbing out. Wooden boxes covered in hessian were set up in each pen to act as hutches. Since most wild rabbits do not have access to free water, the rabbits in these trials were not given water.

Sufficient rabbits for each trial were caught on a neighbouring property or within the park, where possible in areas with vegetation similar to that in the trial area. They were caught using a stunning technique which had been used previously by workers from C.S.I.R.O.(Wildlife and Rangelands Research) and from Adelaide University. The technique involves shining a spotlight at a rabbit, stunning it by shooting between its ears and then catching it in a long-handled net. The rabbits were held in a pen near the trial area for a few days to accustom them to the vegetation.

The rabbits were weighed on being put into the holding pen, at the start of the experiment and again at the end of the experiment.

Not all the trials followed this method exactly. Changes to the method will be described in the relevant section.

1.2 Description of Vegetation Sampling Technique

1.2.1 Introduction

In grazing trials, herbivore offtake of any species is taken to be equal to the decline of this species in the pen over time. The biomass of each species in the pens must, therefore, be measured regularly. In these trials, since any destructive sample large enough to be representative would decrease the total biomass by a significant amount, a non-destructive technique had to be used. The species whose biomasses were to be measured in the trials were largely ground layer species. Despite this, I decided to use a modification of the Adelaide technique (Andrew et al.,1979) even though this was designed for chenopod shrubs. Most non-destructive methods designed for ground-layer vegetation estimate total biomass whereas these experiments required measurement of each species separately. The use of traditional methods of vegetation sampling, such as with point quadrats or visual estimates of cover, was considered. Neither of these methods, however, gives an easy conversion from the index recorded by the operator to a biomass estimate. I, therefore, decided to use the Adelaide technique with the modifications described below. A regular arrangement of fixed quadrats was used for sampling so as to minimize sampling error.

1.2.2 Methods

A regular arrangement of circular, $0.25m^2$ quadrats was laid out in each of the pens. In the first three trials, twelve quadrats were set out as shown in Fig.2.1.1. For the reasons given in the sections on the third and fourth trials, this was changed to eighteen quadrats in the fourth trial. One or two operators made the vegetation measurements, the same operator measuring the same quadrats each time. The operators confined themselves to three paths while they were inside the pens (see Fig.2.1.1). This minimized operator damage to the vegetation. Each operator picked a unit of each of the species which appeared in any of their quadrats. Unit equivalents for each species in each quadrat were recorded before the start of the trial and each day during the trial. A minimum of twelve quadrats were marked outside the pens. They were chosen so as to contain a range of biomasses of as many species as possible. These were then used to gain the calibration data.

The 'Adelaide' technique of biomass estimation is described by Andrew *et al.*(1979). It involves picking a 'hand held unit' of the species to be measured. The unit is then compared to the plant to be measured and an estimation made of the number of units which are equivalent to that plant. A direct multiplication of the weight of the unit by the number of unit equivalents can be very inaccurate. The real biomass can better be estimated by cutting and drying a series of samples of different sizes for which unit equivalent estimates have been made. If dry weight is then plotted against unit equivalents, the gradient of the linear regression line through the origin can be used as a conversion factor for converting unit equivalents of uncut plants into biomasses.

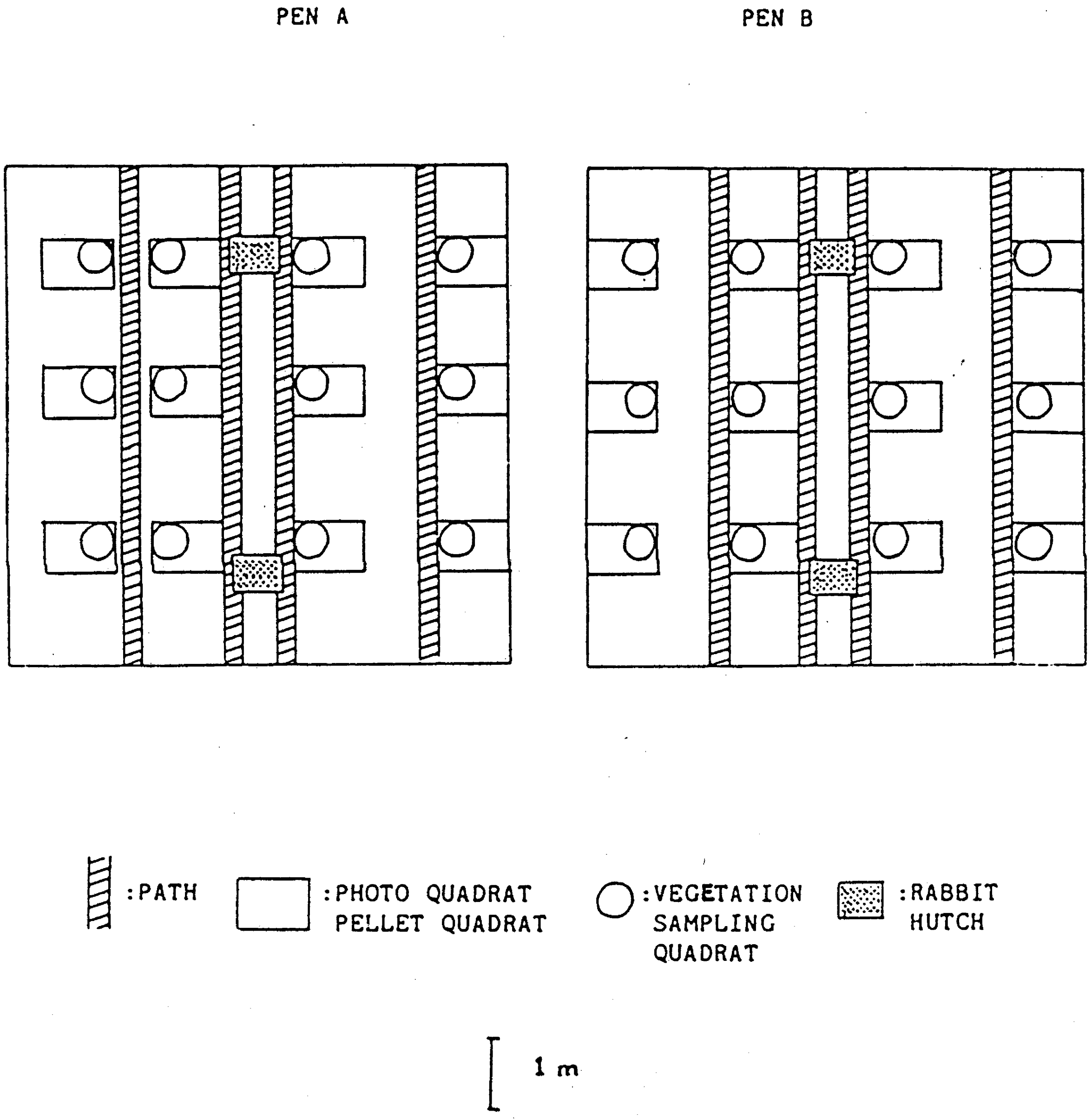
Hand held units of each species in the quadrats inside the pens were picked and kept in plastic bags. The units were chosen to be no larger than twice the smallest amount found in any of the quadrats. They were stored in a refrigerator overnight to minimize water loss. When the initial unit equivalent estimates were made for each trial, the units were taken out of the bags and carefully compared with the plant(s) to be sampled. As the trials progressed, however, and the operators became more experienced, the estimates were made more quickly and without taking the units out of the bags. Each species in each of the quadrats was measured each day of the trial. Measurements were made to the nearest half unit. When a species fell below half a unit, it was recorded as 'trace'. Each species in each quadrat was classed as green, senescent or dead and its flowering, fruiting or seeding status recorded. Where different plants, or parts of plants, of the same species were separable and fell into different phenological categories, standards were cut separately for the different types. This became necessary in the third and fourth trials where the vegetation was becoming drier.

In the Adelaide technique, as described by Andrew *et al.*(1979), the calibration plants (standards) are measured at the beginning and end of each sampling session to record any conversion factor changes. This usually meant measuring the standards twice per day. In these studies there were too many species to be measured to allow us to measure the standards this frequently. Accordingly, the standards were measured at the beginning and again at the end of each trial. It was assumed that any changes in the real biomass of the standards would be small hence any changes in biomass estimates would reflect a change in conversion factor which would have to be taken into account when converting the grazing trial unit equivalents to biomasses. Any species which were not adequately represented in the calibration quadrats had extra standards cut in quadrats chosen to contain roughly the required biomasses of the under-represented species. These extra standards were measured only once due to problems of marking large numbers of quadrats and of time constraints.

As a check on the Adelaide technique at a gross level, and to pick up on any aspects of the vegetation which might reveal themselves as being important on analysis of the results, such as amounts of litter produced or which parts of plants were eaten, photographs of 0.7 m x 1 m quadrats were taken every day. The photographs were taken horizontally from a height of 1 m using a tripod. In the first two trials, twelve quadrats were photographed. This was reduced to three in the other two trials since sufficient information could be obtained from this number.

Various techniques, including the Adelaide technique, were used to estimate relative biomasses of bluebushes, or other shrubs, in the pens. These will be described in the sections on each grazing trial.

Fig.2.1.1 Distribution of sampling quadrats in pens.



2. Grazing trial 1 - Green pasture

2.1 Introduction

The aim of this, the first of four grazing trials, was to provide information about the nature and extent of rabbit offtake on a green, growing pasture. The information gained was to be used to make deductions about the effect that natural populations of rabbits could have on a green pasture in terms of:

1. Total ground layer and *Maireana pyramidata* biomass and
2. Species composition.

The trial took place between the 23rd August 1983 and the 7th September 1983. The pasture which was present during this trial was a fresh growth derived from germinations following 180 mm of rainfall over the previous 6 months which followed 12 months without rainfall sufficient for germination (See Fig.2.2.1). In this trial I set out to measure rabbit offtake from such a green, growing pasture and to assess rabbit selectivity under such conditions.

Two subsidiary aims of the trial were to assess the potential of rabbits, under the green pasture conditions of the trial, to eat and/or damage black bluebush and to assess the viability of using faecal pellet density on a small scale (<$1m^2$) as an index of offtake. If pellet density could be used as an offtake index then I would use pellet counts as an index of grazing pressure at my field sites.

2.2 Methods

2.2.1 Rabbits and rabbit pellets

Eight rabbits were caught on the 20th July. Three rabbits were put into pen A on the 24th July and remained there until the 4th August. Three rabbits were also put into pen B on the 24th July. All three escaped during the first night. One more rabbit was put in pen B on the 27th July and remained there on its own for five nights until five more rabbits had been caught. The eighth rabbit was too small for use in the trial but was kept in the holding pen and its weight recorded at the beginning and end of the trial. The five new rabbits were added to pen B on the 4th August and all six remained there until the end of the trial on the 7th August. In pen A there were, thus, three rabbits for eleven nights while in pen B there were three rabbits for one night, one rabbit for eight nights and six rabbits for three nights. The rabbits were sexed and weighed when they were put into the holding pen and weighed again at the start and end of the trial.

Each day the number of rabbit pellets in twelve 0.7 m by 1 m quadrats in each pen was recorded and the pellets removed.

2.2.2 Vegetation sampling

The changes in the ground layer vegetation were measured using the techniques described above. One operator made all the measurements in both of the pens. The standards were measured only once in this trial. Twelve quadrats were used for the photographs and for the Adelaide technique measurements. Their layout is shown in Fig.2.1.1.

The bluebushes were photographed daily from the same position and with a squared board placed behind them. It was thought that a relative measure of bluebush biomass would be obtainable by counting the number of squares not obscured by the bushes each day.

2.3 Results

Table 2.2.1 lists the species found in each of the pens.

Appendix 1, Table 1.1 contains details of each of the calibration curves used for the Adelaide technique.

Appendix 2, Table 2.1 gives the total biomasses of each species in all the quadrats in each pen on successive days. It also gives the total biomasses in all the quadrats in each pen on each day.

Table 2.2.2 gives the sex of the rabbits and their weights at the start and end of the trial.

Since there was no time to allow the five extra rabbits to become accustomed to being in a pen before being added to pen B, it is possible that their grazing behaviour was affected.

2.4 Discussion

2.4.1 Total biomass removal

Since the numbers of rabbits in the two pens varied during the trial, the grazing effect was measured by using rabbit days (rabbits x days). Figure 2.2.2 shows decline in biomass versus rabbit-days for both pens.

To test the hypothesis that offtake did not decline during the trial, linear and quadratic regressions were carried out on biomass against rabbit days in the two pens. It is possible to carry out an F-test on the quadratic term of a quadratic regression equation. If the quadratic term is significant then a quadratic equation describes the data better than a linear one. Since change in biomass with time is equivalent to rate of offtake, a significant quadratic term would show evidence of a change in offtake rate. No significant quadratic term would indicate that the data show no evidence of such a change. The slope of the line would be the rate of offtake. A significant positive quadratic term in the regression would correspond to a declining offtake with time and a significant negative quadratic term would correspond to an increasing offtake with time.

Figure 2.2.2 shows plots of the regression lines for each pen, both of which are significant ($P<0.05$). A complete analysis of variance for each regression is given in Appendix 7. The quadratic term is significant for the pen A regression but it is not for the pen B regression. The significant quadratic term for pen A indicates a decline in offtake with time. In order to check that this result was not caused by a small number of unusual quadrats, regressions were fitted to the data for each quadrat separately. This also allowed an assessment to be made of the variance associated with the measurements of offtake.

All but one of the linear regressions from pen B quadrat data were significant. One quadrat showed a significant quadratic term. In pen A, however, eight of the twelve quadrats gave significant quadratic terms. Of these, six had a positive quadratic term and two had a negative quadratic term. The positive quadratic terms result from a decline in ground layer offtake in the last two or three days of the trial. The decline in ground layer offtake started in all quadrats when the ground layer biomass was 17 g m^{-2} (at 27 rabbit days). This does not necessarily mean that total offtake declined since the rabbits might, at that time, have started to eat species which did not occur in the sampling quadrats, such as the bluebushes, which the rabbits began to eat at this time in pen A (see Part 2, section 2.4.3 below).

If the reason for the decline in ground layer offtake was an increase in the amount of bluebush being eaten then the lack of a comparable decline in offtake in pen B can be explained since the bluebushes were not touched in this pen (see Part 2, section 2.4.3 below). Since bluebushes are high in salt (Leigh,1972), it is likely that they would only be included in the diet when the palatability of the pasture was low. The next section will show that total pasture palatability declined during the trial in both pens. Since the ground layer biomass in pen B did not fall as low as 17 g m^{-2} (the trial only went for 24 rabbit days), it is likely that the total pasture palatability was still too high for the bluebushes to be included in the diet by the end of the trial.

The two quadrats where there was a significant negative quadratic term (i.e. increasing offtake with time) both had a high biomass of *Tetragonia tetragonioides* relative to the total biomass. The next section shows that this species usually showed an increase in offtake with time. The high relative biomass of *Tetragonia tetragonioides* in the two quadrats thus resulted in an increasing total offtake with time.

The offtake rates, as calculated from the gradients of the linear regression lines were 87 ± 10 g $rabbit^{-1}$ $d^{-1}$and 62 ± 15 g $rabbit^{-1}$ d^{-1}in pens A and B respectively. Using the mean weights of the rabbits in each pen (see Table 2.2.2), these convert to 64 ± 7 g kg^{-1} $d^{-1}$and 39 ± 9 g kg^{-1} d^{-1}.

Before the decline in offtake started in pen A (at 27 rabbit days), the offtake rate was 94 ± 13 g $rabbit^{-1}$ d^{-1} (see Appendix 7 for regression statistics). This is equivalent to 70 ± 10 g kg^{-1} d^{-1}. This is likely to be a more accurate assessment of offtake from a green pasture at the ground layer biomasses present until the bluebushes started to be eaten. It is impossible to know if offtake would have declined if there had been no bluebushes in the pen.

The results for pen A are, therefore, similar to those of Cooke (1974) (57 g kg^{-1} d^{-1}) and Short (1985) (62 g kg^{-1} d^{-1}) although offtake was slightly higher than these before the rabbits started eating bluebushes.

The offtake rates for pen B are significantly lower than published offtake rates. The rabbits in this pen may not, however, have been grazing normally since rabbit densities were high and the five added rabbits had not had time to acclimate to the vegetation or to get used to each other. Table 2.2.2 shows that the rabbits in this pen lost weight whereas those in pen A did not. This suggests that, although the food available would have been adequate to maintain the rabbits' weights, they were not eating sufficient quantities. The results for this pen are unlikely, therefore, to reflect normal offtake rates from such a pasture.

In calculating the offtake rates from the pens, it was assumed that the rabbits were eating equal quantities from the paths as from the rest of the pen. The paths were set up principally to avoid damage to the plants in the quadrats since estimating offtake from quadrats which might also have been damaged by trampling would have been more difficult. The paths make up 14% of the total area of each pen. It is possible that the rabbits avoided the paths to some extent, in which case the offtake measurements above are slight over estimates. Since trampling damage would have increased as the trial progressed, the avoidance of paths would also presumably have increased during the trial. It is impossible to say how significant the effect of decreased grazing in the paths might have been but it could not decrease the estimate of offtake rate by more than 14%.

Bearing in mind the inaccuracies of the technique and that biomass offtake is likely to vary with vegetation type and condition of rabbits, the results for pen A are similar to published results. Those for pen B are not, but this may be because the rabbits in this pen were not grazing normally. The reasons for suspecting this are given above.

2.4.2 Selectivity

A test of the selectivity, or otherwise, of the rabbits is to compare the proportion of each species in the offtake with its proportion in the pasture. If the two are equal, then the rabbits were not selecting. A difference between the two proportions will indicate that the rabbits were selecting between species. If the rabbits were eating each species in proportion to its proportion in the sward then the offtake of each species would be constant, since total offtake is a constant, and the decline curves would all be linear. The linearity, or otherwise, of the decline curves can be checked by looking at the decline in total biomass of each species in each pen.

Figures 2.2.3a and 2.2.3b show plots of the species biomasses against rabbit days. It can be seen that the decline curves show a variety of forms and are not necessarily the same for any species in both pens. The fact that not all species are eaten from the start of the trial and that some decline curves show an increasing, and others a decreasing, offtake with time, shows that the rabbits were being selective.

As a further test of this selectivity, the proportions of each species in the pasture at the start of the trial were plotted against the proportions of those species in the offtake on the first night (see Fig.2.2.4). In both pens there is a weakly significant relationship between proportion in the pasture and proportion in the offtake (Pen A, $r^2 = 0.26$, $P = 0.017$; Pen B, $r^2 = 0.26$, $P = 0.021$). Many species fall consistently above or below the 1:1 lines in both pens. Those which are not eaten in one pen often fall well below the 1:1 line in the other or are not eaten at all. Both groups of rabbits were therefore responding in similar ways to each plant species. It seems, therefore, that some property of each species influenced its offtake rate although proportion in the pasture is also a factor.

Noble (1975) devised a model of offtake of individual species in a pasture grazed by sheep in a grazing trial. In the model, offtake is dependent on the palatability of the species and its biomass in relation to the palatabilities and biomasses of the other species in the sward. He described it thus:

$$c_i / C = (p_i * b_i) / \Sigma(p_i * b_i)$$

where c_i is the consumption of species i, C is the total consumption, p_i is the palatability index of species i and b_i is the biomass of species i. If the unknown factor in determining offtake in this trial is taken to be a function of the species, then it could be taken to equal p_i in this model.

The derivation of the method of calculating the palatability indices is described by Noble (1975). It involves the use of the relationship $c_i = dbi/dt$ and calculating $C*t/B$ where t is the time between measurements and B is $\Sigma(p_i*b_i)$. The gradient of the linear regression line fitted to a plot of $C*t/B$ against $\ln(b_i)$ becomes an estimate of p_i for each species. $C*t/B$ can then be recalculated using the new p_i values and better p_i values obtained. This method gives relative values of p_i. Successive iterations give better relative values. The iteration sequence is complete when there is little change in the values in relation to each other.

I calculated palatability indices for each of the species in pen A and tested the model by comparing predictions of biomass decline of each species in pen B with the actual decline rates. Since palatability indices for the two species which occur in pen B but not in pen A could not be calculated, the predictions might not be accurate even if the model were correct. These species were of low biomass, however, so would not be expected to have a large impact on the offtake of the other species.

Table 2.2.3 gives the palatability indices calculated with each iteration and the final palatability indices used in the model. Five iterations were performed. For each iteration, $\ln(b_i)$ was plotted against C*t/B. The final points where ln(bi) is no longer decreasing were excluded and regressions recalculated. This is justified since, by this stage, the parts of the species left (e.g. grass stumps, stripped stems etc.) are likely to have a different palatability index.

Fig.2.2.5 shows plots of the real and predicted biomasses of each species. It can be seen that, in most cases, the agreement is good. The only species for which the predicted decline curves are not a reasonable fit are *Dactyloctenium radulans* , *Daucus glochidiatus and Babbagia acroptera.* The first of these can be explained by looking at the regressions of $\ln(b_i)$ against C*t/B. A significant quadratic term is an indication of the inconstancy of the palatability factor for a species. If the species were becoming less palatable during the trial then the curve of $\ln(b_i)$ against C*t/B would curve downwards (i.e. have a positive quadratic term) and if it were becoming more palatable then the curve would curve upwards (i.e. have a negative quadratic term). The regressions for four species give significant, positive quadratic terms ($P<0.05$). In three of these, this becomes non-significant when the last few points are removed, as was done for the calculations of their p_i values. This indicates that the palatability indices for these species declined rapidly towards the end of the trial but stayed constant during the earlier part of the trial. Only *Dactyloctenium radulans* retains a significant quadratic term when the last two points are ignored. The plot of $\ln(b_i)$ against C*t/B for this species shows a gradual decline indicating that its palatability index was declining gradually during the trial so that even though the real decline curves for *Dactyloctenium radulans* in the two pens are similar, the predicted decline curve is very different from the real one in pen B. *Daucus glochidiatus* is the other species for which the predicted decline curve is not a good fit. This can be explained by the inaccuracy of the measurements of *Daucus glochidiatus* in pen B. Since the measured biomass in pen B increases by more than a factor of four during the trial, this indicates very inaccurate measurements. This might have been caused by individual plants being missed at the start of the trial then being included later on as the other plants were removed and the small *Daucus glochidiatus* plants became more obvious.

Only *Babbagia acroptera* shows a significant, negative quadratic term ($P<0.05$). In fact, it was obvious in both trials that *Babbagia acroptera* was not touched until late in the trials and even when it was bitten off it was left on the ground. This can be explained by the likelihood that *Babbagia acroptera* is toxic to rabbits since it is toxic to sheep (Cunningham et al. 1981). The poor fit of the model to the real results for pen B can be explained by the small decline in biomass of this species in pen B. Since this species was not eaten, its biomass declined very little during the trial. The accuracy of the biomass measurements was not sufficient to measure such changes although the model predicted, from the overall decline, that they would occur.

The above results show that the proposed model is a good one unless the species being considered gradually change in palatability during the course of the grazing study. In this trial, this appears to be the case for only one species. It is conceivable that a more complicated model could be built which could include the possibility of a changing palatability index. To use this new model for prediction, however, it would be necessary to know the reasons for the changes in palatability indices so as to be able to predict how the palatability would change in a new situation. One approach would be that it would change with proportion of the initial biomass since this would reflect a removal of particular plant parts which might be more palatable. The fact that, in these trials, the p_i values stay consistent for all but one species, indicates that all parts of each species were equally preferred.

The second reason why this model might be criticized is that it can only predict very small initial offtakes and not zero initial offtake . This is, in fact, the same failing as has just been described, since a species which is not eaten at the start of a trial but is eaten later on has a palatability index which increases from zero to some quantity. This is the case for a number of the species in these trials. In this case, however, this does not make a large difference to the predictive value of the model since the predicted offtakes are initially very small. Overall, the model is suitable for this trial.

The predictive value of the model would be enhanced if there were some rules regarding palatability which could be used to estimate the palatability of new species. Table 2.2.4 lists the species in pen A in order of palatability and gives their p_i values. It can be seen that the palatabilities vary widely. No general reason for the particular sequence of the species is obvious. Possible reasons can, however, be suggested for the lower palatabilities of the species in the second half of the list. These are given in

Table 2.2.4 and include toxicity, fibrousness, dryness, a creeping habit, spikyness and saltiness. In general, the species in the first half of the list are erect, green forbs. *Euphorbia* sp.2 is the one exception, being a creeping species. Palatabilities of some new species could, perhaps, be guessed from these general rules but with little accuracy.

2.4.3 Bluebush removal

From the photographs of the bluebushes in each pen, an attempt was made to gain an index of rate of disappearance. The photographs, however, proved to be too variable with respect to the backing board to be able to estimate relative biomass at all accurately. It could be seen, nevertheless, that the bushes in Pen B were little affected (i.e. up to 24 rabbit days) whereas those in Pen A were all grazed down to small stumps. The rates of removal of the four bushes in pen A varied, with some bushes disappearing faster than others. Initially, a large amount of the material removed was left uneaten but, as the trial progressed, even this litter was eaten. It is concluded, then, that most of the bluebush was eaten in the last 6 rabbit days, i.e. when ground layer vegetation was at ≤ 17 g m^{-2}. The pen B trial did not go past the point where bushes were first eaten in pen A (at rabbit days = 27). It seems likely, therefore, that it is necessary for the ground layer vegetation to reach some low threshold of palatability and/or biomass before rabbits will eat bluebushes and this threshold was not reached in pen B.

2.4.4 Rabbit pellets

Figure 2.2.6 shows mean number of pellets produced per rabbit per quadrat per day. The smaller mean number of pellets per rabbit in pen B, despite the greater size of the rabbits in this pen, reflects the variability in number of pellets produced by different rabbits. The wide confidence limits reflect the uneven distribution of pellets throughout the pen.

Figure 2.2.7 shows that there is no correlation between pellet density and offtake on a quadrat basis (Pen A: $r^2 = 0.14$, $P = 0.22$; Pen B: $r^2 = 0.05$, $P = 0.53$). Pellet density does not seem, therefore, to provide a good index of grazing pressure at this scale. This result does not, however, mean that measures of pellet density on a large scale would not reflect relative grazing pressure. Gibb *et al.*(1969) found that, at a larger scale, the mean density of pellets was proportional to the mean density of rabbits in an enclosure over the previous 3 months.

Dung weight, rather than pellet density, might have correlated better with offtake but this information was not collected.

2.5 Conclusions

Rabbits in one of the pens in this trial ate ground layer vegetation at a fairly constant rate of 70 ± 10 g kg^{-1} d^{-1}. This rate fell once they started to eat bluebushes. This result is slightly higher than published results of about 60 g kg^{-1} d^{-1}. Offtake rate in the other pen was much lower but this may have been caused by abnormal grazing behaviour of the rabbits in this pen.

Even in pasture consisting of fresh, green growth, rabbits show definite preferences. In this experiment the preferences were the same in both pens. A model of offtake which incorporates biomass of a particular plant species, a palatability factor for the species, and biomass and palatability factors for all the other species in the pasture, can be used to predict the offtake per rabbit of any species. Palatability factors, calculated from the results from one pen, can be successfully used in an offtake model to predict the decline rates of most species in another, similar pen. The model does not apply when the palatability index of the species in question changes as its biomass declines. This was the case with only one species in the present experiment.

In general, the rabbits preferred green, erect forbs over species which were more fibrous, spiky, toxic or creeping. Within those groupings, however, there were large differences in palatability which cannot be explained.

The black bluebushes (*Maireana pyramidata*) were not eaten until 27 rabbit days into the trial (17 g m^{-2} ground layer vegetation). After that, they were eaten level with the ground within nine rabbit days. This species, however, has the ability to survive even this level of grazing, since all the bluebushes had resprouted by 21st September 1983. This resprouting, however, may have been dependent on the substantial rainfall which fell during the intervening period.

On a small scale (<1 m^2), rabbit pellet density cannot be used as an index of offtake.

Table 2.2.1 Species recorded in grazing trial 1.

Species	Pen A	Pen B
Asphodelus fistulosa	1	1
Atriplex sp.	1	1
Babbagia acroptera	1	1
Beorhavia diffusa	1	1
Brachycome ciliaris	1	1
Chenopodium melanocarpum	1	1
Convolvulus spp.	1	0
Craspedia pleiocephala	1	1
Dactyloctenium radulans	1	1
Daucus glochidiatus	1	1
Enneapogon avenaceus	1	1
Eragrostis sp.	1	1
Euphorbia sp.1	1	1
Euphorbia drummondii	1	1
Goodenia cycloptera	1	1
Helipterum moschatum	1	1
Lotus cruentus	1	1
Plantago drummondii	1	1
Sclerolaena spp.	1	1
Sida spp.	1	1
Stipa variabilis	1	0
Tetragonia tetragonioides	1	1

1 = present, 0 = absent

Table 2.2.2 Weights of experimental rabbits at the start and end of grazing trial 1.

Pen A

Sex	Catch weight 20/7/83	Weight at start of trial 24/7/83	Weight at end of trial 4/8/83	Mean weight during trial
M	1170	1440	1420	1430
M	1270	1420	1420	1420
F	1470----gave--> birth?	1270	1170	1220
			mean	1350

Pen B

Sex	Catch weight 20/7/83	Weight at start of trial 24/7/83	Weight on being put in pen B 27/7/83	Weight on being put in pen B 4/8/83	Weight at end of trial 7/8/83	Mean weight during trial
M	1340	1220				
M	1940	1520				
F	1990---gave-> birth?	1470				
F	1320		1570---------gave-------->	birth?	1370	1470
F				1920	1770	1840
M				1670	1540	1600
F				1670	1520	1590
F				1320	1240	1280
F				1790	1620	1700
					mean	1580

All weights in grams to nearest 10 g.
F = female M = male.

Table 2.2.3 Calculated palatability indices with successive iterations.

	Iteration				
Species	1	2	3	4	5
Asp	2.19	2.82	2.97	3.18	3.02
Atr	.22	.34	.38	.41	.39
Bab	.07	.05	.04	.03	.03
Boe	.37	.26	.23	.20	.25
Bra	1.79	3.59	4.43	5.61	5.42
Con	74.82	18.44	25.86	33.69	34.94
Cra	-	-	-	-	-
Dac	.05	.04	.03	.03	.04
Dau	1.47	2.70	3.43	4.12	3.95
Enn	.10	.08	.06	.05	.07
Era	.24	.16	.15	.12	.16
Eupl	.04	.03	.02	.02	.03
Eupd	1.56	.02	2.72	3.12	2.95
Goo	1.00	1.00	1.00	1.00	1.00
Hel	2.43	4.52	5.76	6.96	6.65
Lop	-	-	-	-	-
Pla	.92	.81	.82	.79	.84
Scl	6.22	.44	.42	.35	.43
Sid	1.70	3.39	4.36	5.34	5.13
Sti	-	-	-	-	-
Tet	.08	.07	.04	.04	.04

Palatability indices have been standardized with P.I. for *Goodenia cycloptera* fixed at 1.00 for ease of comparison.

Species names abbreviated to first three letters of genus. If more than one species occur in one genus then the first letter of the species name is also used.

Palatability indices at fifth iteration are final P.I.'s.

Table 2.2.4 Attributes associated with the species in pen A and their palatability indices.

Species	P.I.	Attributes
Con	103.0	Erect, Flowering, Seeding
Hel	19.6	Erect, Flowering
Bra	16.0	Erect, Flowering
Sid	15.1	Erect, Flowering
Dau	11.6	Erect
Asp	8.9	Erect
Eupd	8.7	Creeping, Seeding
Goo	3.0	Erect
Pla	2.5	Erect, Flowering, Seeding
Scl	1.3	Fibrous, Spiky, Erect
Atr	1.2	Salty, Erect
Boe	.76	Creeping, Flowering
Era	.48	Dry, Fibrous, Seeding
Enn	.20	Dry, Fibrous, Seeding
Dac	.11	Dry, Fibrous, Seeding
Tet	.11	Creeping, Seeding
Bab	.10	Toxic, Erect
Eupl	.07	Creeping

All species were green unless stated to be dry.
Species names abbreviated to first three letters of the genus. If more than one species occurs in one genus then the first letter of the species name is also used.

Fig.2.2.1 Mean monthly rainfall at Kinchega ranger station.

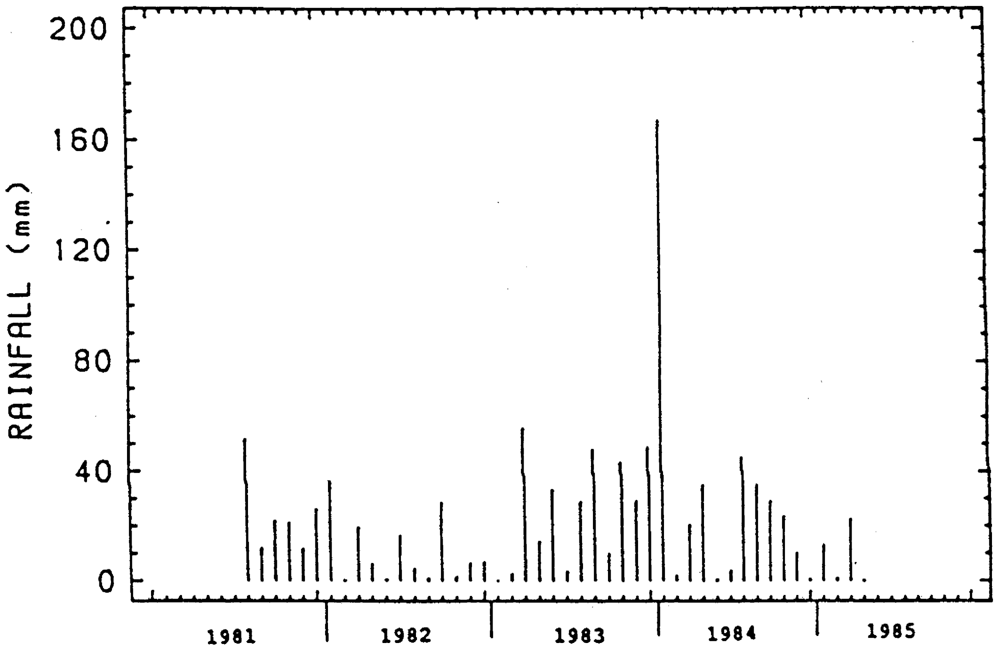


Fig.2.2.2 Decline in total biomass with rabbit days in each pen.

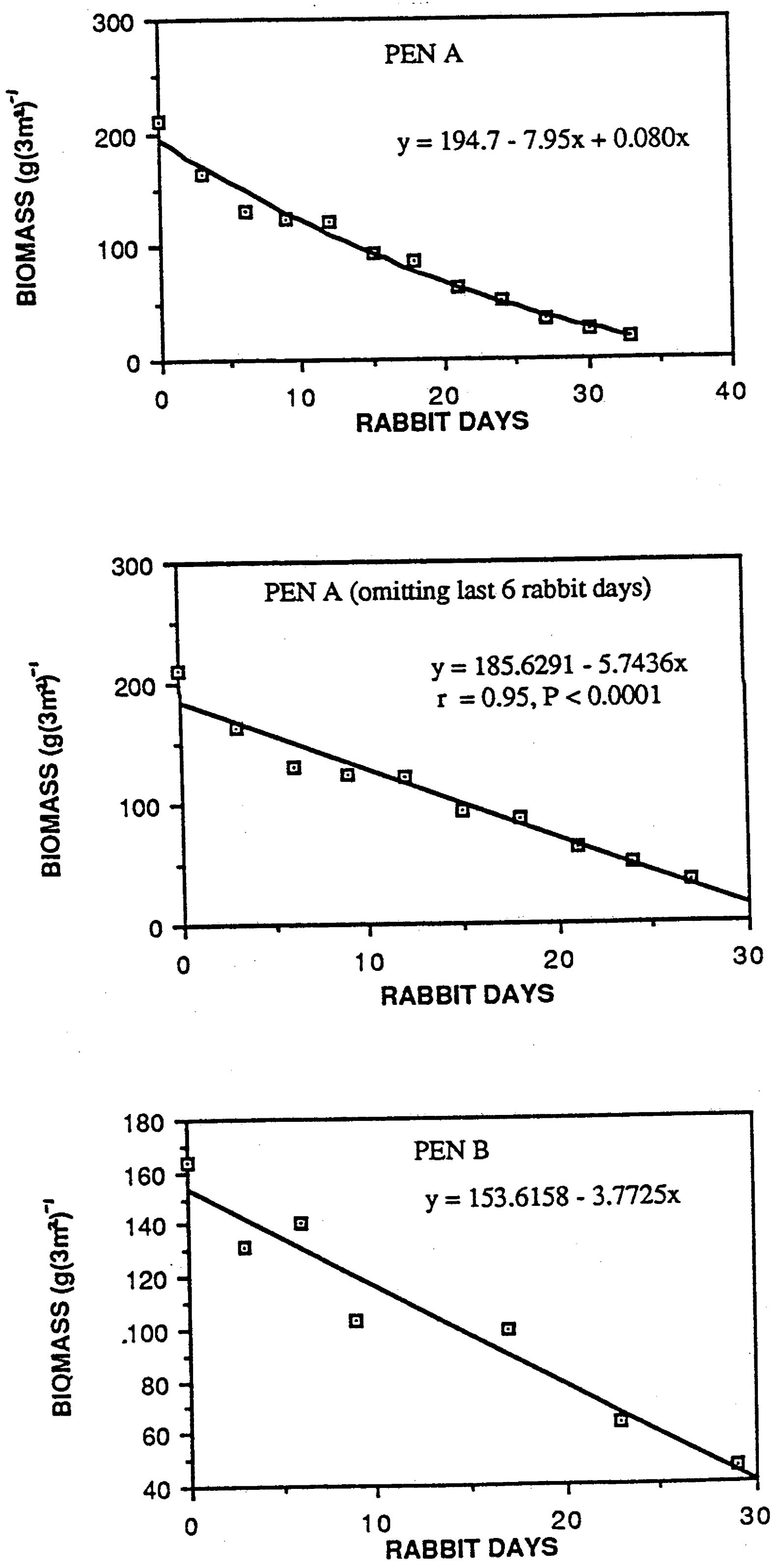


Fig.2.2.3a Decline in biomass (g(3m^2)$^{-1}$) of individual species in pen A.

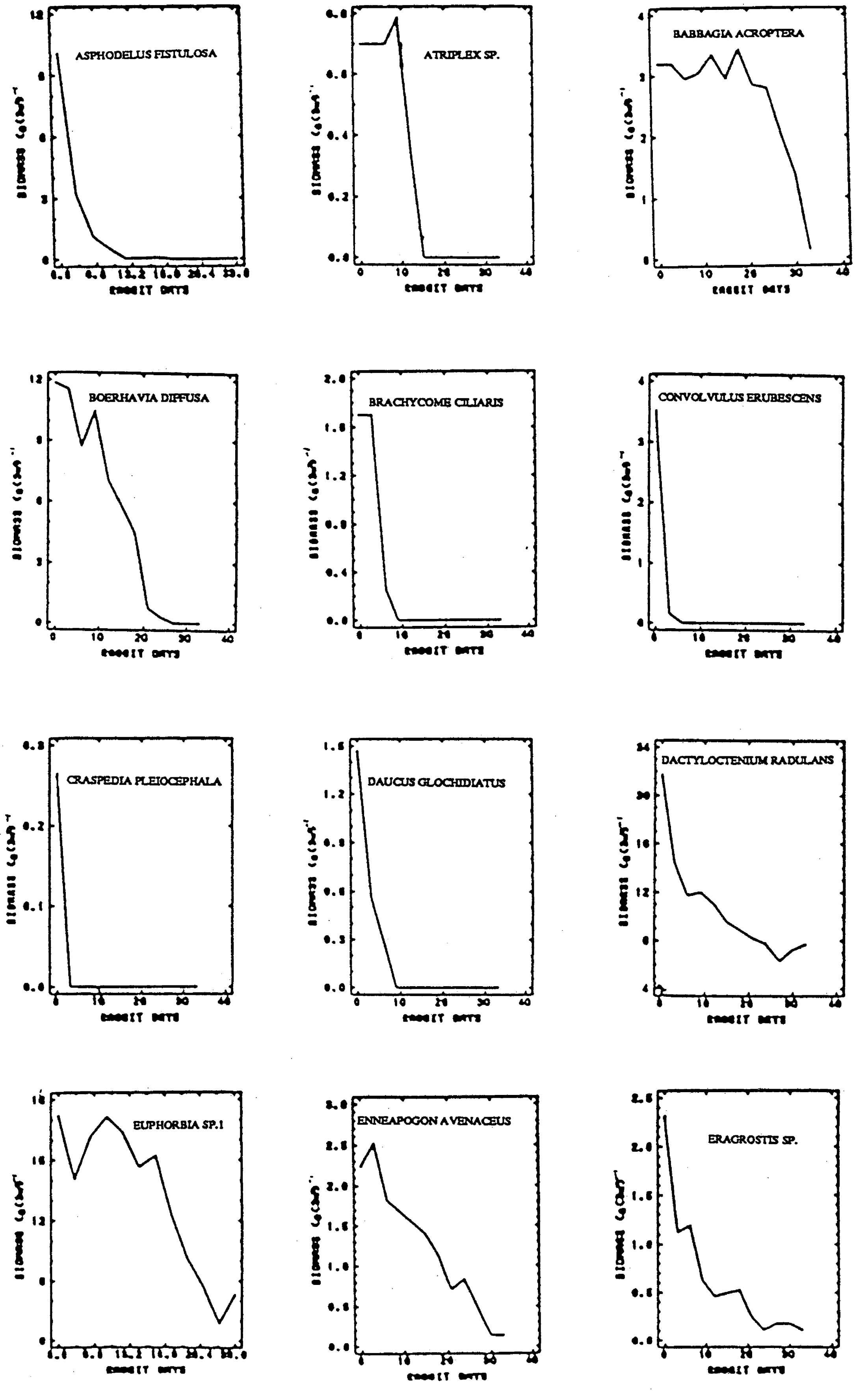


Fig.2.2.3a contd.

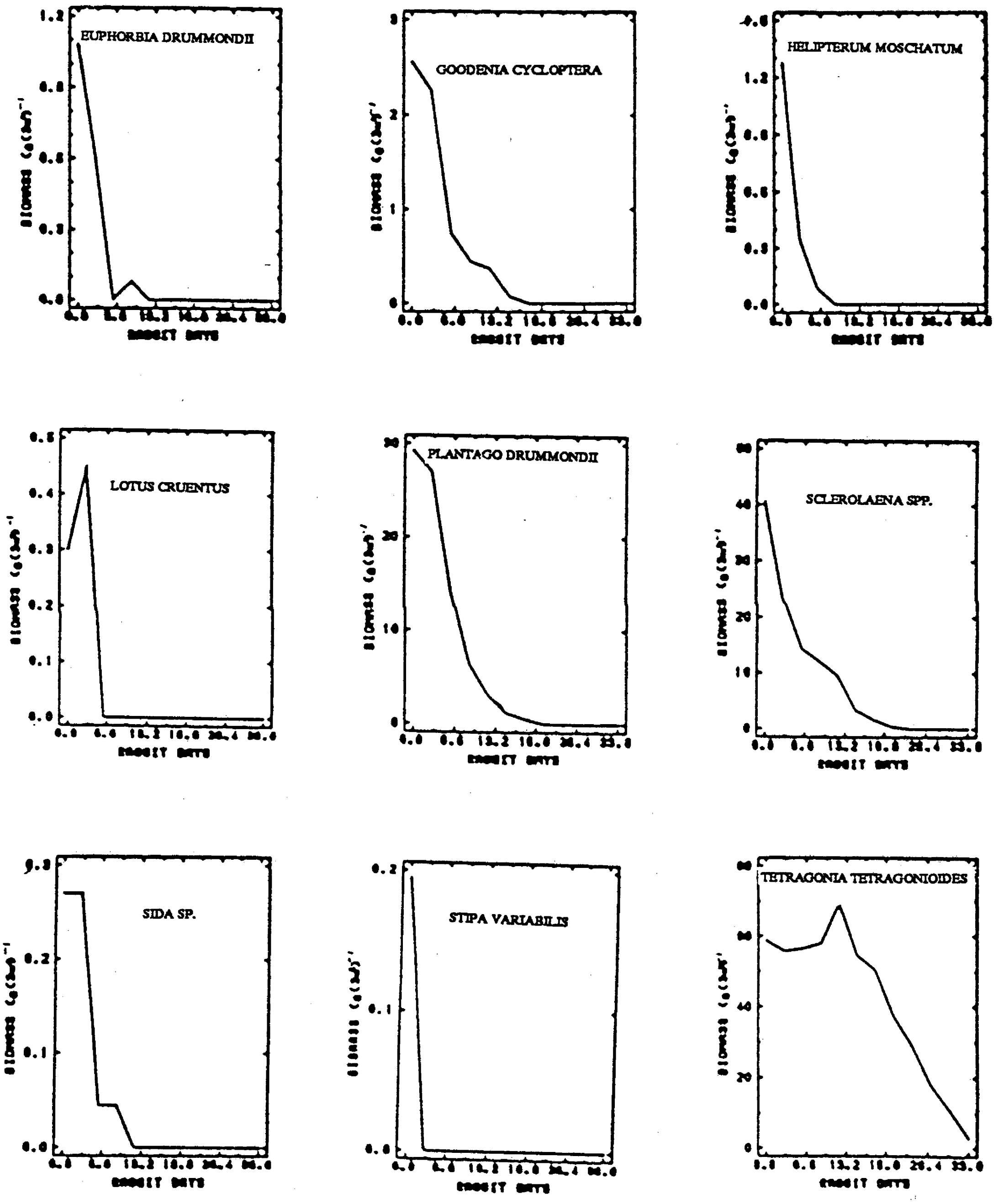


Fig.2.2.3b Decline in biomass ($g(3m^2)^{-1}$) of individual species in pen B.

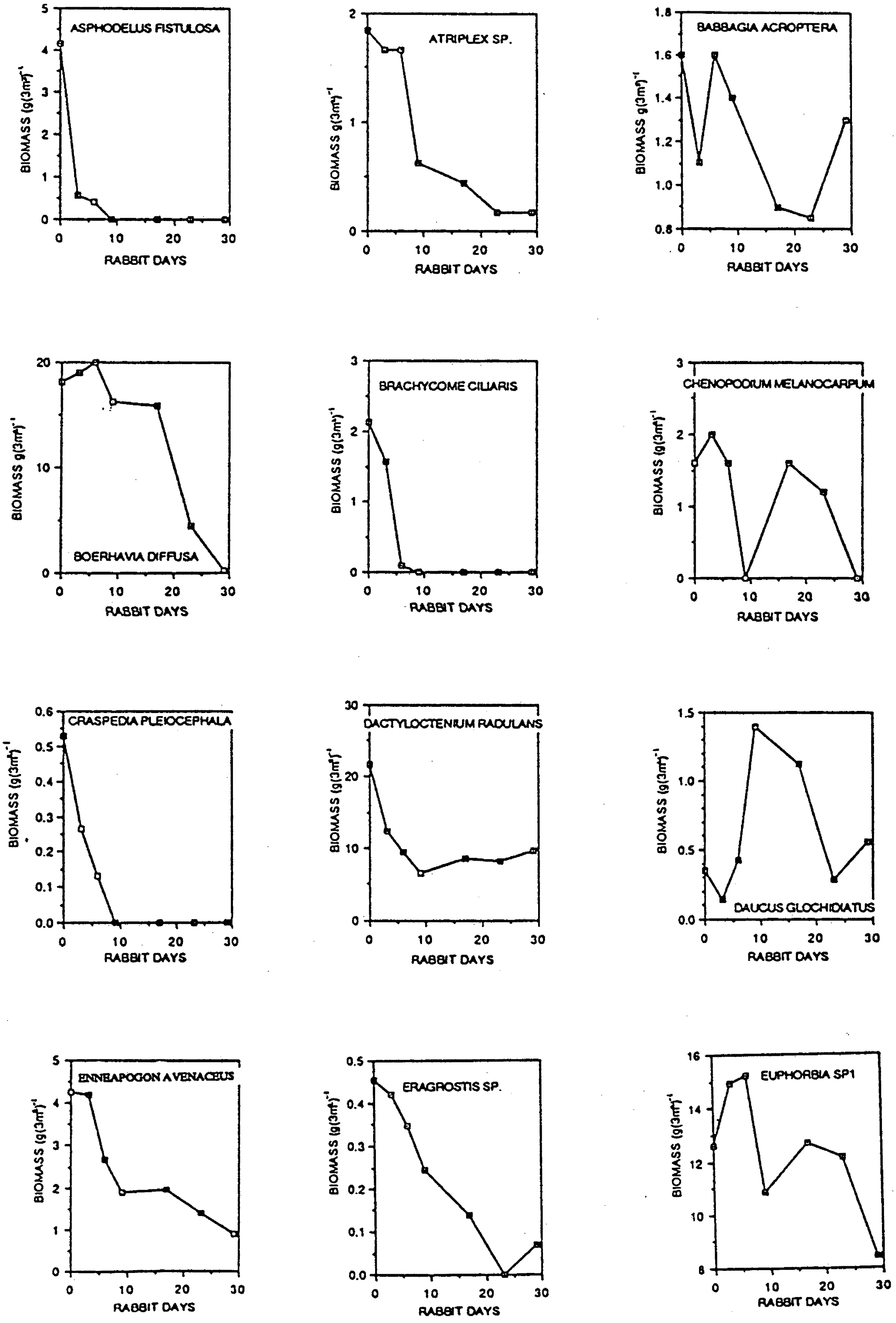


Fig.2.2.3b contd.

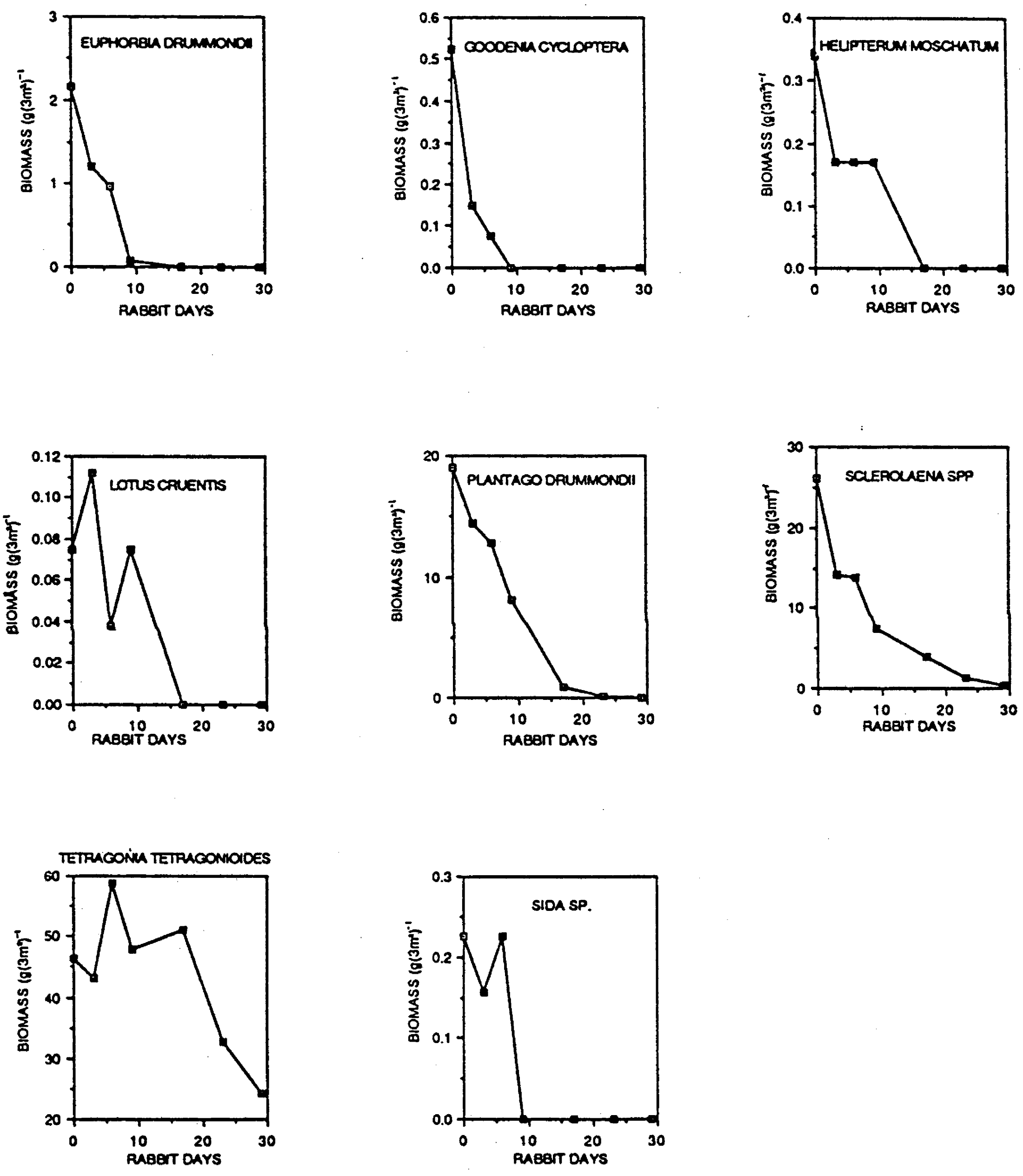


Fig.2.2.4 Proportion of each species in offtake on first night against proportion of each species in pasture biomass on first day.

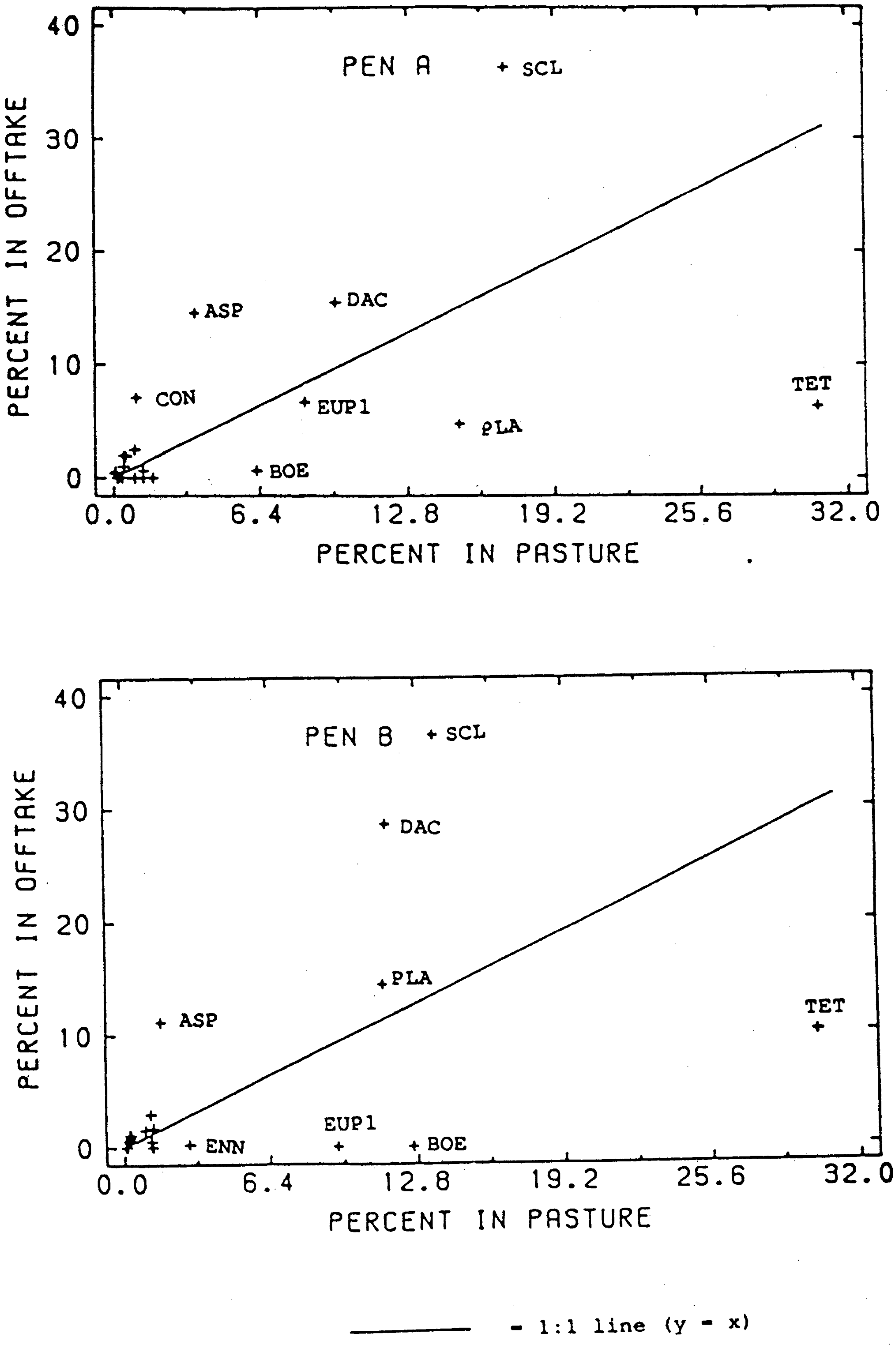


Fig.2.2.5 Real and predicted biomasses of each species with rabbit days in pen B.

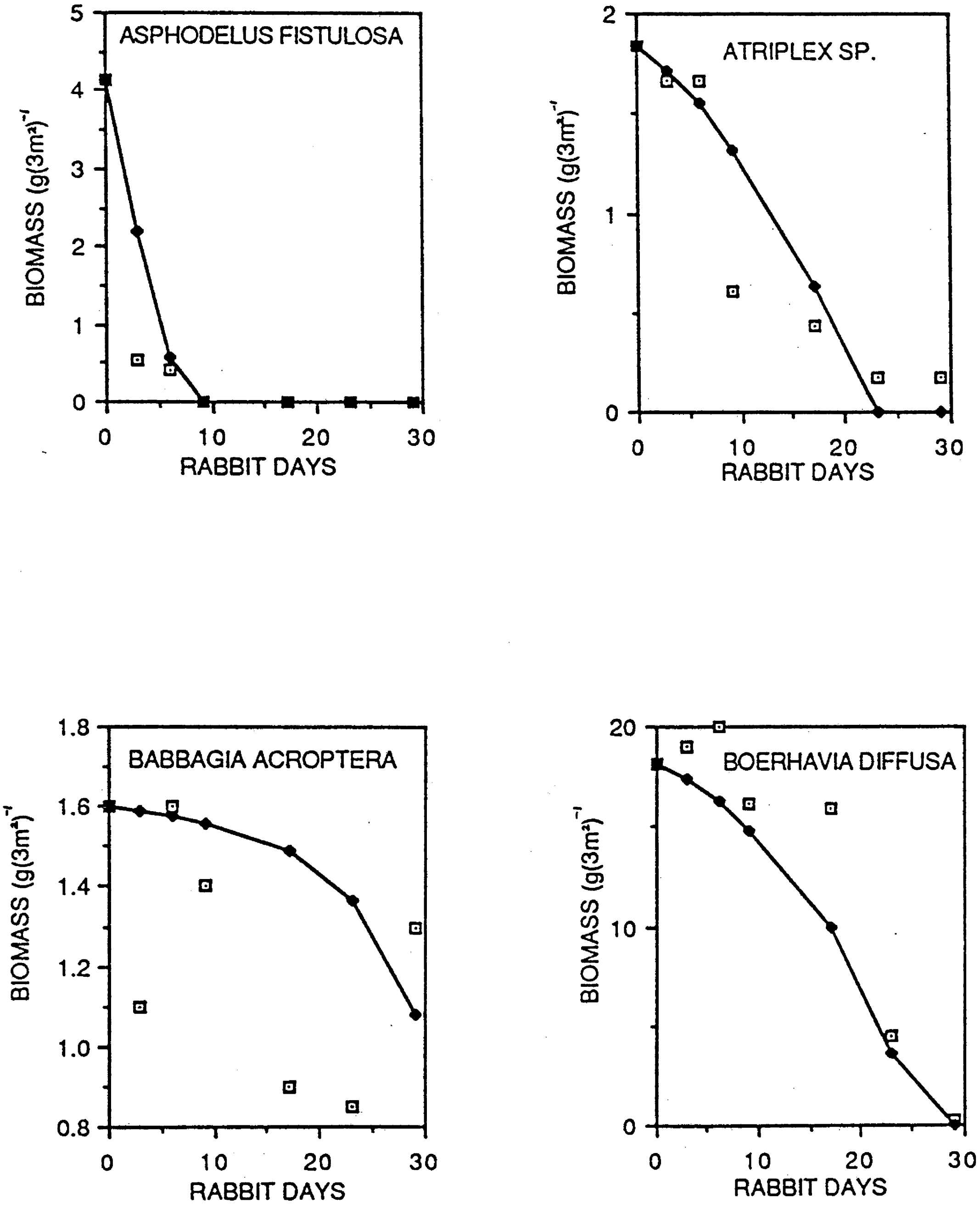


Fig.2.2.5 contd.

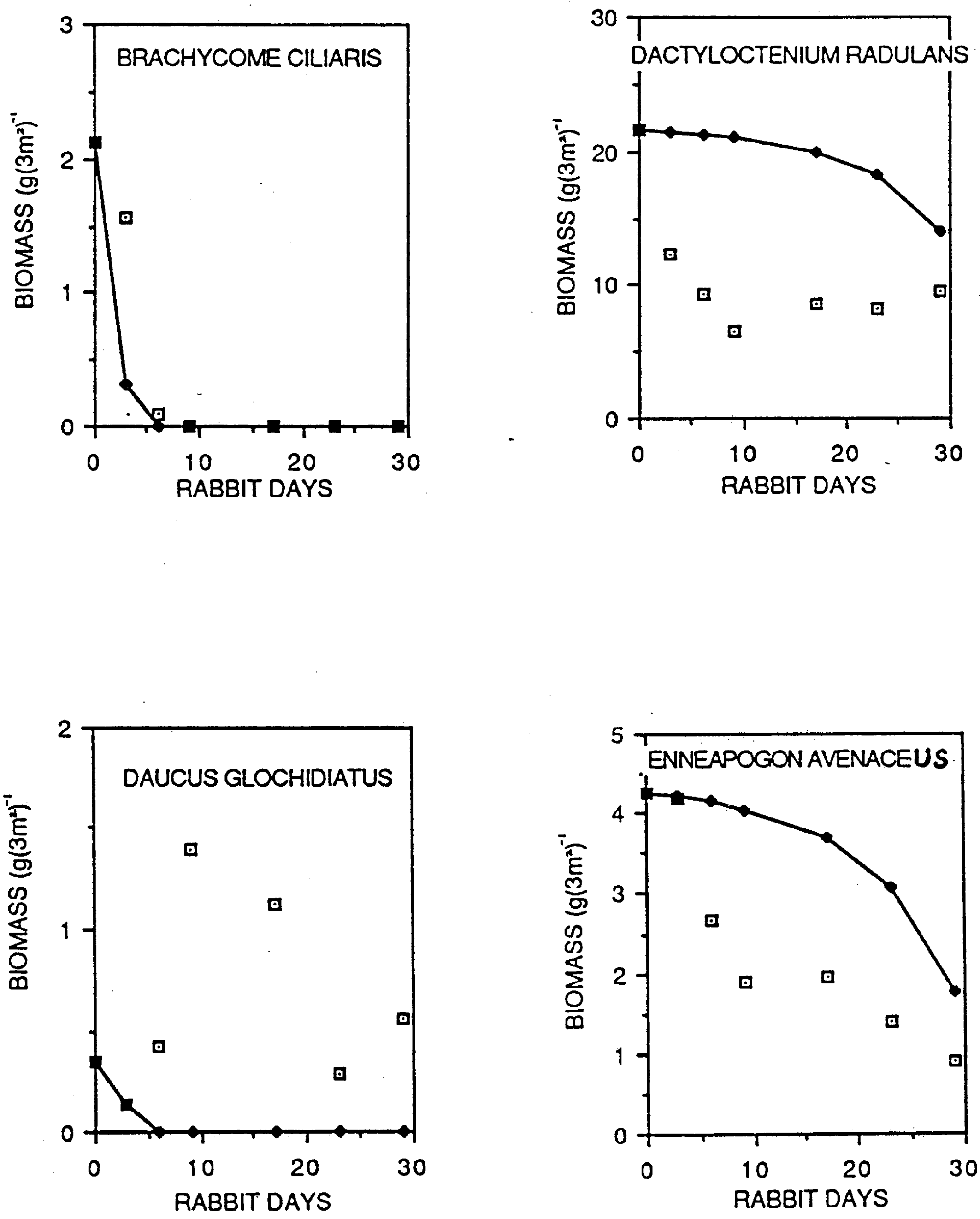


Fig.2.2.5 contd.

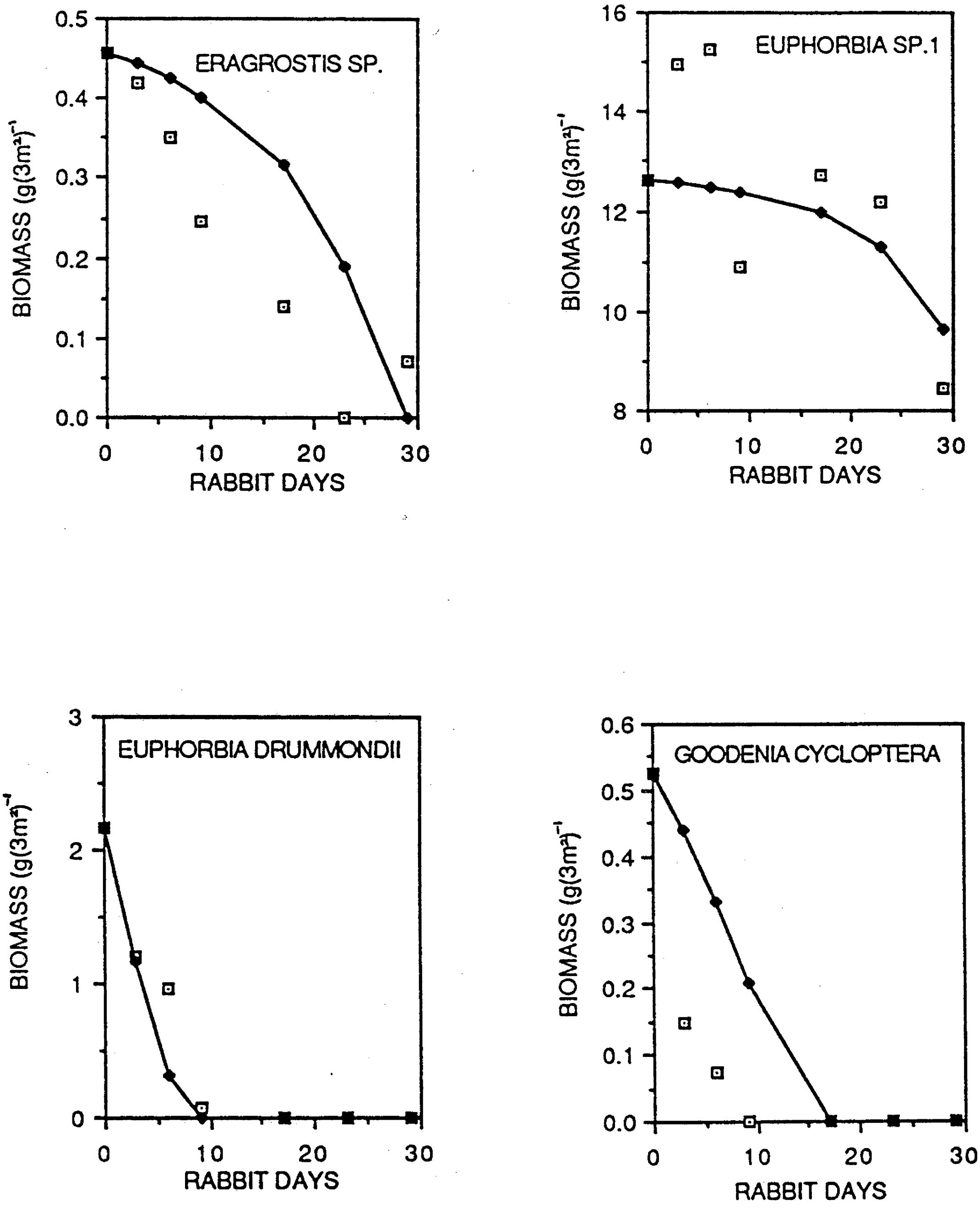


Fig.2.2.5 contd.

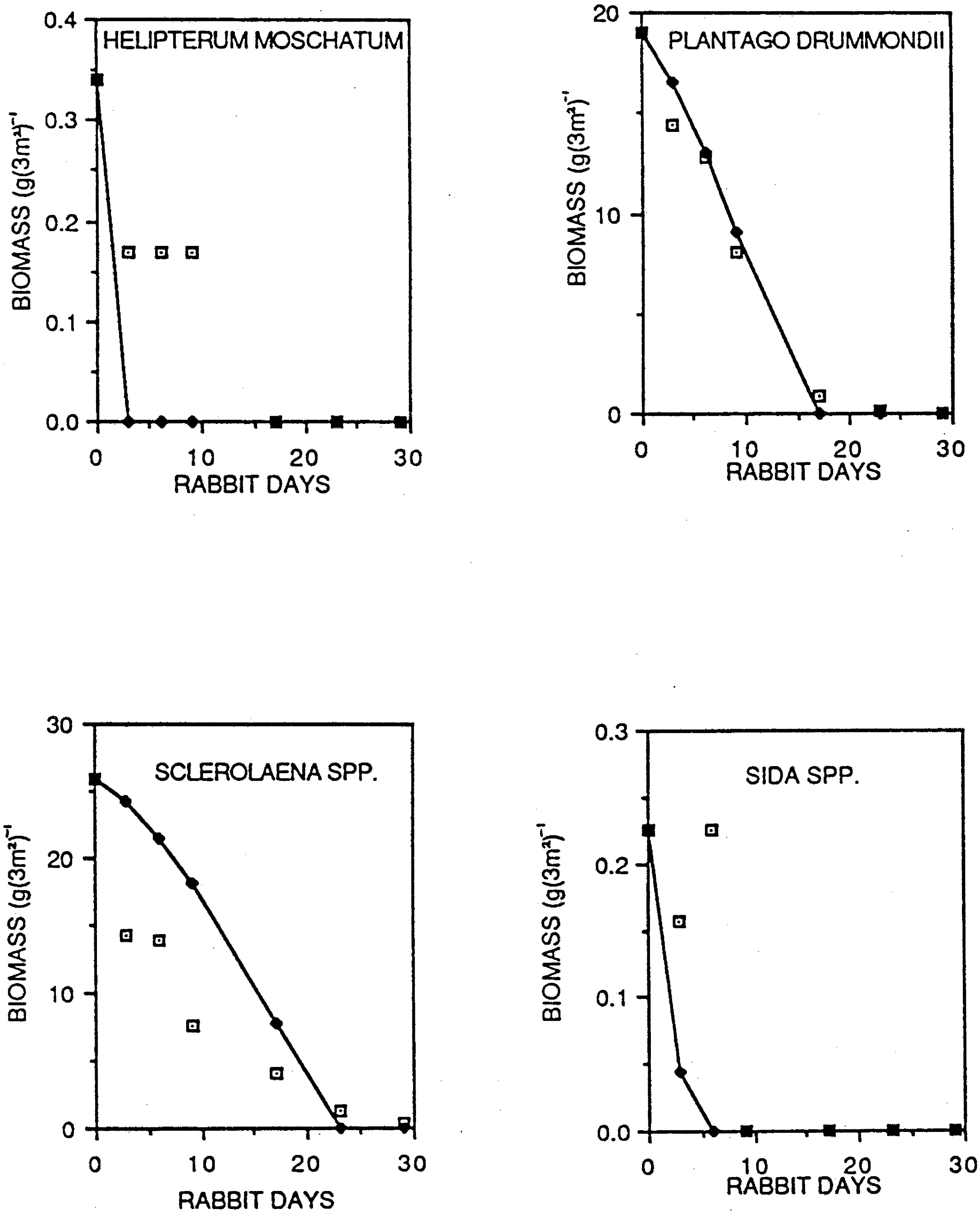


Fig.2.2.5 contd.

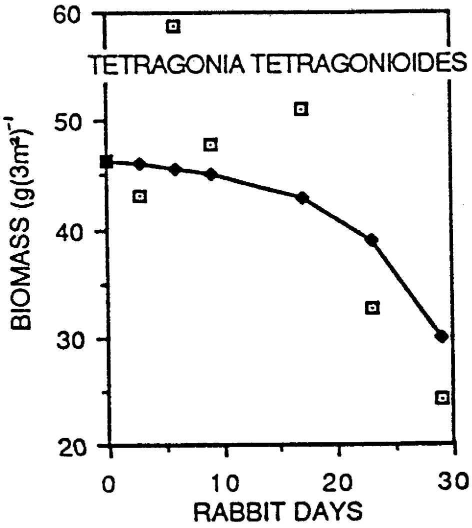
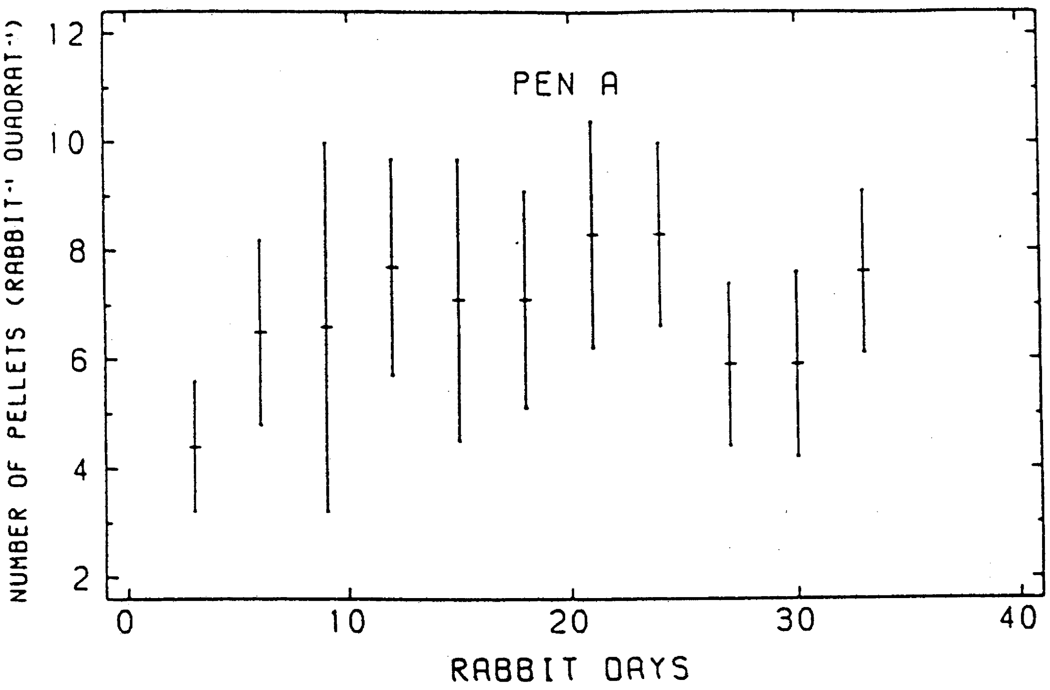


Fig.2.2.6 Number of pellets on each sampling occasion.



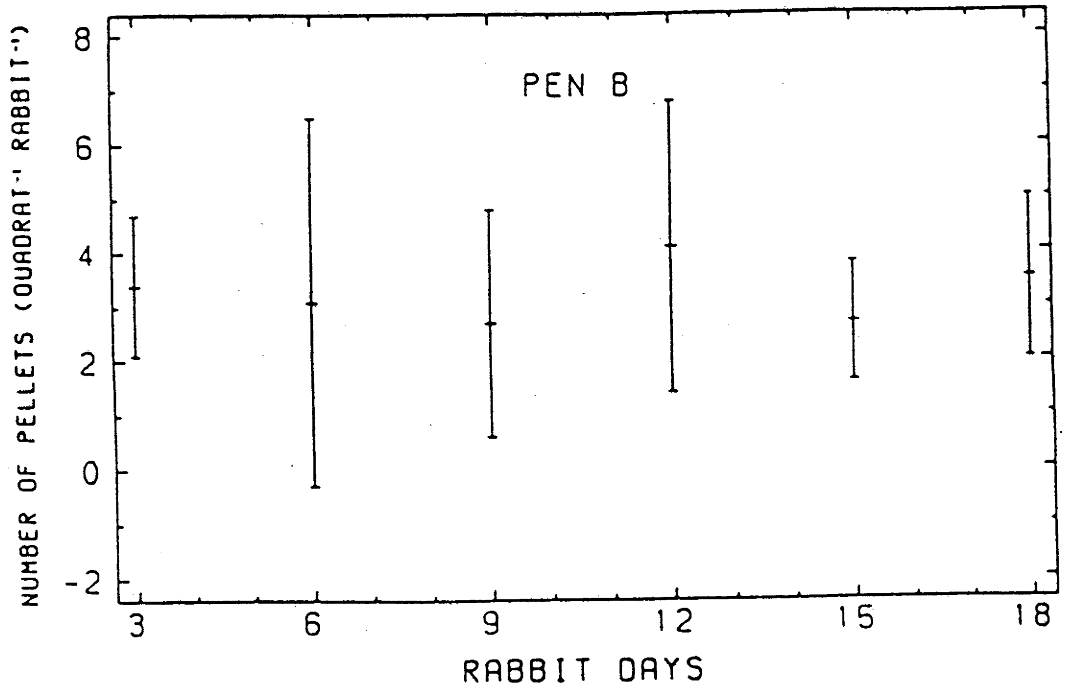
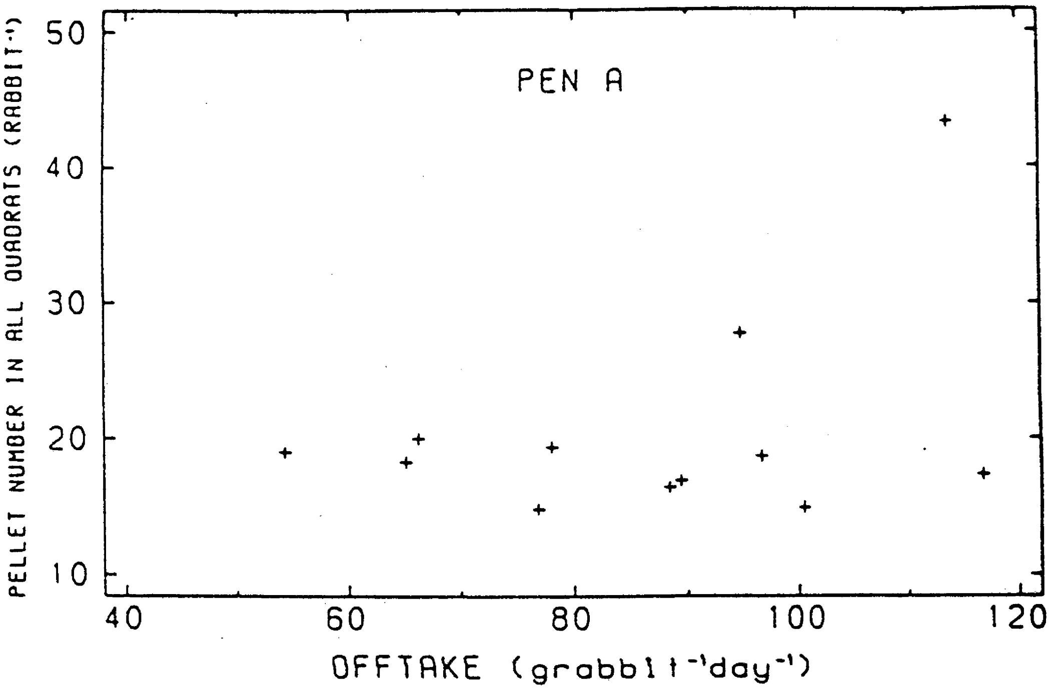
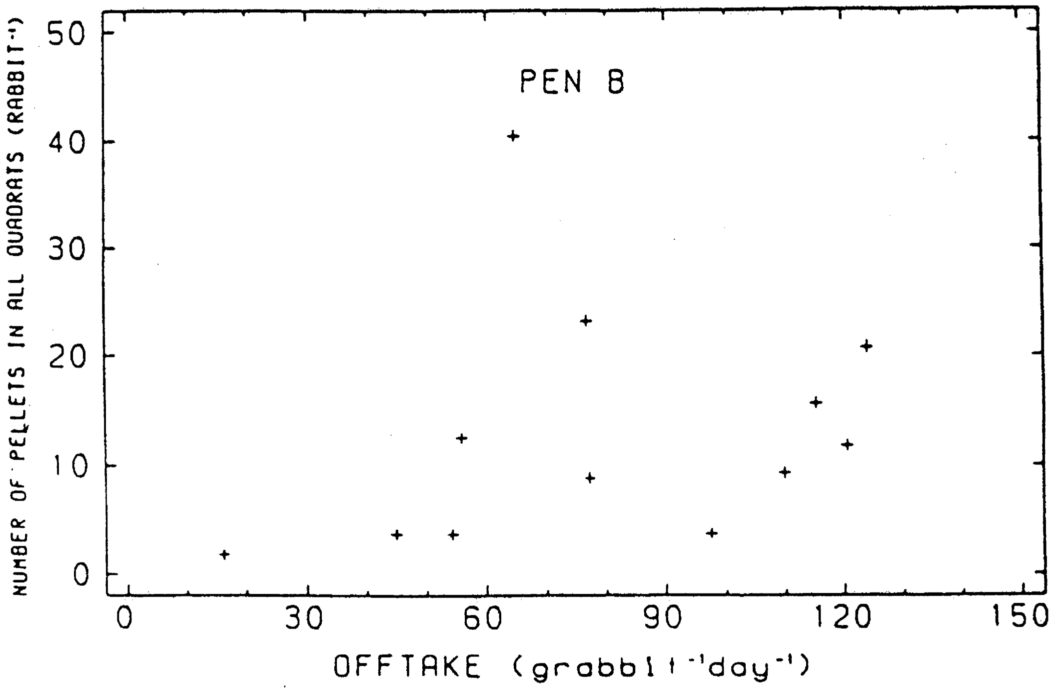


Fig.2.2.7 Relationship between total pellet number in each quadrat and offtake.





3. Grazing trial 2 - Mature pasture

3.1 Introduction

The first grazing trial revealed that rabbits grazing on a green pasture show definite preferences among plant species but that the overall rate of offtake is independent of pasture biomass. This result is as might be expected if the major limitations to intake are fibre and/or water content, as Cooke (1974) proposed. The pasture in the first grazing trial consisted almost totally of green plants hence would be expected to provide an adequate diet regardless of its species composition if no plants were toxic. In extrapolating to the field situation, however, it is necessary to know how rabbits would select, and how much they would eat, under conditions where fibre and/or water content might be limiting. To help provide this knowledge, a second grazing trial was carried out under drier conditions than those of the first.

In this trial the pasture was a mixture of green and dry plants and so would be likely to provide a diet adequate to maintain the rabbits' condition only if a low fibre, high water content diet was selected. Since it would not be possible to select such a diet indefinitely, total offtake might be expected to change as food quality declined. Short (1985) found that offtake declined with biomass and pasture quality even though he provided his rabbits with additional water. Cooke (1974) proposed that offtake of pasture with a low water content would be higher if free water was available. Since most rabbits in the wild do not have access to free water, the rabbits in this second trial were not given water.

The major aims of this trial were, therefore, to assess the degree of selectivity of rabbits grazing on a mature pasture and to deduce the determinants of plant palatability, as well as to measure changes in total offtake with biomass and pasture quality. As before, this information was to be used to make deductions about the potential effect of rabbits on pasture species composition and biomass in the field.

As in the previous trial, a subsidiary aim was to assess the potential of rabbits which do not have access to free water, to damage black bluebush (*Maireana pyramidata*). Rabbits are notorious for their ability to graze and ringbark perennial shrubs and bushes particularly when water is in short supply. This trial would provide suitable conditions to test this effect for the most numerous chenopod shrub in the park.

The trial took place between the 27th September 1983 and the 12th October 1983. The site of the trial was about 1 km from the site of the first grazing trial. This site was chosen because it provided a more uniform pasture than the first site. It would have been impossible at the first site to move the pens to two new positions which were floristically similar. The new site was on a sandier soil hence the species composition was different to that at the first site although many of the species present were the same (c.f. Tables 2.2.1 and 2.3.1).

3.2 Methods

3.2.1 Rabbits

At the time of this trial, rabbit populations were very low (see Part 3, section 1). It proved to be impossible to catch rabbits in the park for this reason. The nearest place where rabbits were still in catchable numbers was on the neighbouring property to the north: Wiri Ilka. The country where the rabbits were caught was similar to that in the park i.e. largely chenopod shrubland. The reason for the relatively high numbers of rabbits on this station, however, is likely to have been the presence of an irrigated lucerne crop. The rabbits were kept in a holding pen for six days before the trial started. They would thus have had some time to adjust to a more natural diet since they were given no extra food or water during this time.

Eight rabbits were caught and placed in the holding pen. They were sexed at the start and weighed at appropriate times during the trial. Some of the females were pregnant but had to be used since time did not allow more rabbits to be caught. As before, three rabbits were put in each pen. Towards the end of the trial one rabbit died and was replaced by another which was being held in the holding pen. Its death may have been precipitated by giving birth since abandoned new born kittens were found in the pen at this time. On the last day of the trial a second rabbit was also found dead and may also have given birth. Both pens, therefore, ran for 16 nights with three rabbits in each pen throughout the trial.

3.2.2 Vegetation sampling

The same techniques were used as in the first grazing trial except that only three ground layer quadrats were photographed. The bluebushes were photographed from one angle only and their biomasses estimated every second day using the Adelaide technique.

Since the vegetation was drying out during the trial, the standards were measured both at the start and end of the trial. All the plants which grew in twelve 0.25 m^2 quadrats were measured at both times. Where species did not occur in all the quadrats, extra standards were cut outside the quadrats. These extra standards were cut about half way through the trial and were measured only once due to the difficulty of marking individual plants. Assessment of any changes in conversion factors between the two times was made by comparing conversion factors calculated using only the plants which were measured twice.

In order to speed up the biomass estimations, two operators did the measurements, each person measuring half the quadrats in each pen.

3.3 Results

Table 2.3.1 lists the species found in the pens and their phenologies at the start and end of the trial.

Appendix 1, Table 1.3 lists the conversion factors calculated for each of the operators from the standards measured both at the start and the end of the trial. Differences in the conversion factors for any one operator would indicate a change in either the hand held units or in the vegetation such that the estimates of numbers of hand held units in the standards were affected. Any changes would most probably be due to the vegetation drying out during the trial. It can be seen that the conversion factors for all species but *Lophochloa cristata* are similar between the start and end of the trial. The conversion factors for *Lophochloa cristata* increased by virtually the same amount for both operators between the two sampling times. The increases may have been due to a change in this species from green to senescent during the trial (see Table 2.3.1). For this species the biomass conversions for the first half of the trial were made using the initial conversion factor and those for the second half of the trial were made using the final conversion factor. The conversion factors for the remaining species were calculated using the mean of the initial and final unit estimates for each standard plant and any extra standards. The extras made little difference to the conversion factors indicating that adequate calibration curves could be obtained with less than twelve points.

Table 2.3.2 gives the sex of the rabbits and their weights on being caught, again at the start of the grazing trial, mid-way through the trial and at the end of the trial. It can be seen that all the rabbits lost weight during their time in the holding pen. The two rabbits which remained in the holding pen after the start of the trial, however, did not lose any more weight. This may indicate some degree of acclimation to the conditions in the pen although it could equally well indicate a reduced social stress with the removal of the six other rabbits. All the rabbits lost weight between weighing times during the trial. This implies that they were eating a non-maintenance diet.

Appendix 2, Table 2.2 gives the total biomass of each species in all the quadrats in each pen on each day of the trial. It also gives the total biomass in all quadrats in each pen on each day.

Figure 2.3.1 shows the biomasses of each of the bluebushes in the pens on each day of the trial. Of the three bluebushes in the trial, only one was damaged. The one that was damaged declined in biomass throughout the trial until the last four days of the trial. At the end of the trial, it was about a third of its original size. Much of the bluebush that was removed was left as litter although some of the litter was eaten later in the trial.

3.4 Discussion

3.4.1 Total biomass removal

Fig.2.3.2 shows biomass in both pens on each day during the trial. It can be seen that offtake declined in both pens with time. The biomass decline can be described by either a quadratic or an exponential curve. Both these curves have been plotted in Fig.2.3.2. Neither one of them is a more accurate description of the data than the other and there is no *a priori* biological reason for either one to be a better description. Both give highly significant fits (Quadratic fits: Pen A, $r^2 = 0.99$, $P < 0.0001$; Pen B, $r^2 = 0.98$, $P < 0.0001$. Exponential fits: Pen A, $r^2 = 0.98$, $P < 0.00001$ Pen B, $r^2 = 0.98$, $P < 0.0001$).

It can be seen that the initial offtakes are very high, even though they are lower when calculated using the quadratic regression equation than when using the measured differences. The smoothed offtakes at the start of the trial are, for pens A and B respectively, 172 ± 35 g $\text{rabbit}^{-1}\text{d}^{-1}$ (91 ± 18 g kg^{-1} d^{-1})and 156 ± 22 g $\text{rabbit}^{-1}\text{d}^{-1}$ (89 ± 13 g kg^{-1} d^{-1}). This is much higher than any previously recorded intake values for rabbits on any diet. Part of the offtake could be accounted for by litter. The photographs taken at the time, however, do not show this to be significant and I did not notice large amounts of litter. Some of the rabbits were pregnant during the trial and this may have led to a slightly raised intake. Pregnancy can increase metabolic rate by about 20% (Cockburn pers.com.). This would cause an increase in energy requirements of less than 20% which could not account for an increase in intake of roughly 60%. A possible explanation is that the seeds of *Tetragonia tetragonioides* and *Swainsona phacoides* were weighed when measuring the dry weights of the standards but were not eaten by the rabbits. If only the foliage of these species was eaten then offtake would have been overestimated. It is also possible that the measured offtakes were real.

In both trials, the high offtakes occur during the first four days of the trial. From then on the offtakes slowly decline. As discussed in the previous trial, the cause of the decline is not likely to be availability of vegetation but is more probably related to its palatability. This will be discussed in the next section.

3.4.2 Selectivity

As in the first trial, the first hypothesis relating to the rabbits' selectivity that I decided to test was that the rabbits were not selecting at all and were, therefore, eating each species in proportion to its proportion in the pasture. Figure 2.3.3 shows plots of the proportion of each species in the pasture against their proportion in the offtake on the first night of the trial. These plots include the species which were not eaten on the first night. Both plots give significant linear regressions ($P = 0.0059$; pen A and $P = 0.0102$; pen B). The scatter around the regression line is large, however, as is shown by the low r^2 values (pen A; $r^2 = 0.31$, pen B; $r^2 = 0.27$). A model of offtake which assumes that there is no selection on the basis of species is inadequate. In particular, it cannot account for the species which are not eaten at all.

A comparison of the two plots in Fig.2.3.3 shows that many species which occur above the 1:1 line in one figure also do so in the other. The same applies to those below the line and those not eaten at all. As in the first grazing trial, this implies that some property of each species could be important in determining its rate of offtake. I, therefore, decided to test the applicability of Noble's offtake model (as described in Part 2, section 2.4.2) to this trial.

The model was used to calculate palatability indices for each species from the data from pen A (Appendix 2, Table 2.2). The same method was used to calculate the palatability indices as was used in Part 2, section 2.4.2. Total consumption at any time was taken to be the instantaneous offtake at that time as calculated from the derivative of the quadratic model of biomass change described above.

There is a wide range of palatabilities (Table 2.3.3). As in the first trial, these indices were used to predict the biomass changes for each species in pen B to test the applicability of the model. The real and predicted biomasses for pen B are shown in Fig. 2.3.4. In general, the fits are good. Some variation between real and predicted biomasses occurs because the initial biomasses used for the model are the initial biomasses in pen B. These measurements are not always very accurate and an inaccuracy in the initial biomass causes the remaining biomasses to be similarly inaccurate. Where this has occurred, the shape of the predicted decline curve is similar to the real one even if the actual values are different. This indicates that the model is a good one despite these apparent discrepancies.

The model was not able, however, to predict the increased offtake later in the trial of four species which start off having very little or no offtake. These species are *Phyllanthus* sp., *Salsola kali*, *Sclerolaena* spp., and *Stipa variabilis*. These discrepancies between the observed and predicted biomasses are most probably due to the failing of the model discussed previously i.e. that it assumes constant palatabilities. If a species is not eaten at all at the start of the trial but becomes palatable later on, the model gives it a palatability index which is higher than it should be initially and lower than it should be towards the end. The model thus predicts an initial offtake which is too high and an offtake towards the end that is too low. This seems to have happened with the four species listed above. The predictions for the other nineteen species, however, are good, indicating that the model is a reasonable description of the system.

As in the previous trial, a better model would be one which could incorporate changing palatabilities. For many purposes, however, the model used will be adequate for prediction as long as the conditions under which it will be inaccurate are known. These will be if the species under consideration changes in important characteristics during the time of interest or if it initially is not eaten but is included in the diet at a later date. Consideration of the factors which contribute to palatability will help to determine which characteristics are important in determining palatability hence also in determining if palatabilities are likely to change under various environmental conditions or with grazing.

Table 2.3.3 lists each of the species in the trial in order of palatability and gives some of their characteristics. The characteristics included are phenology, i.e. greenness and presence or absence of seeds or flowers, habit i.e. whether creeping or erect, presence of spikes and known fibrousness i.e. if the species is woody. Unfortunately, water content was not measured at the time of the trial but the water contents of a few of the species measured two months later are also given for comparison with the greenness of the species at the end of the trial. The species which were green at the end of the trial have, in general, higher water contents two months later than those which were senescent at the end of the trial. This confirms that greenness is linked with water content, as Cooke (1974) found. It also shows that the species which were green at the end of the trial retained a high water content for the next two months whereas those which were senescent at the end of the trial have low water contents or water contents which are very variable between individual plants.

It can be seen that the four species which were recorded as being senescent or partly senescent at the start of the trial occur in the lower half of the table indicating that senescence may contribute to a reduced palatability. Of those species which are in the lower half of the table and are green, most are either creeping or fibrous and/or spiky. Palatability, therefore, seems to be associated with greenness but can be greatly modified by other undesirable characteristics. Most of the high palatability species are non-fibrous, non-spiky, green, erect species. This is not a universal rule, however, since some of the most palatable species are creeping and one, *Emex australis,* is both creeping and spiky. It is possible, however, that they ate this species without eating the spiky seeds. One of the eight species with highest palatability (*Swainsona phacoides*) is also a nitrogen fixer. This attribute may contribute to its high palatability.

Returning to the consideration of the contribution of palatability to total offtake, it can be seen from Appendix 2, Table 2.2 that the seven most palatable species were almost totally consumed in the first five days of the trial. It is during this time that the total offtakes were high. From then on, less palatable species came into the diet or had an increased offtake. The increase in offtake of these species, however, was not sufficient to maintain the high total offtakes and this declined.

All species were eaten at some time during the trial in both pens. In the last three days of the trial, however, there were plants left which were not eaten at all. None of these was green at this time since all the green plants or plant parts had been eaten. The remaining plants may, therefore, have provided a potential diet which was too dry for the rabbits to eat it.

All the rabbits lost weight during the trial (see Table 2.3.2). This may have been due to stressful social conditions, however, offtake for the first four days was not inhibited. This implies that the rabbits were not unduely stressed at that time and there is no reason to suspect that social conditions deteriorated during the trial. Under similar social conditions in the first trial rabbits lost minimal amounts of weight. This also supports the conclusion that the decline in offtake was not due to social stress. Instead it is more probable that their diet was not of sufficient quality and/or quantity to allow them to maintain weight. Since the rabbit which remained in the holding pen where there was plenty of feed throughout, did not lose weight after the initial few days, it seems that removal of the most palatable species decreased the pasture quality to such an extent that the rabbits could not maintain intake and condition.

3.4.3 Bluebush removal

The fact that only one bluebush was eaten and that even this one was not eaten in large amounts at one time, shows that this shrub is not favoured by rabbits (Fig.2.3.1). Many chenopod shrubs have foliage which is high in salt content (Wilson 1966; Lange 1967). This means that the leaves are inedible to rabbits unless they have a good water supply, since rabbits are physiologically incapable of processing a high salt content diet (Wood & Lee 1985). The high water content of the diet of the rabbits in the first trial explains why the bluebushes were eaten on that occasion. The salt concentration in the leaves may also have been lower under the wet conditions of that trial. Since the stems of these shrubs have lower salt contents than the foliage, rabbits are frequently observed to bite off twigs and leave them as litter. They appeared to do this to the one bush in this trial that was eaten. It appeared that the amount of litter diminished later in the trial although we did not measure bluebush litter. Total bluebush offtake in pen A is small compared to ground layer offtake. The variation between pens may be due to differences between individual bluebushes.

3.4.4 Implications for the effect of rabbits in the field

The results of this trial show that, at times when a pasture is mature, species which are green, erect, non-fibrous, non-spiky, and, possibly, leguminous, are most at risk from rabbits. Even at a grazing pressure inside the pens of 612 rabbits ha^{-1}, however, the most preferred species were not removed completely on the first night. A permanent effect on these species would, therefore, only be likely where rabbit grazing pressure is high e.g. near to warrens, or at times of high rabbit density. Species which remain green longer than most others will be very susceptible. Even if the palatability of a green species does not increase as other species dry out, its offtake will increase since the palatabilities of the other species will be decreasing.

Of the most palatable species in this trial, *Convolvulus erubescens*, *Convolvulus arvensis*, *Sida* spp and *Swainsona phacoides* remained green until the end of the trial and still had high water contents two months later. This means that they are likely to be particularly susceptible to rabbit grazing. While these species are still in existence and are green, rabbits will be able to obtain a diet on which they can maintain condition. Species such as the sclerolaenas, *Stipa variabilis* and *Salsola kali*, although they can remain green for prolonged periods, and also had high water contents two months after the trial, are likely to be less at risk since, by the time they start to be eaten, rabbits are beginning to lose condition. When this happens, they become more susceptible to predators since they are weaker and have to spend more time looking for high quality food. Rabbit populations, therefore, fall quickly at these times hence grazing pressure is likely to become low too quickly for them to have a large effect on these plant species. In the field, rabbits may be able to acclimate, to some extent, to a low water content, high fibre diet. In practice, however, rabbit numbers fall dramatically as pastures dry out, particularly if grazing pressure is high (see Part 3, section 1 and Cooke 1974).

This trial confirms that offtake per rabbit, when pastures provide an adequate diet, is at least 100 g rabbit $^{-1}$ d^{-1}. Under the conditions at the start of this trial, offtake may have been as high as 170 g rabbit^{-1} d^{-1}.

The fact that the rabbits could not eat the dry material left at the end of the trial and could not maintain condition on the pasture, implies that they would be unable to denude a pasture before its quality became too low for large numbers to persist. They could, thus, deplete pasture quality but could not remove a large proportion of the standing biomass.

The bluebush results show that these shrubs are not uniformly palatable under conditions of potential water shortage. Since only one bush was eaten and at a slow rate relative to its biomass, it seems unlikely that rabbits could do much damage to bluebushes, especially since this species is well able to regenerate after severe grazing (see Part 2, section 2). Shrub pruning does occur at Kinchega and bluebush litter was very evident under many bluebushes in September 1983, about seven months after effective rainfall (Fig.2.2.1). Sampling at that time revealed that the litter amounted to about 2 kg ha^{-1}; a small proportion of total bluebush biomass. Fresh litter did not accumulate after this time, presumably because the rabbits were no longer in high enough numbers to have a noticeable effect. It is possible that rabbits which have access to free water would be able to process the salt in bluebush foliage. Reports of this species of chenopod shrub being completely defoliated by rabbits are likely to refer to areas which are within a few hundred metres of a water supply.

3.5 Conclusions

The initial offtake of the rabbits was not less than the expected result of 100 g rabbit^{-1} d^{-1} and may have been as high as 170 g rabbit^{-1} d^{-1}. It was impossible to gain an accurate estimate of the initial offtake of the rabbits in this trial since the seeds of two species were included in the calculation of conversion curves and may not have been eaten by the rabbits.

When grazing on a mature pasture, rabbits show definite preferences. Greenness, an erect habit, and possibly non-fibrousness and an ability to fix nitrogen are traits which tend to be preferred whereas dryness, a creeping habit and spikeyness are traits which are not preferred. This selectivity puts certain species at risk from rabbit grazing in high grazing pressure areas.

Total offtake declines with pasture palatability and rabbits lose condition rapidly. Although some acclimation may occur under natural conditions, rabbits most probably cannot survive long once the preferred species have been removed if there is no rainfall sufficient to cause resprouting. This removal of preferred species will take differing lengths of time depending on rabbit densities. If rabbit numbers are low, the preferred species are likely to dry out before they are removed.

Adult bluebushes are not a preferred species and are, therefore, at little risk from rabbits which have no access to free water.

Table 2.3.1 Species recorded in grazing trial 2.

Species	Phenology 26/8/83	 12/9/83
Boerhavia diffusa	G/F	G/S
Calotis cymbacantha	G/F,S	S/S
Chenopodium melanocarpum	G,S/S	S/S
Convolvulus arvensis	G/S	G/S
Convolvulus erubescens	G/S	G/S
Craspedia pleiocephala	S,G/F	S/F
Emex australis	G/S	S/S
Enneapogon avenaceus	S/S	S/S
Eragrostis dielsii	S/S	S/S
Eragrostis sp.	G/S	G,S/S
Euphorbia drummondii	G/S	G,S/S
Helipterum floribundum	G/F	S/F
Helipterum moschatum	G/F	S/F
Lophochloa cristata	G/S	D/S
Phyllanthus sp.	G/S	G/S
Plantago drummondii	G/F	S/F
Salsola kali	G	G
Sclerolaena spp.	G	G
Sida spp.	G/S	G/S
Stipa variabilis	G/S	G/S
Swainsona phacoides	G/S	G/S
Tetragonia tetragonioides	G/S	S/S

G,S,D/F,S = green, senescent, dead/ flowering, seeding.
All species were recorded in both pens.

Table 2.3.2 Weights of experimental rabbits in grazing trial 2.

Pen A

Sex	Catch weight	Weight at start of trial	Weight 2	Weight at end of trial
F	1970	1690	1320	940
F	1620	1470	1190	920
F	2070	1470	1190	1120
Mean weight	1890	1540	2470	1610

Pen B

Sex	Catch weight	Weight at start of trial	Weight 2 or when put into pen	Weight 3	Weight at end of trial
F	1670	1440	1120--gave-->950(dead) birth?		
F	1870	1660--gave-->920(dead) birth?			
F	2070	1470	1190		1120
F	1970	1320	1320		920
M*	1170	1120			940
Mean weight	1750	1400	1140		1000

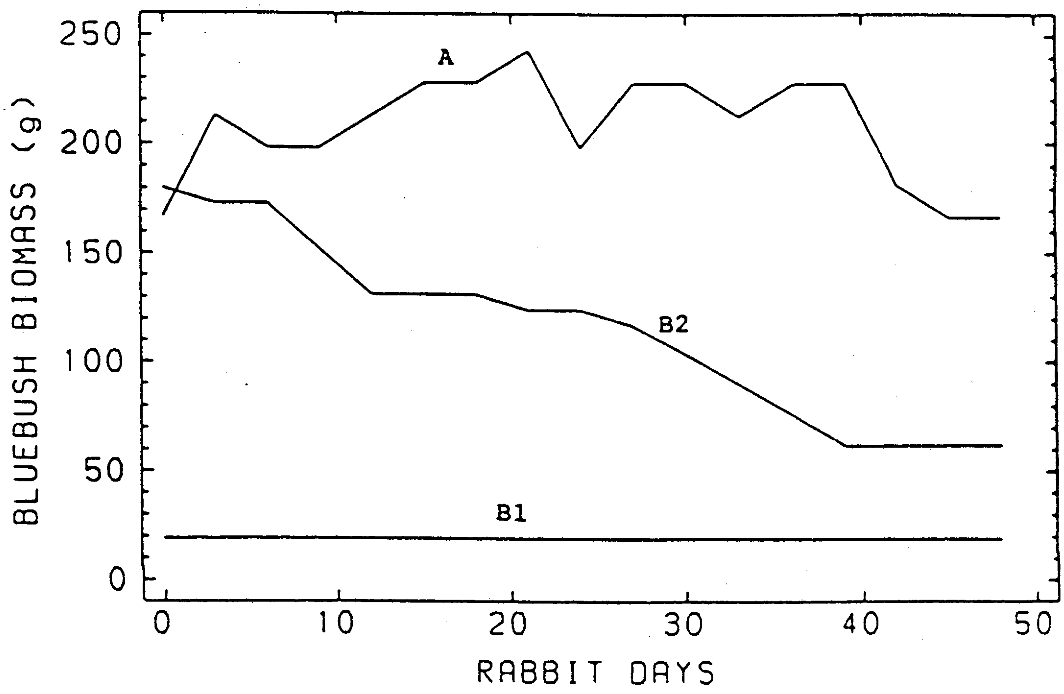
* = in holding pen throughout trial.
Weights to nearest 10 g.

Table 2.3.3 Attributes associated with species in pen A and their palatability indices.

Species	Palatability Index	Phenology		Water Content(%) (13-15/11/83)	Attributes
		26/8/83	12/9/83		
Cone	22	G/S	G/S	59.6	Erect
Cona	23	G/S	G/S		Erect
Eme	12	G/S	S/S		Creeping/ Spiny
Sid	5.7	G/S	G/S	53	Erect
Eup	5.6	G/S	G,S/S	42	Creeping
Swa	5.5	G/S	G/S	70,57,60,58	Erect
Boe	4.4	G/F	G/S	60,62.5	Creeping
Lopg	3.9	G/S	D/S		Erect
Hel	3.0	G/F	S/F	0,6	Erect
Era	2.7	G/S	G,S/S	0,42,0	Erect
Cal	2.0	G/F,S	S/S		Erect
Dau	1.8	G/S	S/S		Erect
Pla	1.4	S/S	S/S	38,0,57	Erect
Che	.90	G,S/S	S/S		Creeping
Tet	.84	G/S	S/S	10	Creeping
Sti	.79	G/S	G/S	54,36	Erect
Scl	.74	G	G	57,51	Erect, Possibly Fibrous Spiky
Erad	.72	S/S	S/S	50	Creeping
Sal	.65	G	G	57,51	Erect, Possibly Fibrous
Hel	.61	G/F	S/F	0,7	Erect
Cra	.60	S,G/F	S/F	46(green) 28,0(dry)	Erect
Phy	.21	G/S	G/S	63	Creeping

Abbreviations use first three letters of genus. Where there is more than one species in one genus, the first letter of the species is also used.

Fig.2.3.1 Changes in biomass of bluebushes in grazing trial 2.



A - Bluebush in pen A

B1,B2 - Bluebushes in pen B

Fig.2.3.2 Decline in total biomass with rabbit days in each pen.

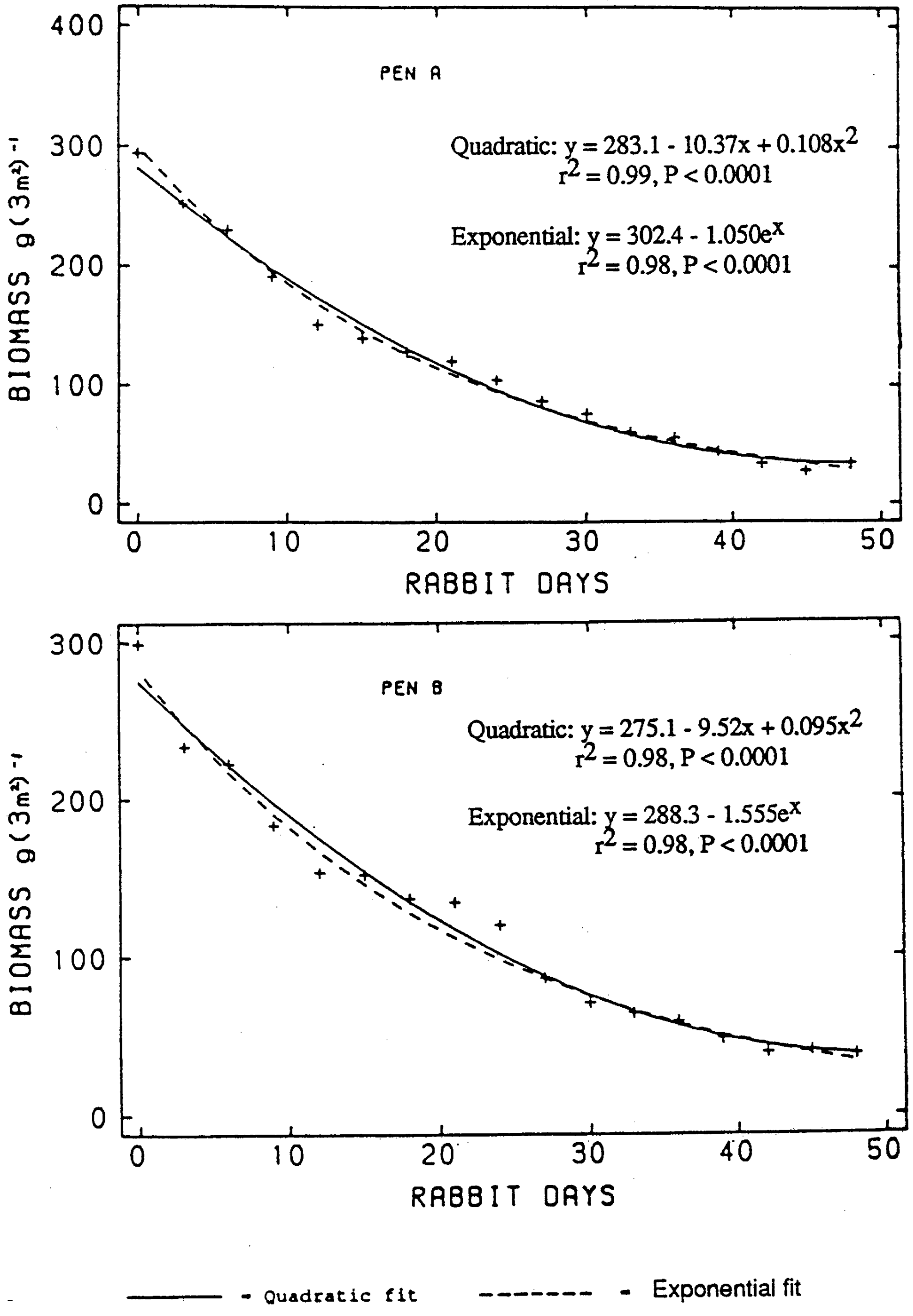


Fig.2.3.3 Proportion of each species in offtake on first night against proportion of each species in pature on first day.

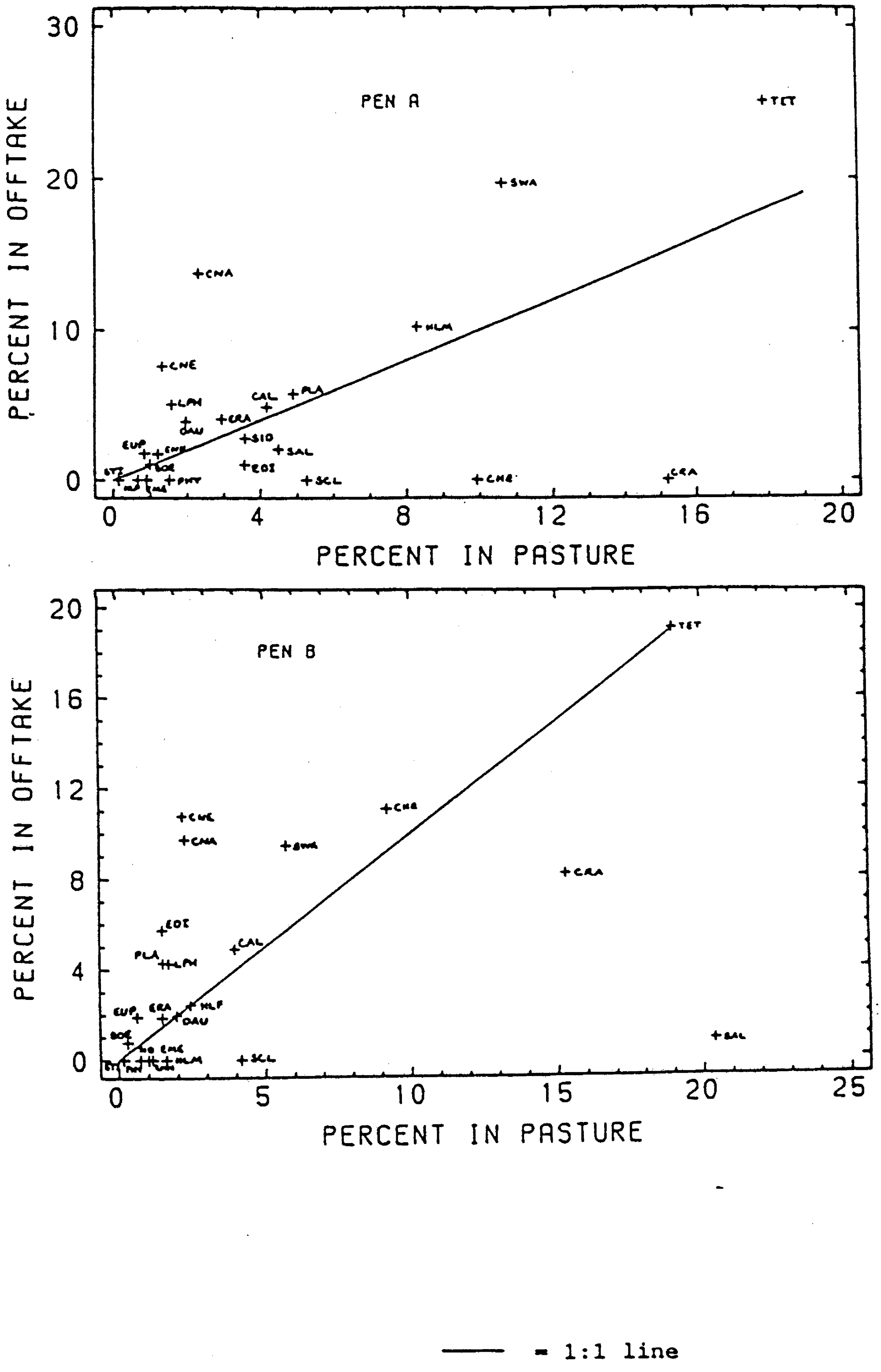


Fig.2.3.4 Real and predicted biomass of each species in pen B against rabbit days.

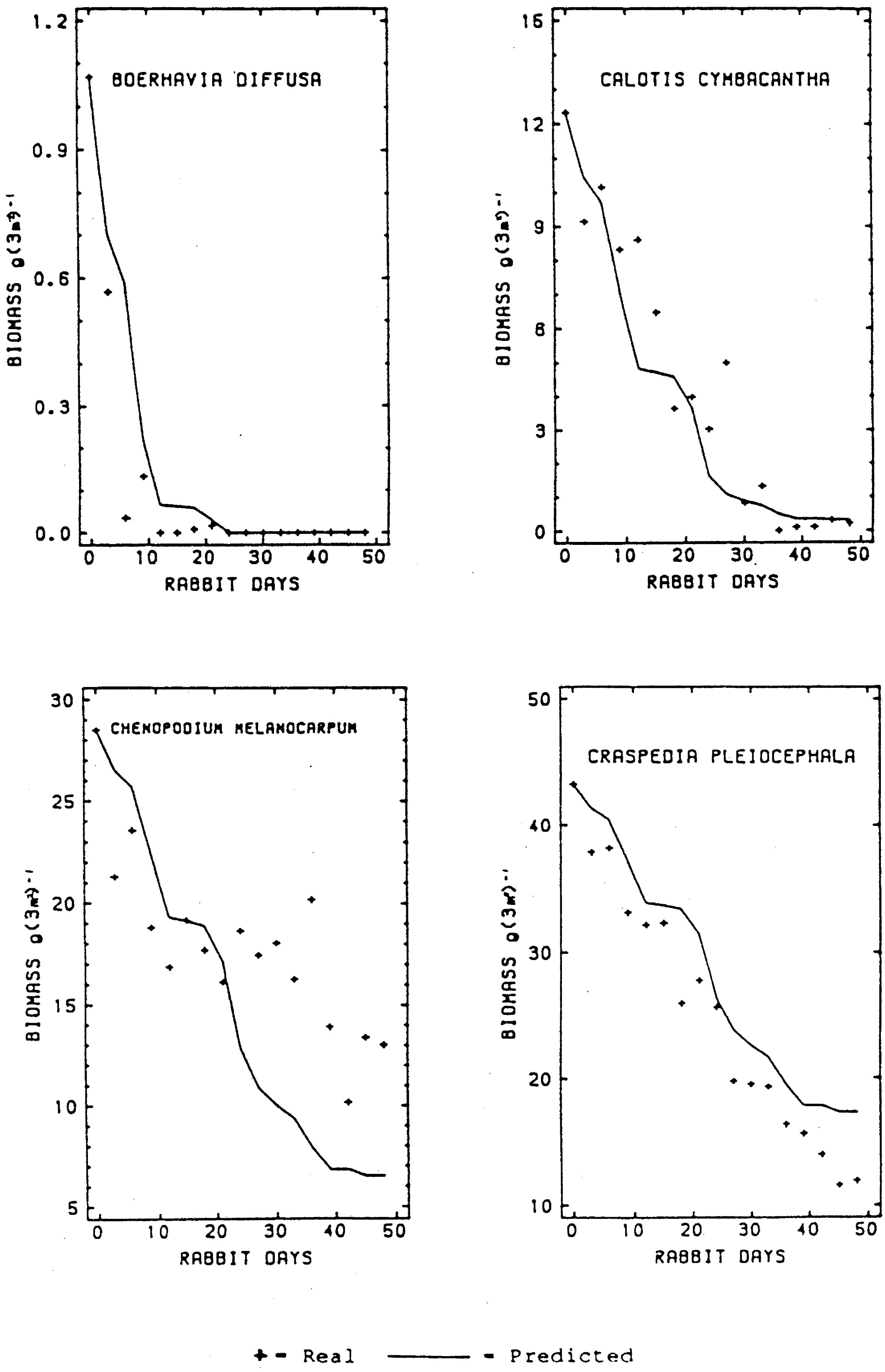


Fig.2.3.4 contd.

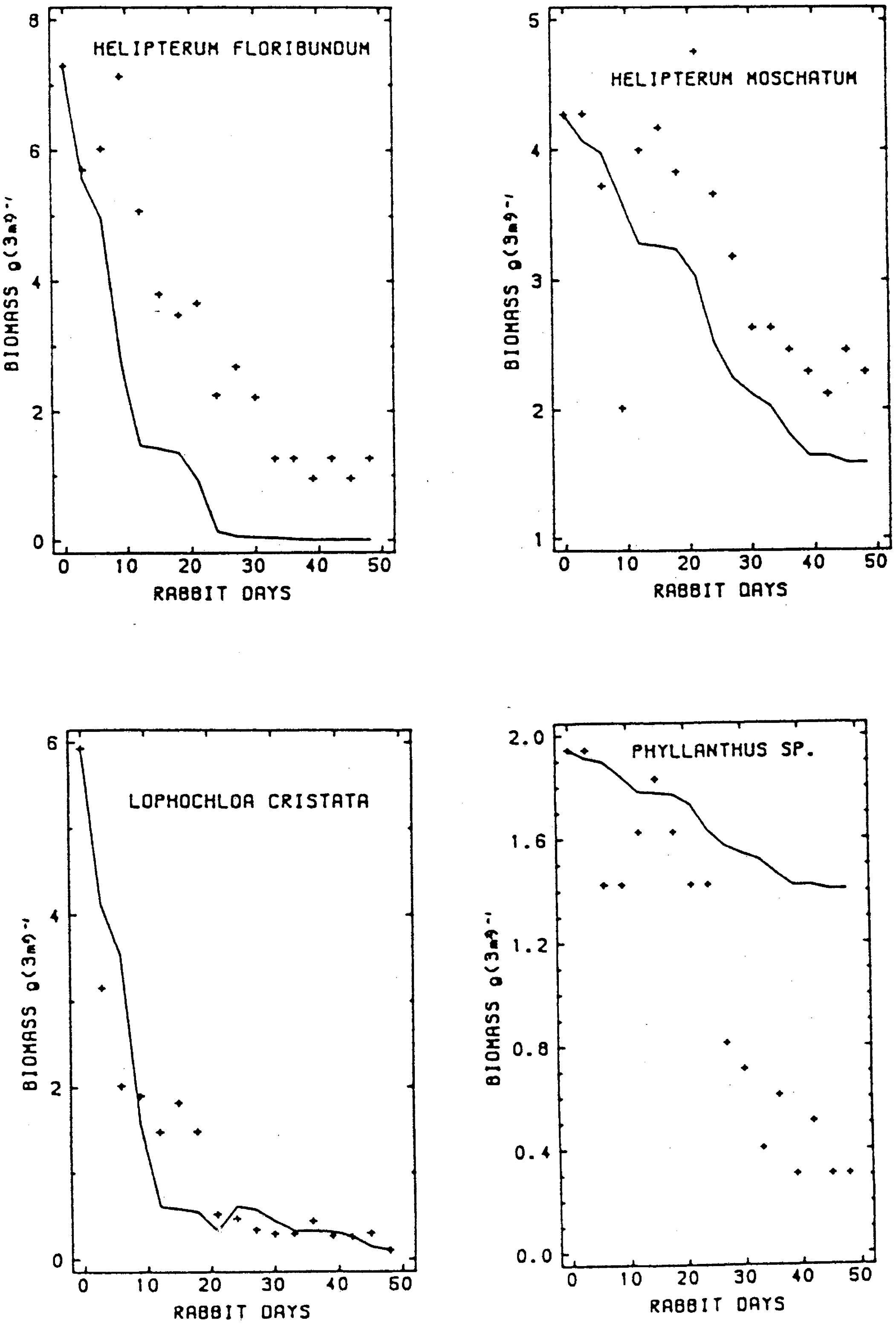


Fig.2.3.4 contd.

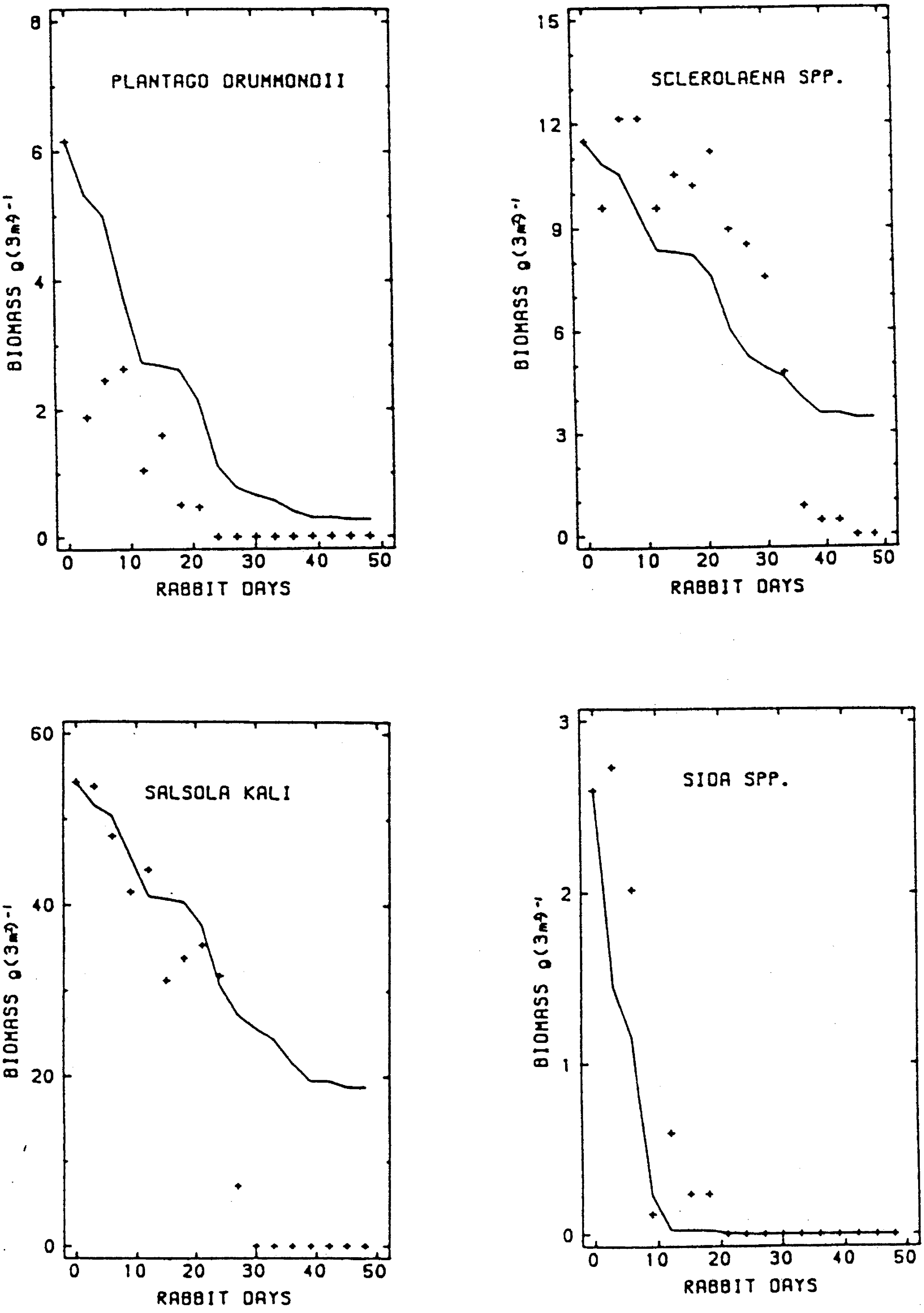


Fig.2.3.4 contd.

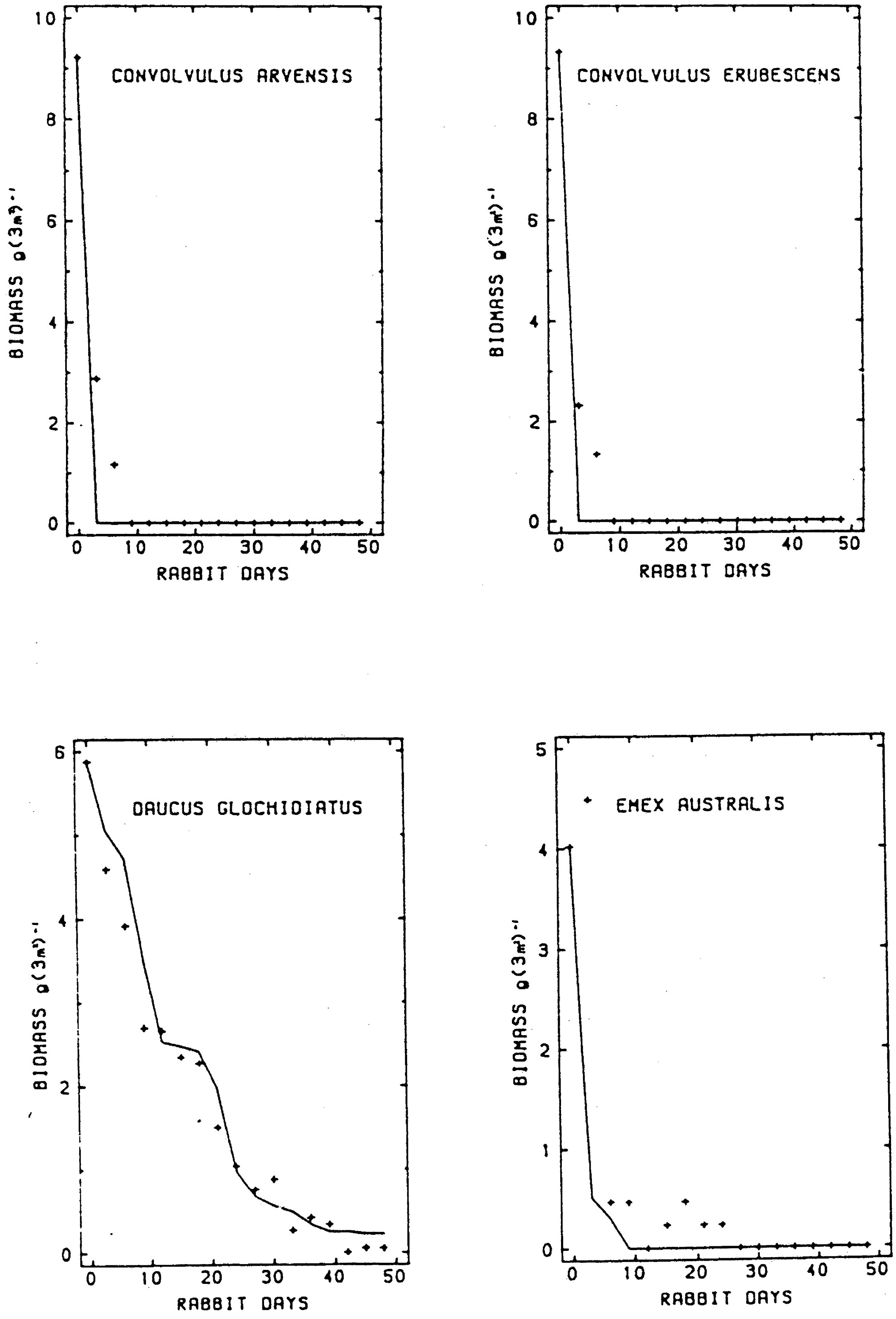


Fig.2.3.4 contd.

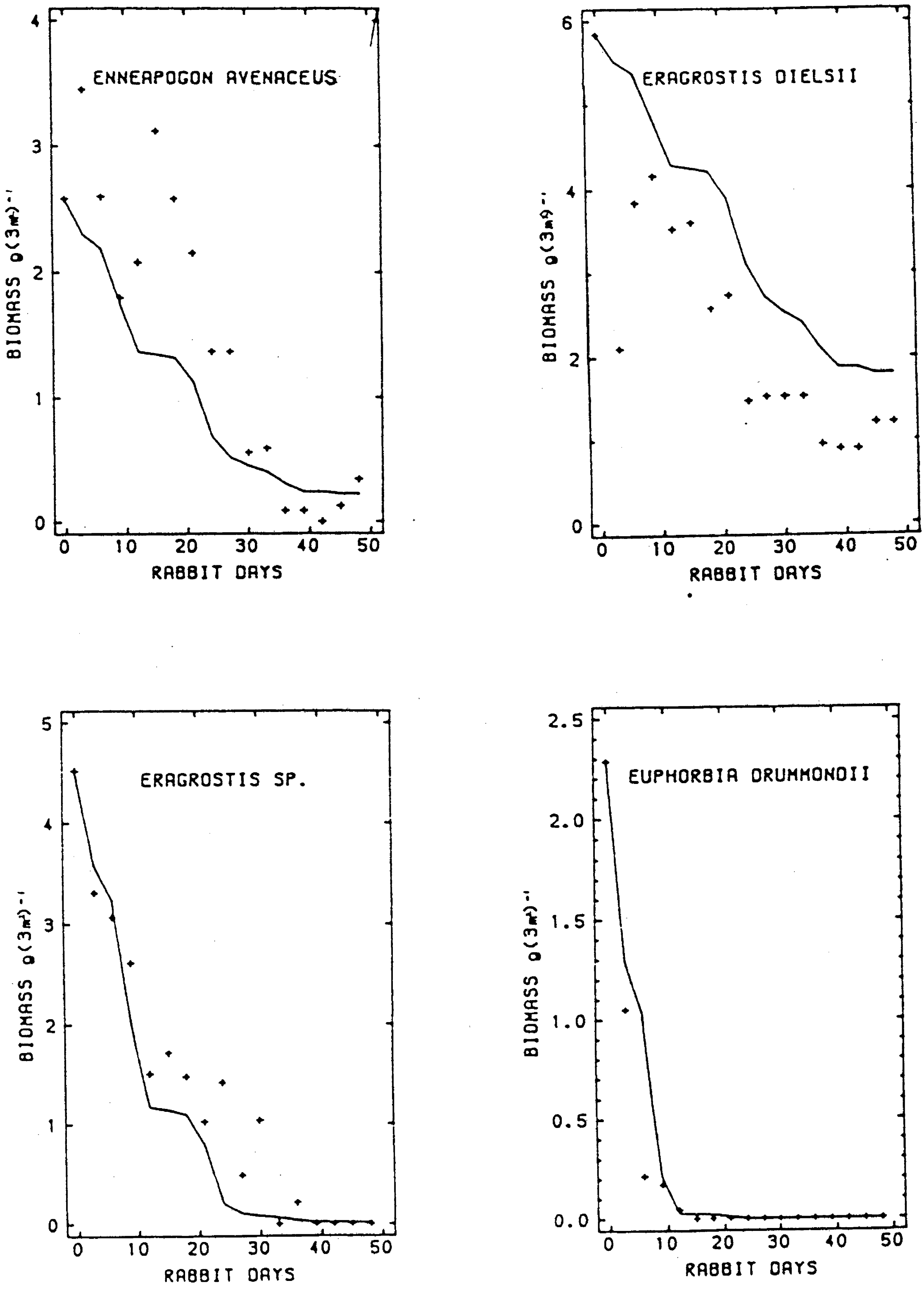
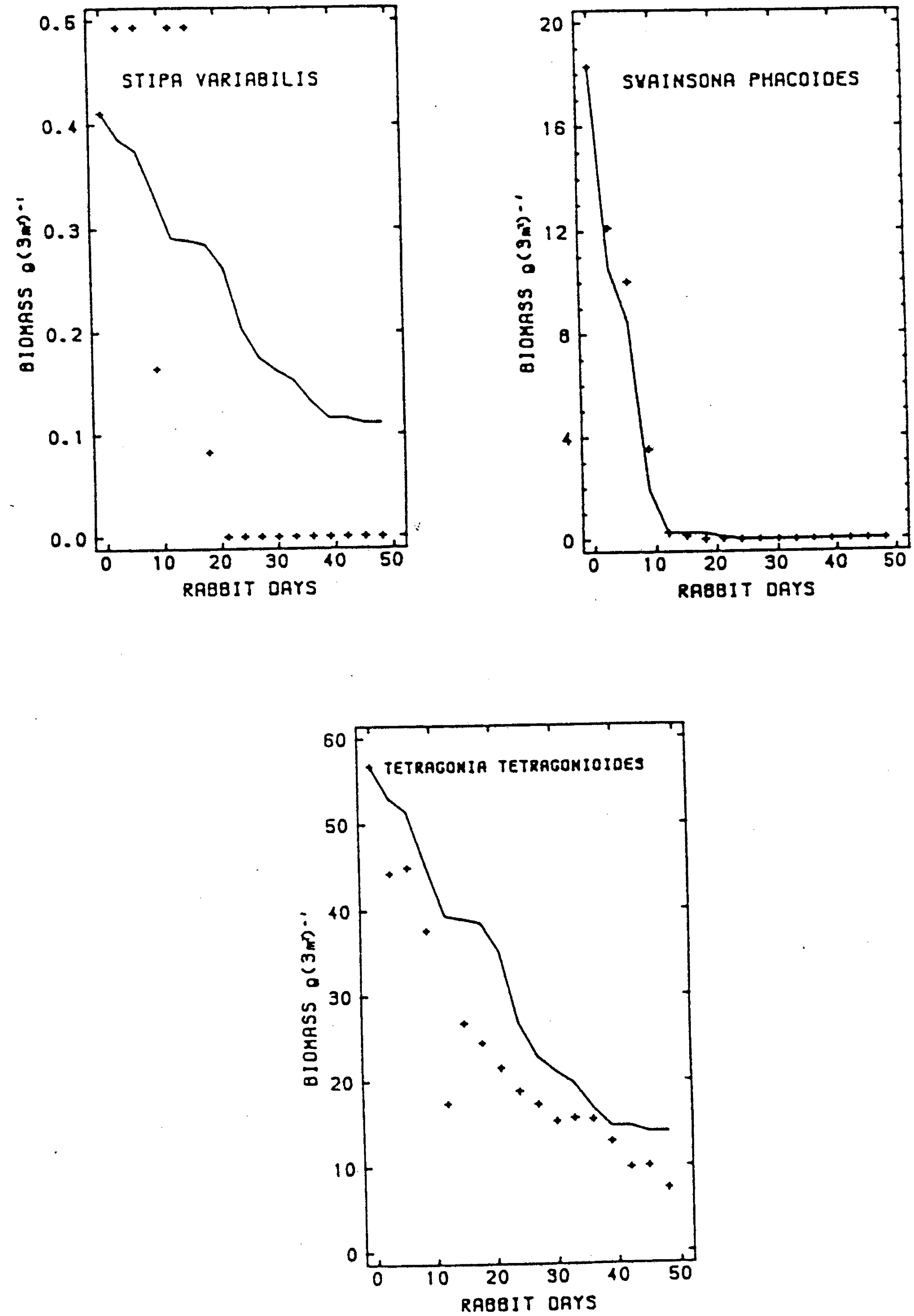


Fig.2.3.4 contd.



4. Grazing trial 3 - Dry pasture

4.1 Introduction

The previous grazing trial showed that when rabbits are grazing on a mature pasture and have no access to free water, one of the main determinants of palatability is greenness. Although there was evidence that greenness is correlated with water content, water content itself was not measured during the second trial; only at a later date. In this trial I set out to verify the selection criteria proposed in the previous two trials and to test the hypothesis that rabbits select for species with high water contents.

The trial took place between the 30th October and the 8th November 1984, just over a year since the previous trial.

4.2 Methods

4.2.1 Pens

Since very little difference could be seen between the vegetation inside and outside the pens which had been used for the previous trial, they were kept in the same position and used for this trial.

4.2.2 Rabbits

All rabbits were caught in areas of bluebush inside the park. I was limited in the amount of time that I could run this trial since one of the operators could only be at the site for two weeks. I, therefore, decided to put four rabbits in each pen instead of only three as had been used in previous trials. Accordingly, four rabbits were put into pen A on the morning of 28th September and four put into pen B on the morning of 30th September. Unfortunately, one rabbit escaped from pen B on the first night and, in pen A, one escaped and two were found dead on the morning after they were put in. Three more rabbits were added to pen A on 30th September. Three more mortalities occurred in pen A during the trial. One rabbit was found dead on 3rd November and two on 4th November. All the rabbits appeared to have been killed by either a fox or a cat despite the electric fence. The numbers of rabbits in pen A during the trial was, therefore, one for two nights, four for three nights, three for one night and one for one night. The rabbit left at the end of the trial in pen A could not be weighed because it had dug itself a burrow so could not be caught. Pen B retained its three rabbits until 5th November when a fourth rabbit, which had been held in the holding pen since the start of the trial, was added in order to increase grazing effect before time ran out. Pen B therefore, contained three rabbits for six nights and four rabbits for two nights.

4.2.3 Vegetation sampling

The same techniques were used for the ground layer vegetation as in the previous trial but with one variation. This was that each operator measured the vegetation in one pen only. This simplified data analysis. Any differences in biomass estimation accuracy would be picked up as differences in the goodness of fit of the calibration curves.

Standards were not cut for the bluebushes since adequate information could be gained from the unit estimates.

4.2.4 Water contents

Samples of each of the species found in the pens were collected pre-dawn. They were placed in plastic bags and kept in an insulated cold box until all the samples had been collected. They were then weighed, dried at 80° C for 48 hours and reweighed. I had previously determined that plant weights did not decrease further with longer drying. We were unfortunately unable to find samples of three of the species. These were *Triraphis mollis*, one of the *Sclerolaena* species and *Helipterum moschatum*.

4.3 Results

Table 2.4.1 lists the species present in each pen.

Table 2.4.2 gives the sex and weights of the rabbits at the start and end of the trial.

Appendix 1, Table 1.4 gives the conversion factors and regression statistics for both operators at the start and end of the trial.

Appendix 2, Table 2.3 gives the biomasses of each species in all quadrats on each day of the trial and the total biomasses on each day.

4.4 Discussion

4.4.1 Accuracy of biomass estimates

The conversion factors did not change greatly between the start and end of the trial (Appendix 1, Table 1.4). Accordingly, the means of the two conversion factors were used for all species except for dead *Eragrostis dielsii*, *Swainsona phacoides* and *Triraphis mollis*. For these species, although the initial and final conversion factors were similar, the initial calibration curves did not give significant regressions. The final conversion factors were, therefore, used.

Four species gave poor regression fits overall. These were *Convolvulus spp.*, *Enneapogon avenaceous*, *Swainsona phacoides* and *Triraphis mollis*. The biomass measurements for these species and for the initial measurements of dead *Eragrostis dielsii* must, therefore, be regarded with less confidence than those for the other species.

Appendix 2, Table 2.3 shows that the estimates of total biomass for each species often show an increase from one day to the next. Although this occurred in the previous trials, the number and extent of the increases is greater in this trial. Total biomass also apparently increases on some occasions. Since increases in biomass are impossible, this indicates that the biomass estimates are more inaccurate than in the previous trials. Even the species which are not mentioned above as having inaccurate conversion factors often show apparent biomass increases. The explanation for this lies in the differences in composition between this and the previous trials as well as in the inaccuracy of some of the calibration curves in this trial. The error associated with the total biomass estimate for any species is the sum of the calibration errors for each quadrat biomass divided by the square root of the number of biomass estimates. The total error is therefore large if the calibration errors are large and/or if the number of individual biomass estimates is small. Since calibration errors increase as the value diverges from the mean in either direction, both large and small values of biomass have large associated errors. This means that the total error is also increased if the biomass estimates for any one species tend to be large and/or small relative to the mean biomass used for the calibration curve. The three factors which contribute to giving inaccurate biomass totals are, therefore; a high calibration error, the occurrence of the species in a small number of quadrats and a tendency of the quadrat biomasses to diverge from the mean biomass used for the calibration curve. Similarly, the factors which will contribute to an inaccurate estimate of total biomass for all species are; few species, a high error associated with the estimates of individual species biomass and high variability in biomasses of different species. This last factor is important since the absolute error associated with an estimate of individual species biomass is greater for a high biomass species than for a low biomass species for a given fit of calibration curve.

Appendix 3 gives the initial biomasses of each species in each quadrat on the first day of each of the three grazing trials. Grazing trial 3 has fewer species than previous trials, a lower mean number of quadrats containing each and the widest range between the high and low biomass species. It also has a greater proportion of species with poor calibration regression fits. All these factors contribute to causing a lower accuracy of the biomass estimates for this trial compared to those for the previous trials. Despite this, useful information can still be gained by looking at trends over time since this has the effect of reducing the error by a factor which is directly proportional to the number of sample times.

4.4.2 Total biomass removal

The estimates of biomass of *Enneapogon avenaceous* and *Stipa variabilis* in pen A were very inaccurate as can be seen by the apparent increases in biomass of these species (Appendix 2, Table 2.3). For this reason and since the rabbits in this pen were also disturbed by predators, I decided to use only the results for pen B to calculate total offtake.

As before, the biomass in pen B can be plotted against rabbit days to gain an estimate of rate of offtake. Figures 2.4.1 shows total biomass against time together with the linear regression lines of best fit.

A significant linear regression ($r^2 = 0.82$, $P = 0.0009$) can be fitted to the total biomass data with time for pen B. An attempt at fitting a quadratic regression gives a non-significant quadratic term. The rate of offtake calculated from the gradient of the linear regression is 108 g rabbit^{-1} d^{-1}. It seems, therefore, that in this pen, the offtake was as predicted and did not decline during the trial.

4.4.3 Selectivity

For the resasons given above, I have not attempted to use the results for pen A to calculate palatability indices. Instead, I have applied the model to the pen B results using the mean offtake given above as the total daily consumption. Table 2.4.3 gives the palatabilities calculated for this pen. It also gives the water contents of each species. Fig.2.4.2 shows water content plotted against palatability index. It can be seen that the four species with the highest water content also have three of the highest palatability indices. These species all have water contents of 55% or more. These would, therefore, be the only species capable of providing an adequate water intake for the rabbits. Although it contained no measurable water, *Craspedia pleiocephala* has a high palatability index. Since some of this species was left as litter, the calculated palatability index may be higher than it should be. The amount of litter was not measured. Water content does not seem to be important in determining the palatability indices of the remaining species. The water contents of the three species for which it was not measured have been estimated from the water content of similar species in similar conditions of dryness.

The water content of the rabbits' diet in this trial can be estimated by using the offtake model with the calculated palatability indices. If the model is taken to be a reasonable representation of reality then idealized offtakes of each species can be calculated. The data for pen A in this trial were inadequate for testing the model but the previous two trials have shown that the model is a reasonable representation of rabbit behaviour. Since the water contents of most of the species in the trial were known and the species composition of the diet could be predicted from the model, the water content of the total diet could be calculated for any day. Table 2.4.4 gives the calculated water contents of the rabbits' diet for a simulated trial under pen B conditions.

The initial water content of the diet is 57% and this declines throughout the trial to 41% at the end. There are several assumptions that have been made in running this model which could change this result. The water content of *Triraphis mollis* has been taken to be 50% but might have been higher. Similarly, I assumed that the rabbits could not select out the green from the dead *Enneapogon avenaceus* but since we did not measure which of these the rabbits were eating, this may not have been the case. Finally, it is possible that the rabbits were not eating any *Craspedia pleiocephala* but were leaving it all as litter. If a combination of the above which gives the highest water contents is used, and *Triraphis mollis* is taken to have a water content of 55%, then offtake water content starts at 60% and ends at 49%. Under these conditions, the water contents are still close to or below the minimum necessary water content of 55%

calculated by Cooke (1982). It is possible that the rabbits, by selecting individual plants with a particularly high water content, in reality obtained more water than has been calculated but the opportunities for this would be limited. It seems, therefore, that the rabbits were living on a diet which provided their required water intake at the start of the trial but did not provide it towards the end.

Despite the lack of succulent plants, rabbits did not eat out all the high water content species before starting on the others. As in the previous trials, they ate a mixed diet from the start although there were distinct preferences.

All the rabbits lost weight during the trial. This implies that their diet was not adequate for them to maintain condition. Social stress cannot be excluded as the indirect cause of the weight losses but since the rabbits were eating normal amounts of food this is unlikely. There were still some green plants left at the end of the trial but even these were not able to sustain the rabbits at their original weights. Not all green plants, on their own, are therefore able to provide an adequate diet for rabbits.

4.4.4 Bluebush Removal

Figure 2.4.3 shows the number of units estimated for each bluebush on each day of the trial. Although there is a large variation associated with the estimates, they show that only small amounts of bluebush were removed and, even then, most of this was left as litter.

4.5 Conclusions

Under conditions of low species diversity and low pasture water content, rabbits eat approximately 100 g rabbit^{-1} d^{-1}. This result comes from only one of the trials' two pens since the other one was disturbed by predators.

Under the conditions of low pasture water content rabbits select for the highest water content species. This causes the water content of their intake to decline with time as these species are removed. Despite this selectivity, water content is not the only criterion for palatability, particularly amongst plants with a water content near or below 50%.

Even with selective feeding, the rabbits lost weight with time indicating that rabbits might decline in numbers before large changes in pasture species composition occurred.

Rabbits graze only very small quantities of bluebush under these conditions.

Table 2.4.1 Species recorded in grazing trial 3.

Species	Pen A	Pen B
Asphodelus fistulosa	0	1
Convolvulus spp.	1	0
Craspedia pleiocephala	1	1
Daucus glochidiatus	1	1
Enneapogon avenaceus	1	1
Eragrostis dielsii	1	1
Goodenia cycloptera	1	1
Helipterum moschatum	1	1
Sclerolaena sp.1	1	1
Sclerolaena sp.2	1	1
Sclerolaena sp.3	1	1
Sida spp.	1	1
Stipa variabilis	1	1
Swainsona phacoides	1	1
Triraphis mollis	1	1

1 = recorded   0 = not recorded

Table 2.4.2 Weights of rabbits used in grazing trial 3 (g).

Pen A

Sex	Weight 29/10/84	Weight 30/10/84
F	1320	
F		1870
M		1720
F		2320

Pen B

Sex	Catch weight 30/10/84	Weight on being put in pen 5/11/84	Weight at end of trial 7/11/84
M	1720		1420
M	1720		1420
M	1570		1320
M	1270	1270	1070
Mean weight	1570		1310

Weights to nearest 10 g.

Table 2.4.3 Palatability indices and attributes of each species.

Species	P.I.	Water content (%)	Phenology 30/10/84	Phenology 4/11/84
Asp	33.7	79±2	G/S	G,S/S
Swa	25.2	67±4	G/S	G/F,S
Sid	10.7	57±1	G/S	G/S
Cra	7.7	0	D/F	D/F
Dau	4.1	57±5	G,S/S	S/S
Era(g)	4.0	24±6	G/S	G/S
Tri	3.2	50*	G/S	G/S
Hel	3.1	0*	D/F	D/F
Scl2	2.8	51±4	G/S	G,S/S
Era(d)	2.5	51±3	D/S	D/S
Enn	1.6	33±5	G,S/S	G,D/S
Scl3	.7	52*	G/S	G/S
Scl1	.6	53±4	G/S	G/S

* = assumed water content (see text).

Table 2.4.4 Water content (%) of hypothetical intakes for pen B.

Rabbit days into trial	Conditions 1	2	3	4	5
3	51	52	53	55	58
6	48	49	51	53	54
12	42	43	46	46	52
15	40	42	44	44	50
18	39	41	44	42	49
22	39	41	44	41	48
26	39	41	45	40	48

1 = Enn water content = 33%, Cra included in calculation, Tri water content = 50%
2 = Enn water content = 33%, Cra included in calculation, Tri water content = 55%
3 = Enn water content = 44%, Cra included in calculation, Tri water content = 50%
4 = Enn water content = 33%, Cra excluded from calculation, Tri water content = 50%
5 = Enn water content = 44%, Cra excluded from calculation, Tri water content = 55%

Fig.2.4.1 Decline in total biomass with rabbit days in pen B.

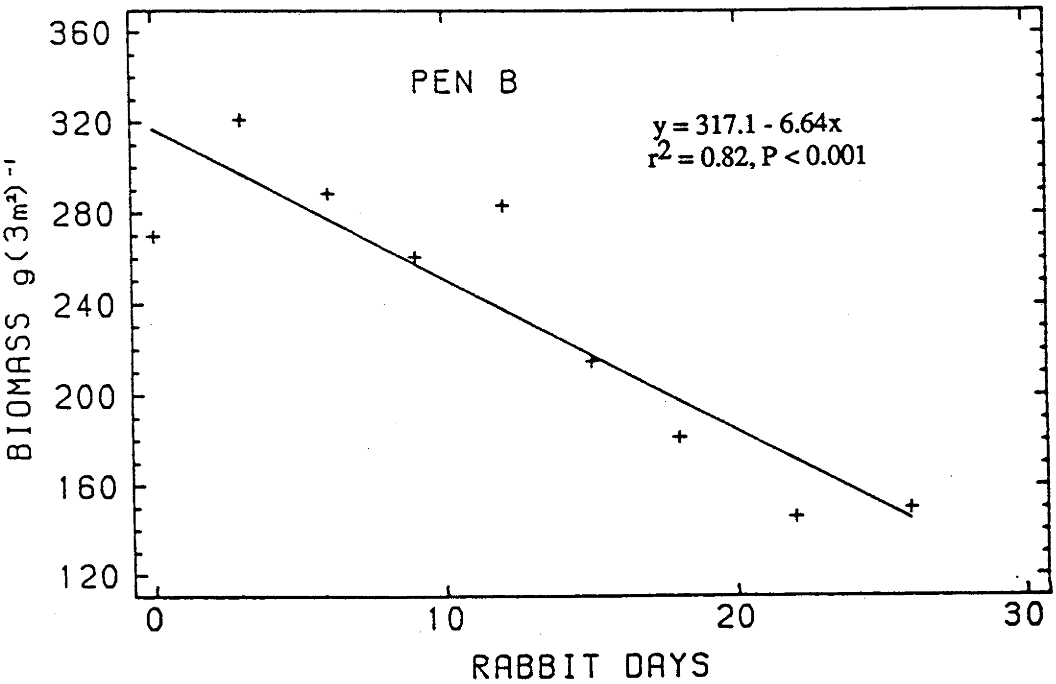


Fig.2.4.2 Relationship between water content and palatability index.

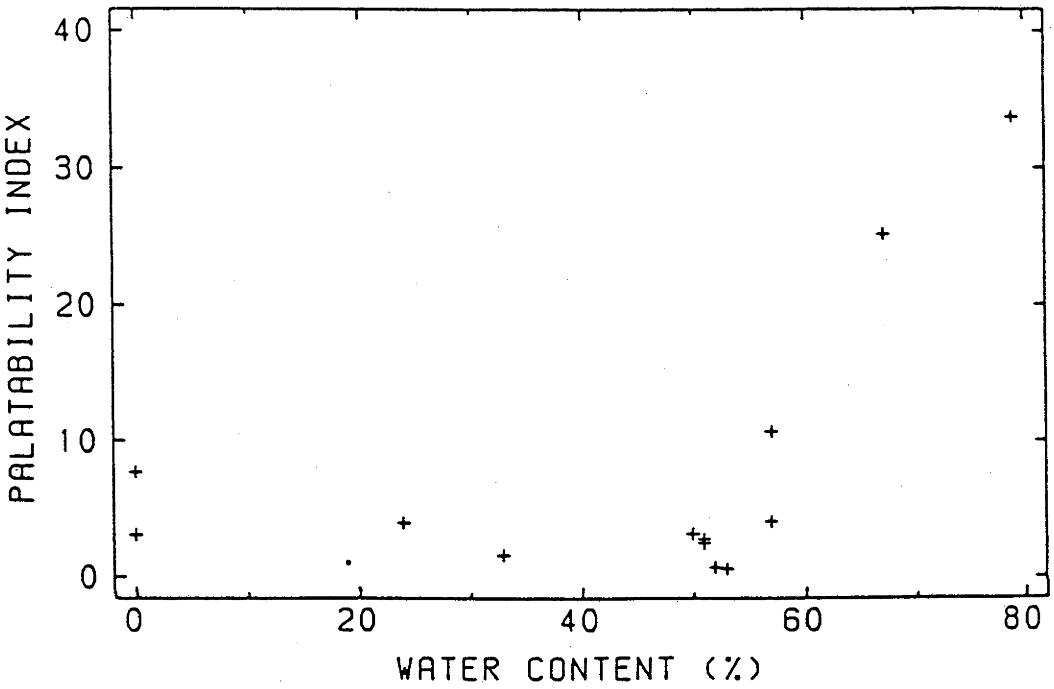
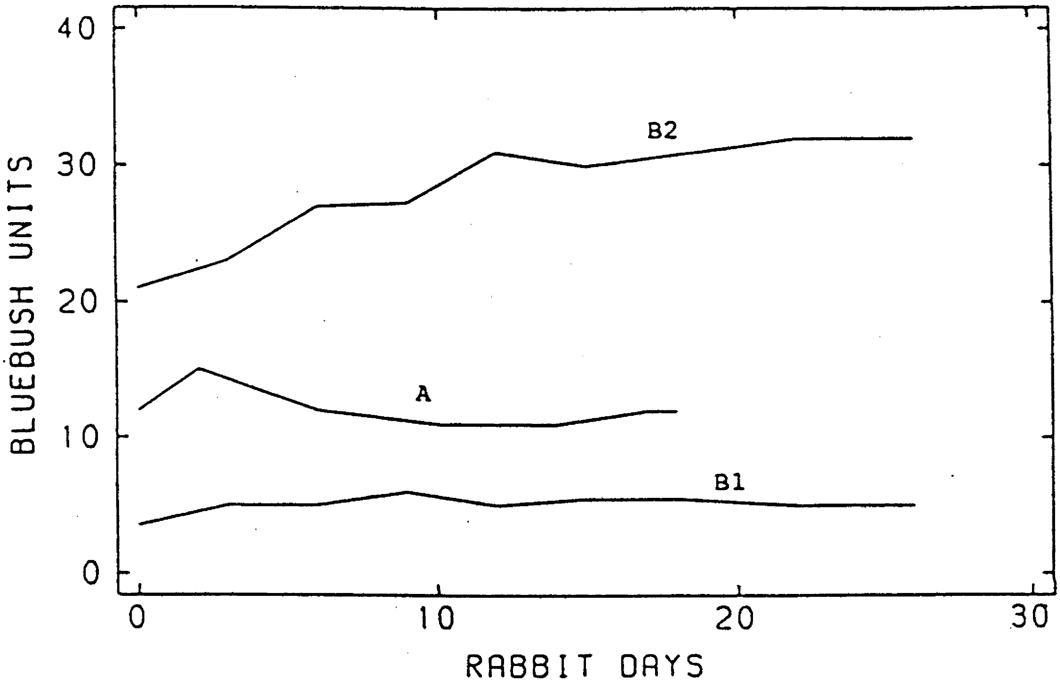


Fig.2.4.3 Biomass units of the bluebushes in both pens against rabbit days.



A = Bluebush in pen A B1,B2 = Bluebushes in pen B

5. Grazing trial 4 - Dry, unpalatable pasture

5.1 Introduction

In the third trial, the rabbits did not decrease their intake as pasture quality declined. This result differs from that of the second grazing trial where offtake declined with time. In this trial I set out to test whether rabbits would eat anything at all on a pasture which was very dry, had a low species diversity and was made up of species which had been shown in previous trials to be of low palatability. At the time of the trial, rabbits were in very low numbers (see Part 3, section 1). The rabbits which were used for the trial must have had access to a food supply which was of higher quality than the pasture in the pens otherwise they would not have been alive. It was, therefore, a valid hypothesis that the rabbits would not have been able to eat anything in the pens. If the rabbits did eat the pasture then this trial would be another test of the hypothesis that offtake declines with pasture quality. In the third trial, litter was observed to accumulate and since this could have contributed to the lack of offtake decline, the biomass of litter, as well as of standing material, was measured in this trial.

The trial took place between the 19th March and the 31st March 1985, five months after the previous trial and at the end of a hot, dry summer (see Fig.2.2.1). Unfortunately, there was a fall of rain on the 23rd March which was sufficient to stimulate germination during the course of the trial. This meant that I was not able to use this trial for its intended purpose. I was, however, able to measure the effect of a high density of rabbits on survival and growth of new germinants.

5.2 Methods

5.2.1 Pens

In the five months since the previous trial the vegetation had grown sufficiently that the species composition and structure of the vegetation inside and outside the pens had become similar enough that no differences could be seen. The pens were, therefore, left in the same positions.

5.2.2 Rabbits

All the rabbits were caught within the park in areas of bluebush.

The three rabbits which were originally put into pen A all escaped on the first night. Two of these rabbits were small and may, therefore, have been able to squeeze through the mesh of the pen. Three new rabbits were added later on but one escaped after two days and one was found dead the day after being put in. There was no evidence that predators were involved. The escapes and short time that the trial was run in this pen led me to abandon it.

Three rabbits were put into pen B on the 18th March. One small rabbit escaped through the mesh as soon as it was put in and a new rabbit was added on the 20th March. In pen B there were thus two rabbits for two nights and three rabbits for eleven nights.

From the 20th March onwards the rabbits in pen B were living in burrows which they had dug. The numbers of rabbits in the pen could not be checked from then on since catching the rabbits each day would have been too much of a disturbance. By smoothing the soil at the entrance to each burrow, I was able to show that there was at least one rabbit in the pen. Difficulties of catching the rabbits prevented their being counted and weighed at the end of the trial.

5.2.3 Vegetation sampling

The same techniques were used as in the previous trial except that eighteen quadrats were used instead of twelve in an attempt to increase the accuracy of the biomass measurements and the amount of litter of each species was measured in each quadrat every day.

Since *Sclerolaena* sp.2 was rare both inside and outside the pens, we could not find enough plants of this species to construct a separate calibration curve. I, therefore, pooled the standards for both sclerolaena species but kept the dry and green standards separate. There are, therefore, two calibration curves for both these species; one for green plants and one for dry plants.

Enneapogon avenaceus resprouted after the rain. I initially intended to measure the green and dry parts separately but this proved to be too difficult as they were too closely intermingled.

The germinants were sampled using twelve 100 cm^2 square quadrats placed in a regular pattern inside the pen. Twelve similar quadrats were randomly positioned outside the pens. The number of germinants inside each quadrat was counted each day. Any sign of rabbit damage was noted. At the end of the trial the germinants were harvested above ground, dried at 80 °C for 24 hours and weighed.

5.3 Results

Table 2.5.1 lists the species present in pen B.

Table 2.5.2 gives the sex and weights of the rabbits in pen B at the start of the trial. The rabbit which was added later in the trial was not weighed.

Figure 2.5.1 shows germinant numbers over time inside and outside the pen.

Appendix 1, Table 1.5 gives the conversion factors and regression statistics for the pen B biomass measurements.

Appendix 2, Table 2.4 gives the biomasses of each species in all quadrats on each day and the total biomass in all quadrats on each day. The biomasses include litter for each species.

5.4 Discussion

5.4.1 Accuracy of biomass estimates

The results of the calibration curves are given in Appendix 1, Table 1.5. Four of the seven species gave significant regressions through the origin for both the initial and final calibration curves. One of the other species gave a significant regression through the origin for one calibration curve but not for the other. Only one calibration curve each was constructed for the other two species. Both of these were non-significant. The biomass estimates of both these species, *Craspedia pleiocephala* and *Daucus glochidiatus*, are likely to be more inaccurate than those of the others. These species contribute little to the total biomass in the pen (see Appendix 2, Table 2.4) hence their inaccuracy will have little effect on the accuracy of the total biomass measurements. There were no significant differences between the initial and final conversion factors for any species so the means of the two were used for the conversions.

Some plant species in this trial, as in the previous one, were seldom encountered despite the larger number of quadrats. *Craspedia pleiocephala* and *Sclerolaena* sp.2 occurred in only three quadrats (Appendix 3, Table 3.4). Although the other species occurred in at least five quadrats each, the biomasses vary widely between quadrats for *Sclerolaena* sp.1 and *Stipa variabilis*. These factors tend to lead to wide confidence limits on the biomass estimates for these species (see Part 2, section 4.4.1).

As discussed in Part 2, section 4.4.1, the accuracy of the total biomass measurement decreases if there are few species and if there is a large amount of variability between species biomasses. In this trial, the number of species was low and *Enneapogon avenaceus* dominated the pasture, making up about 70% of the biomass (see Appendix 2, Table 2.4). As in the previous trial, this has tended to reduce the accuracy of the measurements although the larger number of quadrats will have compensated for this to some extent.

5.4.2 Germinant removal and damage

Figure 2.5.1 shows the number of germinants in pen B and in the control quadrats at different times. In the control quadrats, the number of seedlings increased until about eight days after they were first counted. From then on they declined slightly in number. In pen B the number of germinants rose initially but then fell. Although there was another increase subsequently, the final number of germinants was lower than that in the control quadrats despite the initial numbers being higher. The reduction in germinant numbers was not due to their death since no dead germinants were recorded. The mean weight of germinants at the end of the trial is given in Table 2.5.3. It was significantly higher ($P = 0.0001$) in the control quadrats than in pen B. Towards the end of the trial, damage to germinants which were still present was frequently recorded in the pen. The differences in germinant weight and number were, therefore, likely to be due to rabbit disturbance and/or grazing. There was no significant difference between the amounts of litter in pen B and in control quadrats. The differences between the control and pen quadrats could not, therefore, have been due to any differences in the mulching effect of litter.

After eight days of growth, there was a difference of 64% in germinant biomass between the pen and the control area. If this difference is assumed to be due totally to the rabbits and not to unmeasured site differences, then the potential effect of rabbits at field densities can be caluculatd. In the pen, the grazing pressure was between 204 and 625 rabbits ha^{-1}. If the 'worst case' is assumed, and it is taken that only one rabbit was responsible for the germinant removal, then a 'worst case' offtake for rabbits at high field densities can be calculated. At a density of 25 rabbits ha^{-1} offtake of germinant biomass under conditions similar to those in the trial, would be 7.8%. Since this density of rabbits is unlikely to occur when pastures are dry, removel of germinant biomass by rabbits is likely to be less than this amount. Close to occupied warrens, where grazing pressure is likely to be high, (see Part 3, section 1.2) offtake of germinants is likely to be higher than elsewhere and may be significant in some cases.

The results of this trial show that rabbits can graze extremely small seedlings. The effect of such grazing by rabbits in the field is likely to be insignificant except, possibly, close to occupied warrens.

5.4.3 Total biomass removal

A regression of the decline in non-germinant biomass with time in pen B (Fig.2.5.2) has a significant, positive, quadratic term ($P = 0.008$) which implies that offtake declined with time. It is impossible to calculate offtake per rabbit since I was uncertain about the number of rabbits in the pen throughout most of the trial.

5.4.4 Selectivity

Despite the rain and the presence of germinants, palatability indices could still be calculated for the ground layer species. Selection would not necessarily be expected to be on the basis of water content since the rabbits would be deriving water from the germinants. If it is assumed that the germinants contained about 90% water (Wellard, pers. com.) then the maximum water intake derived from them would have been 2.4 litres. Since each rabbit would require roughly 100-120 ml d^{-1} of water, 2.4 litres would have been sufficient for about eight days if there were three rabbits in the pen and longer if there were fewer rabbits. Water content may still have been an important factor in diet selection early on since most of the germinant biomass became available towards the end of the trial.

Palatability indices for each species were calculated and water content measured as in the previous trial (Table 2.5.4). The green parts of *Sclerolaena* sp.2 have the highest palatability index and the highest water content but there is little relationship between the palatability indices and water contents of the remaining species (Fig.2.5.3). As in the previous trial, *Craspedia pleiocephala* had a very low water content yet had a high palatability index. This trial confirmed that offtake of this species was being consumed and not left as litter. The erect habit of *Craspedia pleiocephala* may have accounted for its high intake by rabbits despite its lower water content. This species made up only a small proportion of the total intake and would have had little effect on the water content of the rabbits' diet.

5.4.5 Bluebush and acacia removal

The bluebush in pen B remained untouched throughout the trial.

An *Acacia victoriae* seedling completely disappeared on the first night. The water contents of the three acacia seedlings which we harvested varied from 29% to 45%. A relatively high water content of the seedling which was removed may have been sufficient incentive for its removal since only the green parts of the sclerolaenas and the bluebush leaves would have had a higher water content.

5.5 Conclusions

The rabbits in this trial reduced the number of germinants after a rain event and reduced the total biomass of the remaining germinants. The grazing pressures in this trial were, however, much higher than they would be in the field under similar conditions. The rates at which germinants were affected were too low for rabbits at field densities to have a significant effect on germinant numbers except, possibly, close to occupied warrens. It is, therefore, unlikely that rabbits could have a significant effect on the biomass of a new growth flush.

On the dry pasture present at the start of this trial, the rabbits selected strongly for the two species with the highest water content (green *Sclerolaena* spp. and *Acacia victoriae*).

The results of this trial support the hypothesis that rabbits will select strongly for any species which remains green when most of the pasture is dry. The exception to this is the bluebushes which remain green but are avoided presumably because of their high salt contents. The effect of such selective grazing by rabbits in the field is hard to predict since, by the time the pasture is in a condition similar to the one in this trial, rabbit numbers are already low and offtake may be insufficient to have much effect on the species which remain green.

Table 2.5.1 Species recorded in grazing trial 4, pen B.

Species
Craspedia pleiocephala
Daucus glochidiatus
Eragrostis dielsii
Enneapogon avenaceus
Sclerolaena sp.1 (soft)(green)
Sclerolaena sp.1 (dry)
Sclerolaena sp.2 (dry)(prickly)
Stipa variabilis

Acacia victoriae recorded in pen
but not inside sampling quadrats.

Table 2.5.2 Weights of rabbits in pen B, grazing trial 4 (g).

Sex	Weight 15/3/85
F	1620
F	1420
F	1220 (escaped)

Weights to nearest 10 g.

Table 2.5.3 Dry weights of all germinants in each quadrat inside pens and in control area at end of trial.

Quadrat	Germinant weight (g)	
	Pen B	Control area
1	0.04	0.08
2	0.02	0.11
3	0.02	0.09
4	0.01	0.10
5	0.02	0.04
6	0.03	0.05
7	0.06	0.14
8	0.03	0.06
9	0.03	0.08
10	0.003	0.04
11	0.06	0.05
12	0.01	0.09
Mean	0.028	0.077

Table 2.5.4 Palatability indices, water contents and phenology of each species.

Species	P.I.	Phenology 19/3/85	 31/3/85	Water content (%)
Scl1(G)	51.4	G	G	57±9
Cra	45.7	D	D	0
Dau	13.7	D	D	-
Scl1(D)	9.6	D	D	28±6
Scl2(D)	5.1	D	D	28±6
Sti	2.6	D	D	17±3
Enn	1.6	D	D,G	26±3
Era	1.0	D	D	15±7
Aca		G	G	36±14

P.I. = palatability index.

Fig.2.5.1 Number of germinants in control and pen B quadrats over time.

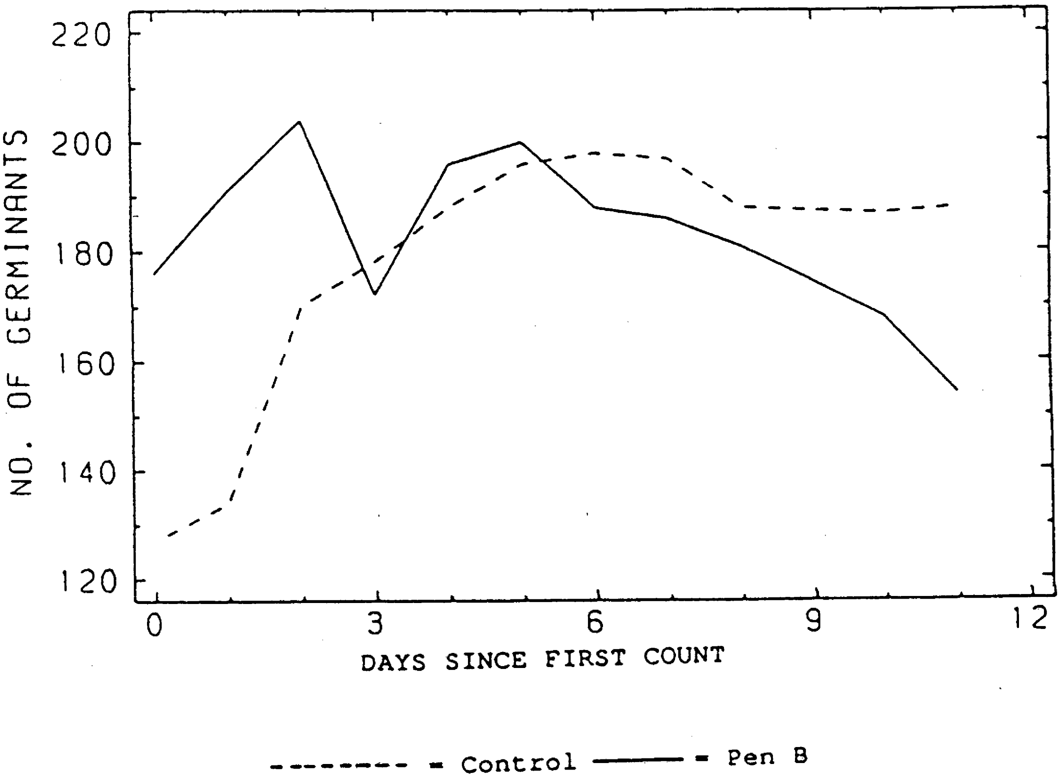


Fig.2.5.2 Decline in total biomass with rabbit days.

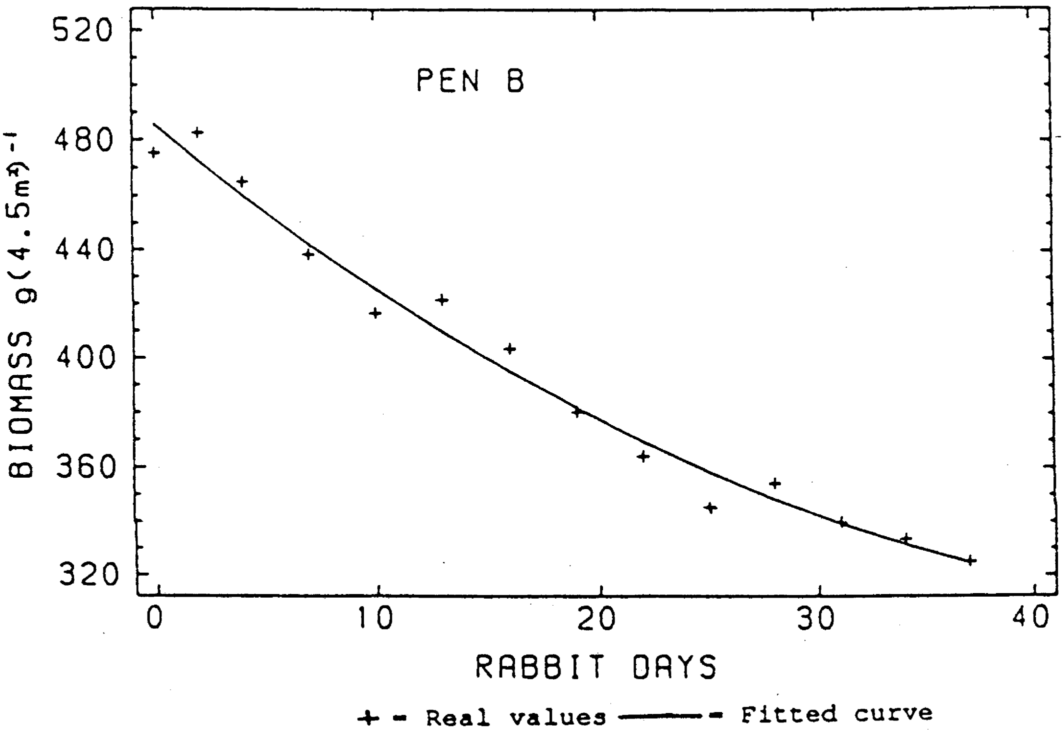
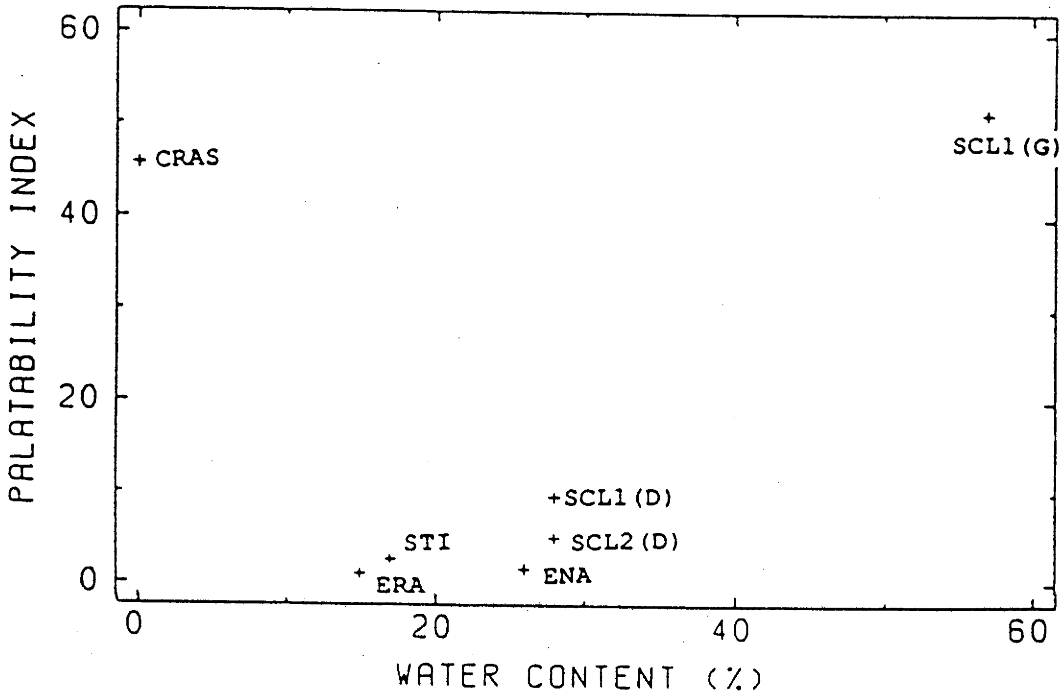


Fig.2.5.3 Relationship between palatability index and water content.



CRAS - Craspedia pleiocephala STI - Stipa variabilis
ERA - Eragrostis dielsii ENA - Enneapogon avenaceous
SCL1(D) - Sclerolaena sp.1 (dead) SCL2(D) - Sclerolaena sp.2 (dead)
SCL1(G) - Sclerolaena sp.1 (green)

6. General discussion of results of grazing trials.

6.1 Total offtake

The aim of the grazing trials was to draw conclusions about rabbit offtake under different conditions in the field and about the potential effect that their patterns of selectivity will have on pasture species composition.

Experimental data have shown that offtake is often a function of pasture biomass with offtake increasing with biomass until an upper limit is reached (e.g. Short 1985). This is the functional response. A plot of smoothed offtake against smoothed pasture biomass for the three trials for which suitable information was obtained (Fig.2.6.1) shows that this relationship did not hold for the rabbits in these trials. I used the best fit relationships derived in the previous chapters to smooth the biomass changes over time and to calculate offtake. If a single functional response curve could represent the field situation in the case of rabbits in the arid zone then the offtake curves for each grazing trial would each fall on part of the same curve. This is not the case.

The likely reason for the lack of a simple functional response curve for rabbits in this system is that the rabbits were having to select a diet which fulfilled their water and/or energy requirements. This means that not all biomass was available as food. Cooke(1979) classed plants as available if they contained more than 55% water and less than 40% fibre. He then calculated the biomass of available vegetation as the total biomass of all such species. This method does not necessarily include all edible biomass since it is the water and fibre content of the total diet which must fall within these limits. If, therefore, part of the diet is very high in water and low in fibre then some high fibre and/or low water content species can also be eaten. This was confirmed in the third trial where the rabbits ate very dry species as well as succulent ones when they had the option of only eating the succulent ones.

The offtake curves for the three grazing trials can be interpreted in the light of rabbits' dietary requirements. In the first trial, offtake was near the average of 100 g rabbit^{-1} d^{-1} throughout the trial despite the low biomasses in the pens at the end of the trial. This can be explained by the high level of hydration of the pasture in the first trial i.e. the rabbits were experiencing no nutritional limits to intake. In the second trial, total biomass declined no further than it did in the first trial but offtake declined to zero. This can be explained by the decreasing water content of the pasture. In the third trial, offtake again remained at around 100 g rabbit^{-1}d^{-1} throughout the trial. This can be explained by the maximum water contents. The initial water contents are adequate (60%) and the final ones were just below maintenance(49%). This decrease in water content may not have been sufficient to cause a decrease in intake. As discussed in Part 2, section 3, the higher than expected initial offtakes in the second grazing trial may indicate that, as pasture quality initially declines, offtake increases. As quality declines further, offtake then starts to decline as well and eventually falls to zero. If this model of the relationship between offtake and pasture quality is the correct one then, from the results of grazing trial 2, rabbit offtake could be as high as 170 g rabbit^{-1} d^{-1} from some mature pastures. The work presented in this thesis is not sufficient to distinguish between two models of offtake. One predicts a lower than maximum offtake from very high quality pasture and the other predicts maximum offtake from any pasture whose quality is above a certain level.

The possible reasons for the reduction in offtake with decreasing pasture quality have not been investigated for rabbits. It is common for ruminants to increase the passage time of food through the gut as diet quality declines (McIntosh 1966). This allows more efficient digestion to take place. If the gut does not expand, and is normally filled, then intake must also decline. Since the rabbits in this trial would not, at any time, have had problems of finding or being able to remove vegetation, it was not availability which limited intake. The same mechanism as for ruminants may, therefore, have been operating.

As a test of the hypothesis that offtake is a function of amount of feed containing suitable water and fibre contents, I determined the relationship between green biomass and total offtake in each trial (Fig.2.6.2). The curves for the first grazing trial remained the same as in Fig.2.6.1 except that the biomass of *Dactyloctenium radulans* is not included since all the species except this one were green. I calculated the green biomass in the other grazing trials using the information on growth state for each species in each grazing trial. I included only those species which remained green throughout each trial. I then smoothed the green biomass decline curves by fitting linear or quadratic regressions to the declines with rabbit days. I plotted these against the total offtake measures used for the total biomass offtake curves (Fig.2.6.1).

In grazing trial 2, offtake fell below 100 g rabbit^{-1} d^{-1} when green biomass was at 50 and 100 kg ha^{-1} in pens A and B, respectively. These green biomass levels were reached in both these pens at the same time; 24 rabbit days (see Appendix 2, Table 2.2). At this time *Sclerolaena* spp. made up the majority of the green biomass in both pens. The higher green biomass in pen B was due to a higher biomass of *Sclerolaena* spp. Since these species are woody and can have high fibre contents (Cooke 1974), they may have exceeded the fibre limits of the rabbits' diet and this fall in dietary quality may have induced the fall in offtake.

In grazing trials 1 and 3 offtake remained at about 100 g rabbit^{-1} d^{-1}. In these trials, green biomass fell to 38 and 105 kg ha^{-1} in grazing trials 1 and 3 respectively. In both these trials, species other than *Sclerolaena* spp. remained at the end of the trials.

The low level of green biomass in pen A at the end of grazing trial 1 suggests that rabbits will eat about 100 g rabbit^{-1} d^{-1} even if the quantities of green biomass are extremely low, unless *Sclerolaena* spp. make up a large proportion of the green biomass.

It seems, therefore, that a functional response curve relating offtake to pasture biomass, regardless of its quality, is not appropriate for the calculation of offtake of rabbits. When there is any green biomass available, apart from *Sclerolaena* spp., offtake will be at, or above, about 100 g rabbit^{-1} d^{-1} and may be as high as 170 g rabbit^{-1} d^{-1}. If green biomass consists solely of *Sclerolaena* spp. then offtake will be below maximum. At Kinchega, these species are unique in that they remain green longer than other species and also tend to be fibrous. Presumably rabbits, at other sites, will respond similarly to other species possessing similar properties. On such a diet, rabbits will lose condition. If there is no green biomass then rabbits are likely to eat little and lose condition. This remains to be tested since I was unable to do so in this study. Rabbit numbers are likely to fall rapidly at such times. Part 3, section 1.1 gives an example of such a rapid fall in rabbit numbers. This occurred at the start of 1985 when conditions were extremely dry (see Fig.3.1.2).

If a high proportion of green biomass was made up of toxic species, such as *Babbagia acroptera* and possibly *Phyllanthus* sp., then offtake would presumably also be less than maximum. Thus, in assessing rabbit offtake in the field, toxic species should not be included in an assessment of green biomass.

6.2 Species composition

The selection model $c_i/C = p_i{*}b_i/\Sigma p_i{*}b_i$ was an adequate description of the rabbits' behaviour in all the grazing trials. Since offtake of individual plant species is not purely a function of their proportion in the pasture, species composition will be affected in the short term by rabbit grazing. The degree of change will be dependent on grazing pressure and on the extent of differences in palatability between plant species. Table 2.6.1 gives the palatability indices of each species in each of the grazing trials. Palatability differed markedly between species at all times although in grazing trial 4, when most of the pasture was dry, there were no high palatability species. Changes in the palatability of individual species between grazing trials might be due to changes in the species such as drying out or increased fibrousness. Such changes to the *Sclerolaena* spp., which have been set at a palatability index of 1.0, would also cause inconsistencies between measures of palatability index of individual species in different trials. In general, however, the most and least palatable species remain so at all times.

Among green species, palatability is increased by an erect habit and possibly an ability to fix nitrogen. It is decreased by spineyness, possibly fibrousness and toxicity. Green species are preferred over dry species.

Rabbit grazing pressure decreases rapidly with distance from rabbit warrens (Part 3, section 1.2). Short term changes will, therefore, be greatest close to large, active warrens and at times when rabbit numbers are high. The likely extent of short term changes in species composition will be discussed in Part 4.

Short term changes in species composition will result in long term changes, if the regenerative capacity of preferred species is reduced to such an extent that they cannot replenish stocks when rabbit numbers are low. Many species rely solely on the seed bank for regeneration and even the 'perennial' species must rely on the seed bank when all above ground parts decay or are grazed, as at the end of a long drought. If rabbits, by selectively grazing, can change the composition of the seed bank, then they have the potential to change species composition in the long term. The susceptibility of a plant species to such depletion, will depend on its palatability and on the number of seeds it produces. The concept of susceptibility will be discussed further in Part 3, section 2 and some evidence for the existence of a long term effect will be presented.

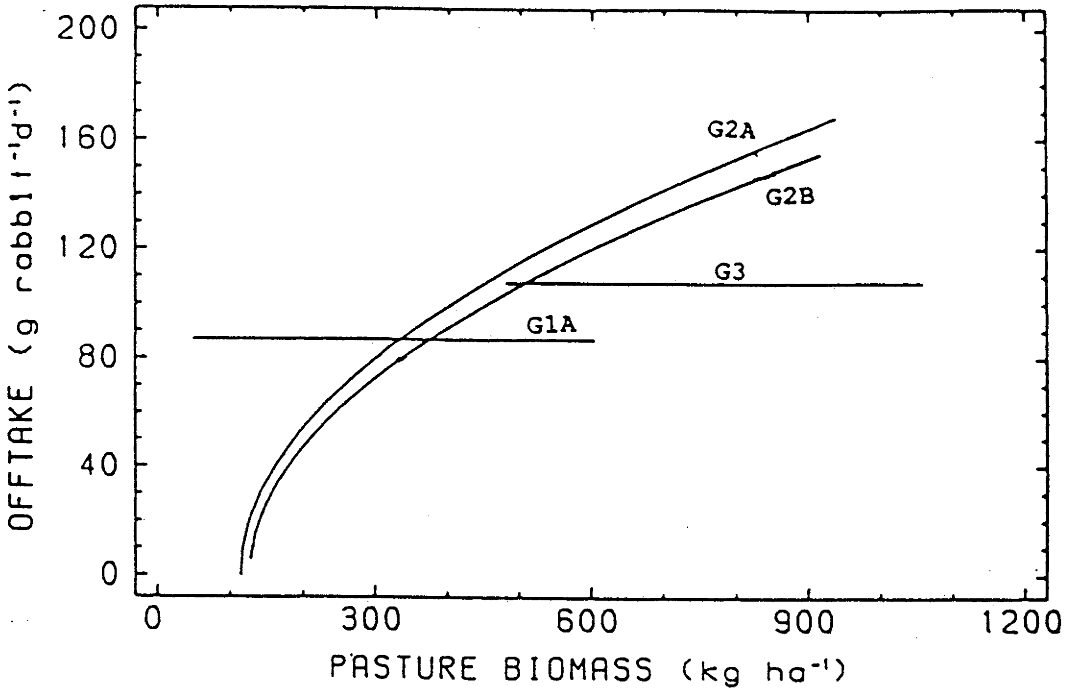
The implications of rabbit biomass removal and selectivity on intra- and inter-specific competition between herbivores will be discussed in Part 4.

Table 2.6.1. Palatability indices of all species in all grazing trials. For comparison between times P.I. of green *Sclerolaena* sp. has been taken as one and other P.I. values adjusted accordingly.

Species	Grazing Trial 1	Species	Grazing Trial 2	Species	Grazing Trial 3	Species	Grazing Trial 4
Con	80.5	Cne	31.5	Asp	24.6	Scl1(G)	1.0
Helm	15.5	Cna	27.5	Swa	18.4	Cra	0.89
Brach	12.5	Eme	15.2	Sid	7.8	Dau	0.27
Sid	11.8	Sid	7.7	Cra	5.5	Scl1(D)	0.18
Dau	9.1	Eup	7.6	Dau	3.1	Scl2(D)	0.09
Bul	6.9	Swa	7.4	Era(D)	2.9	Sti	0.05
Eup	6.8	Boe	6.0	Tri	2.2	Enn	0.03
Goo	2.3	Lop(G)	5.3	Helm	2.2	Era	0.02
Pla	1.9	Helf	4.1	Era(G)	1.8		
Scl	1.0	Era	3.6	Enn	1.2		
Atr	0.91	Cal	2.7	Scl2	1.0		
Boe	0.59	Dau	2.4	Scl3	1.0		
Era	0.38	Pla	2.3	Scl1	1.0		
Enn	0.16	Enn	2.0				
Dac	0.08	Che	1.2				
Tet	0.08	Tet	1.1				
Bab	0.08	Sti	1.1				
Phy	0.06	Scl	1.0				
		Erad	1.0				
		Sal	0.89				
		Helm	0.83				
		Cra	0.77				
		Phy	0.28				

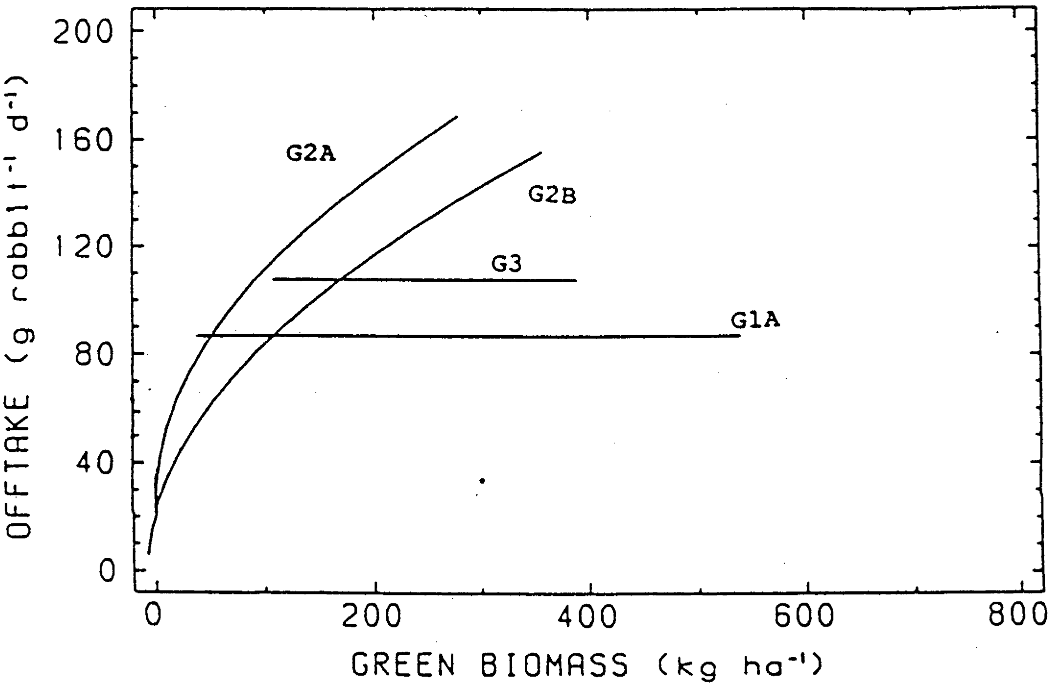
Each species is denoted by the first three letters of the genus. If there are two species in one genus then the first letter of the species name is also used. (G) = green (D) = dead. In the third grazing trial, the average P.I. for the three *Sclerolaena* spp. has been taken as 1.0.

Fig.2.6.1 Functional response curves derived from three grazing trials.



G1A = Grazing trial 1, pen A,
G2A = Grazing trial 2, pen A, G2B = Grazing trial 2, pen B,
G3 = Grazing trial 3, pen B,

Fig.2.6.2 Functional response curves using green biomass only.



Part 3.

Measurement of Rabbit Effects in the Field

The work described in Part 2 led to the conclusion that rabbits select strongly enough between pasture species for them to significantly alter species composition, particularly at times when they are in high numbers. It is possible that such short term effects will build up over time and lead to long term changes in species composition.

In this section I describe the results of different methods used to investigate both the long and short term effect of rabbits under natural conditions.

The area chosen for this work is described in Part 1.

1. Rabbit grazing pressures: past and present

In order to predict the effect of rabbits on vegetation, it is necessary to know how rabbit numbers are likely to change with environmental conditions. Although rabbit population dynamics have been studied in the arid zone (see Part 1), actual densities have seldom been measured. I decided to provide information on rabbit dynamics and densities for Kinchega by measuring rabbit populations throughout my study period by two different methods. In section 1.1 I will report on the results of these measurements.

To estimate the long term effect of rabbits on vegetation I needed to compare areas which had been subject to different levels of rabbit grazing. Initially, I assumed that the effect of rabbits would decrease with distance from a warren and I took the distance of any site from the nearest warren to be an indication of past grazing pressure. This proved to be inadequate (see Part 1 section 2.3.2) and a more detailed index of past grazing pressure was developed. In section 1.2 I describe the calculation of this index.

In this chapter, I report on my results for these various measures of rabbit numbers and past effects.

1.1 Active entrance surveys and spotlight counts

1.1.1 Methods

The position and size of all the warrens inside the kangaroo exclosure were recorded as were those of the warrens inside a 500 m by 500 m unfenced area of similar vegetation type situated about a kilometre to the north. Each of these warrens was visited every two months and the number of active entrances on each one noted. The number of occupants of all the warrens was calculated for each sampling period using Parer's (1982b) equation relating number of active entrances in sandy soils to population sizes. Active entrance surveying started in mid 1982 but since no definite active entrances were found at that time spot checks were made but no full surveys were carried out until rabbits started to breed in April 1983. No active entrances were found before that time.

The spotlight count method of obtaining an index of rabbit numbers has been used often e.g. Martin (1977); Rogers (1981); King and Wheeler (1985). It involves driving along set transects at a constant speed and counting all rabbits seen within a spotlight beam on either one or both sides of the vehicle. The index is usually improved if a transect is counted on several consecutive nights, and if repeat counts are always started at the same time in the evening.

If an estimate of density is required then an estimated distance limit for counting rabbits must be used. Any estimates of rabbit densities obtained this way, however, will be inaccurate since different vegetation types allow different visibility and bias may be introduced since rabbits are not necessarily at representative densities along transects, which are frequently roads. Even when used only as an index, care must be taken in making comparisons from one sample time to the next as vegetation changes can change visibility thereby exposing a different proportion of the population. I have used the spotlight counts only as an index of rabbit numbers.

Between May 1981 and August 1982, G. Robertson of the National Parks and Wildlife Service of New South Wales, at irregular time intervals, carried out spotlight counts along a 17 km stretch of road which ran round the south western boundary of the Park (see Fig.3.1.1). The counts were made from inside a vehicle driven at a constant speed of 20 km h^{-1}. Counts were made on the Park side of the vehicle only. The area sampled is distant from water and contains similar vegetation to that on my study site. Population trends for this area were more likely to be typical of trends in

Australian arid zone rabbit populations than would population trends for areas close to water. I, therefore, decided to continue these counts. I recorded rabbit numbers on this transect in November 1982, again in March 1983 and approximately every two months from then on until March 1985. Normally three runs were done at each sampling period but, if fewer than five rabbits were observed on the first run, then no replicates were done. I judged that, at these times, one run was sufficient to confirm that rabbit numbers were still low. Since I was not aiming to obtain accurate population density information from these counts this was sufficient for my purposes.

1.1.2 Results

Figure 3.1.2 shows the spotlight count indices and rabbit densities from active entrance counts for each of the sampling times.

1.1.3 Discussion

The trends in numbers of rabbits during the study are broadly similar for all methods of population assessment. They reflect both the rainfall regime during the period and the incidence of myxomatosis. I observed rabbits with this disease during 1983. During the long period of low rainfall in 1982 (Fig.3.1.2), the spotlight counts show that rabbit numbers maintained low levels. At the start of 1983, the numbers dropped and fell to zero about a month after rainfall had induced vegetation growth in March of that year. Just prior to the rain, P.Bayliss, of the National Parks and Wildlife Service of New South Wales, ran a spotlight transect through the south west corner of the Park. He was mainly concerned with counting kangaroos but his observations of rabbits led him to conclude that they were evenly spread throughout the area. At that time, and during the previous year, no active entrances could be identified with confidence in either of the areas surveyed for warrens although rabbits were occasionally seen in the area. This is most likely because the rabbits were ranging widely and using different burrows each day. This method will, therefore, underestimate rabbit numbers when they are low.

The numbers started to increase after the rain although a myxomatosis epidemic in the last quarter of 1983 reduced the population again. The subsequent rates of increase recorded by the two different techniques were different during this time. The numbers recorded by the spotlight count method increased more slowly than those recorded by the active entrance method. This is probably because kittens are too small to be counted in spotlight counts whereas they increase the proportion of used entrances on a warren. Parer and Wood (1986) comment that the equation for estimating populations from number of active entrances may not be accurate during breeding seasons since kittens use warrens more than adults do. Nevertheless, the population estimates are good enough to show that populations increased until about October of 1984. From then on they fell until the end of the study. All three plots of population trend show a decline in the rate of decrease with time even though the vegetation was drying out during this time. This may indicate that the remaining rabbits were better adapted to the dry conditions than those which died first. It is possible that the juveniles were the first to die since Richards (1979) found that juveniles of between one and two months old had a significantly higher rate of water turnover than adults under the same conditions. Nevertheless, the numbers declined by, at least, two thirds during only four months. This fast rate of decline is consistent with the results of Hayward (1961) who found that rabbits in a 2-acre enclosure with no access to water, 'after onset of very dry summer conditions lost weight slowly over two months then most died after losing nearly 50% of their original weight'. Hayward, however, states that rabbits respond very quickly to the availability of water and therefore benefit greatly from intermittent rainfall since the water allows them to increase their dry food intake. Unless plant growth was stimulated, however, this benefit would be only short-lived and rabbit numbers would still be expected to crash unless small rain showers occurred frequently.

1.1.4 Conclusions

These results show that rabbit populations at Kinchega behave in a way which is consistent with previous knowledge of rabbit population dynamics in arid areas (see Part 1). The data are not extensive enough to warrant looking for correlations between different rainfall parameters or pasture growth indices and rabbit population sizes. They do show, however, that the rabbit population responded to plant growth by increasing except when myxomatosis kept the population low. When the vegetation started to dry off, rabbit numbers fell rapidly. During the winter of 1982 when conditions were very dry, rabbits maintained themselves at low densities and, although the numbers started to fall during summer, there is evidence that rabbits were thinly spread throughout the country by the time that some fresh vegetation finally appeared in autumn. There is no evidence that rabbits were using only warrens close to water during 1982, as suggested by Myers and Parker (1975b) but the 'drought' may not have gone on long enough for this to occur. The warrens they were using may have been favoured for other reasons. The rabbits took one year to achieve the highest densities I recorded when between 60% and 70% of warren entrances were active.

It would thus take less than two years of favourable breeding conditions i.e. the presence of growing vegetation and an absence of myxomatosis, for all the warrens to be filled. When this occurs, rabbit densities would be about 5 ha^{-1} at one of my sampling sites and 8 ha^{-1} at the other. If food availability did not limit population growth at this stage then social factors probably would (see Part 1). The consequences of these conclusions for the vegetation will be discussed in Part 4.

1.2 The grazing index

In Part 1 I described experiments which I carried out to look at different aspects of vegetation in relation to distance to the nearest warren. None of these experiments showed any relationship between distance and the vegetation parameters. This may have been for one or more of the following reasons;

1. Rabbits have had no effect on the vegetation;
2. The effect is too small to be detected by the vegetation sampling methods that I used;
3. Grazing time is not related to distance from a warren, or
4. Distance to the nearest warren, alone, is not the only factor determining relative use by rabbits.

In order to test the assumption of decreased grazing pressure with distance from warrens, I used data collected by P.Fullagar and C.Davey. These data record movements of wild rabbits under natural conditions. From their results I was able to calculate a rate of decline in grazing pressure with distance from the warren. With this I was then able to calculate a grazing index for each of my vegetation sampling sites which was based on the maximum grazing pressure at that site due to all the warrens within a range of 240 m (the maximum distance from warrens that rabbits were recorded by Fullagar and Davey). This section describes the method used to calculate these indices which are used for the analysis of vegetation data in Part 3, section 2.

1.2.1 Method of data collection

The data used in this section were collected by P.Fullagar and C.Davey in 1973 and 1974 at Calindary Station in western New South Wales. The property is situated 150 km north and 30 km east of Broken Hill. Calindary, like Kinchega, is in the semi-arid zone and falls within the region of non-seasonal rainfall. The vegetation in the area consists of scattered trees of *Eucalyptus largiflorens*, *Acacia aneura* and *Grevillea stricta*. There are few shrubs and a ground layer of *Enneapogon avenaceus*, *Aristida browniana* and various other grasses and forbs. I considered the ground layer vegetation to be similar enough to that at Kinchega that behaviour of rabbits would also be similar at the two sites.

Information on movements of individual rabbits was collected in March 1973 and September 1974. The 1973 observations followed several months of low rainfall. Since this occurred at the end of summer, green vegetation would have been relatively sparse. In 1974, the observations followed several months of good rainfall and winter temperatures. The vegetation would, therefore, have been greener and more abundant. The two observation times would, thus, have been at times of contrasting amounts of food availability.

The data were collected by tracking individual rabbits from time of first emergence at dusk to their return to the burrow. Each rabbit was fitted with a light-emitting collar and its position and behaviour recorded at regular intervals. The methods are fully documented in Fullagar (1981). In 1973 six rabbits were tracked, three of them for one night and three for two nights. In 1974 nine rabbits were tracked for one night each. All but one of the rabbits were different from those used in 1973.

As well as regularly monitoring the position of each rabbit, the observers recorded its behaviour at each observation time (once every minute). There were nine categories of behaviour only one of which was related to grazing.

1.2.2 Relationship between grazing pressure and distance from warren

Data were available regarding the distribution in space of each of the behaviour categories. Unfortunately, the computer programs for separating the behaviours and printing the maps were outdated by the time I came to do this study and I did not have the time or the skills to update them. I, therefore, made the assumption that total use reflected use for grazing. Some confirmation of this comes from a comparison of 'centres of activity' for different behaviours. A 'centre of activity' is a measure of the centre of distribution of each behaviour type (Fullagar 1981). Fullagar and Davey calculated these for ten rabbits observed near Canberra and for seven behaviour categories. The centres of activity for grazing always fell close to the centres of activity for all behaviours combined. This suggests that the distribution of grazing is little different to the distribution of all behaviours combined. This is supported by observations of Fullagar (pers.com) that rabbits continuously intermix grazing with other activities. If this is the case then the distribution of total use reflects the distribution of grazing pressure.

The behaviour data were manipulated by Fullagar and Davey so that they could be presented on maps of the whole study area divided into 5 yd by 5 yd cells. In each cell, the total number of observations of a rabbit during one watch in that cell was recorded. One map was produced for each watch.

I constructed a transparent overlay which marked the position of the warren and concentric circles round the warren at 5 yd intervals to 300 yds. By placing the overlay on the maps, I was able to calculate the number of sightings in each annulus. I calculated the proportion of sightings per unit area in each of the annuli to obtain an index of rabbit use. Rabbit use falls off rapidly with distance from the warren in both years and becomes insignificant past 240 m (see Fig.3.1.3). In 1973, there was an increase in rabbit use at 150 m. This was probably due to a topographic depression at this distance (Wood pers.com.). Since these results were obtained at the end of summer when this depression is more likely to have still supported green plants, there would have been a strong incentive for rabbits to go there. Apart from this anomaly, the curves for the two years are similar. I, therefore, combined the data for the two years for use in the estimation of decline in grazing pressure with distance from warren. The results for both years show the maximum distance that rabbits will travel from the warren to be about 240 m since there were only occasional sightings beyond this distance in either year.

If the results for Calindary are taken to be representative of the behaviour of rabbits in similar areas then the relationship between distance from warren and rabbit use for this area can be used to predict rabbit use in other areas. To do this it is necessary to find a function which describes the decline in rabbit use with distance from the warren. This can be done by deriving an empirical relationship between distance from the warren and rabbit use or by using models of rabbit behaviour to derive expected functions whose validity can be tested by fitting them to the data. I tested three empirical, and two behavioural, models.

The best fit linear relationship between distance from warren and rabbit use gives a significant but poor fit ($r^2 = 0.24$, $P = 0.0101$). The best fit quadratic relationship gives a better fit ($r^2 = 0.46$, $P = 0.0002$) but a linear relationship using logarithmically transformed observation data gives the best fit of the empirical models ($r^2 = 0.89$, $P < 0.0001$).

Of the two behavioural models which I considered, one assumed that rabbits move in a random manner once out of the warren and the second assumed that a rabbit moves in one direction and at a constant speed out from the warren.

The first model is equivalent to diffusion and the pattern of rabbit use with distance from the warren which eventuates can be described by a modified Bessel function (Pielou 1969). To test this model I calculated the expected numbers of observations per unit area in each annulus and regressed these against the real values. If the model were a good one then a linear regression through the origin would be significant. This was the case ($r^2 = 0.75$, $P < 0.0001$). A positive quadratic regression equation, however, fitted these data significantly better ($r^2 = 0.98$, $P < 0.0001$). This would be expected if the rabbits spend more time on, and near to, the warren, than the model predicts. This phenomenon is confirmed by observations which indicate that rabbits, on first emerging from the burrows, spend some time on the warren checking conditions before they move away (Fullagar pers. com.).

The second model results in rabbit use being proportional to the reciprocal of the distance from the warren. If this model were a good one then there would be a significant linear relationship between the reciprocal of distance from the warren and the number of sightings per unit area. This was the case ($r^2 = 0.987$, $P < 0.0001$). As with the first model, however, a positive quadratic regression gave a significantly better fit ($r^2 = 0.996$, $P < 0.0001$). If the first 20 m are excluded from the data set then a linear regression gives a better fit than a quadratic one ($r^2 = 0.93$, $P < 0.0001$ for the linear fit) thus confirming that higher than expected rabbit use of the first 20 m from the centre of the warren caused the quadratic term to be significant.

The constant speed, one direction model with increased use on, and near, the warren, produced the function which best described the model. The random walk model also fitted the data well but the fit was poorer and there is less behavioural evidence to support this model. Since the rabbits in the study which were tracked on two occasions went out in the same direction from the warren each time, and rabbits are known to have fairly fixed territories, the one direction, constant speed model probably better represents the normal behaviour of rabbits. I, therefore, decided to use this function to produce an index of past accumulated grazing pressure for each of my vegetation sampling sites.

1.2.3 The grazing index

The relationship between the proportion of the total number of sightings at each distance per unit area and the reciprocal of the distance can be used to calculate the grazing pressure at any distance from a warren if the number of rabbits in the warren is known. For the Calindary data, this relationship is;

$$y = -0.03161 + 9.374(1/x) + 30.77(1/x^2)$$

where y is the proportion of all sightings per ha at distance x metres from the warren (see Fig.3.1.4). The grazing pressure at a given distance, and for a given number of rabbits using a warren, can be calculated by multiplying the number of rabbits in the warren by the value of this equation for x equal to the reciprocal of the distance in metres. The derivation of this calculation is given in Appendix 4.

A relative measure of past accumulated grazing pressure can be obtained for different sites if the number of burrows is taken to be representative of past numbers of occupants of the warren. Since rabbit densities are related to number of active entrances (Parer 1982b), this is a reasonable assumption when rabbit numbers are at a maximum. At other times, however, different warrens may 'fill up' faster than others hence grazing pressure will not be related to warren size. In calculating grazing indices for my vegetation sampling sites, I have assumed that all warrens fill up at the same rate and, therefore, that grazing pressure at a given distance from a warren is related to number of burrows in the warren.

Using the relationship obtained above and estimates of maximum rabbit numbers in each warren calculated from Parer's equation, I calculated the total grazing pressure due to all warrens at each of my sampling sites at maximum rabbit densities. This, I have taken to be an index of past accumulated use which can be compared with vegetation parameters. Even if the estimates of maximum warren populations were inaccurate, the grazing indices should still reflect differences between sites as long as the assumption that use is related to warren size is true. The grazing indices are given in Table 3.1.1.

Table 3.1.1 Grazing index associated with each sampling site.

Sample site	Grazing index
1	1.34
2	2.20
3	3.56
4	4.83
5	5.24
6	2.89
7	1.58
8	0.72
9	0.23
10	0.02
11	0.31
12	0.94
13	2.57
14	6.87
15	7.63
16	3.50
17	2.53
18	1.79
19	1.01
20	0.40
21	0.66
22	0.23
23	0.29
24	1.03
25	2.62
26	4.38
27	4.75
28	4.68
29	2.51
30	0.63

Fig.3.1.1 Location of spotlight count transect (xxxxxxxx).

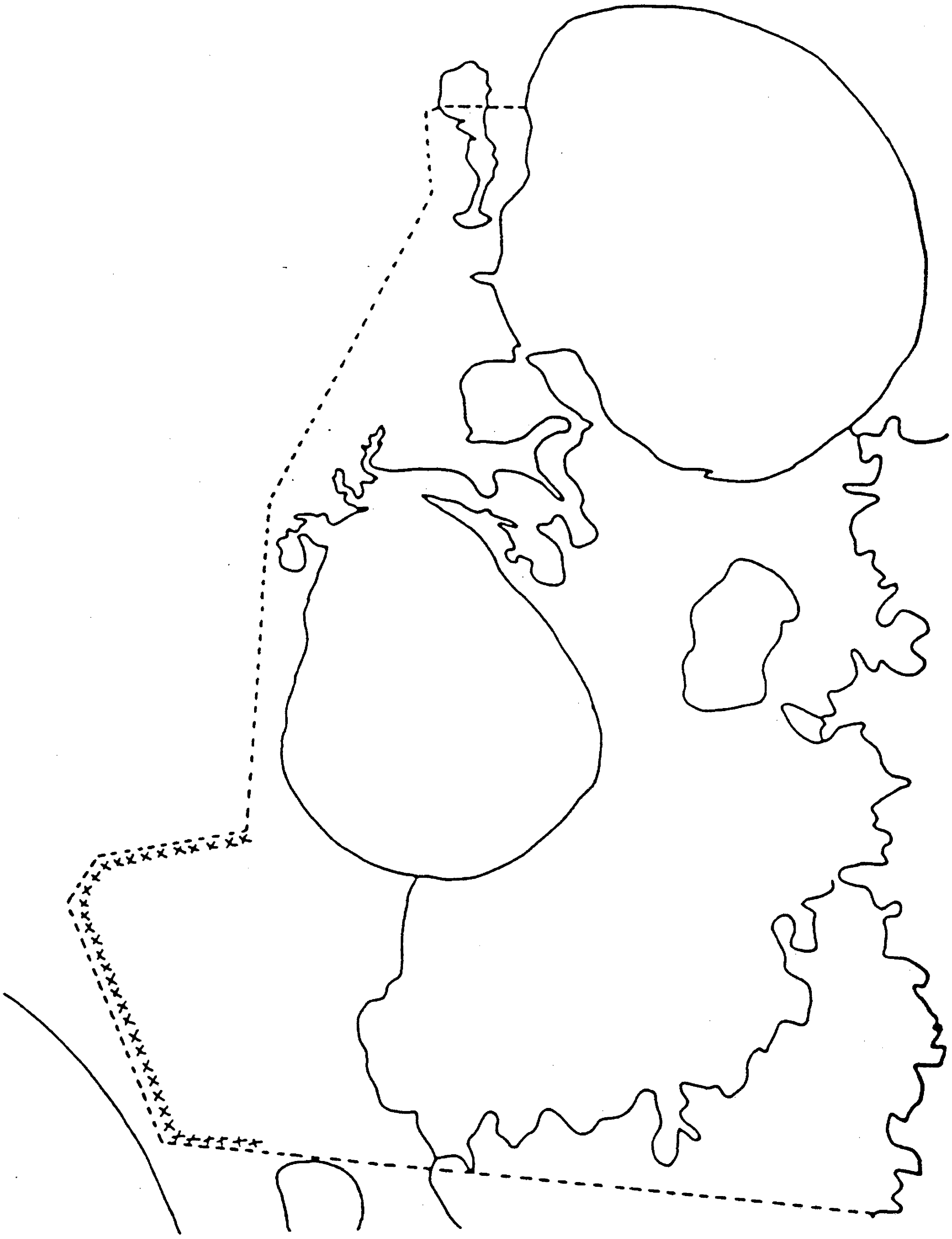


Fig.3.1.2 Rabbit densities and mean monthly rainfall throughout the study period at Kinchega National Park.

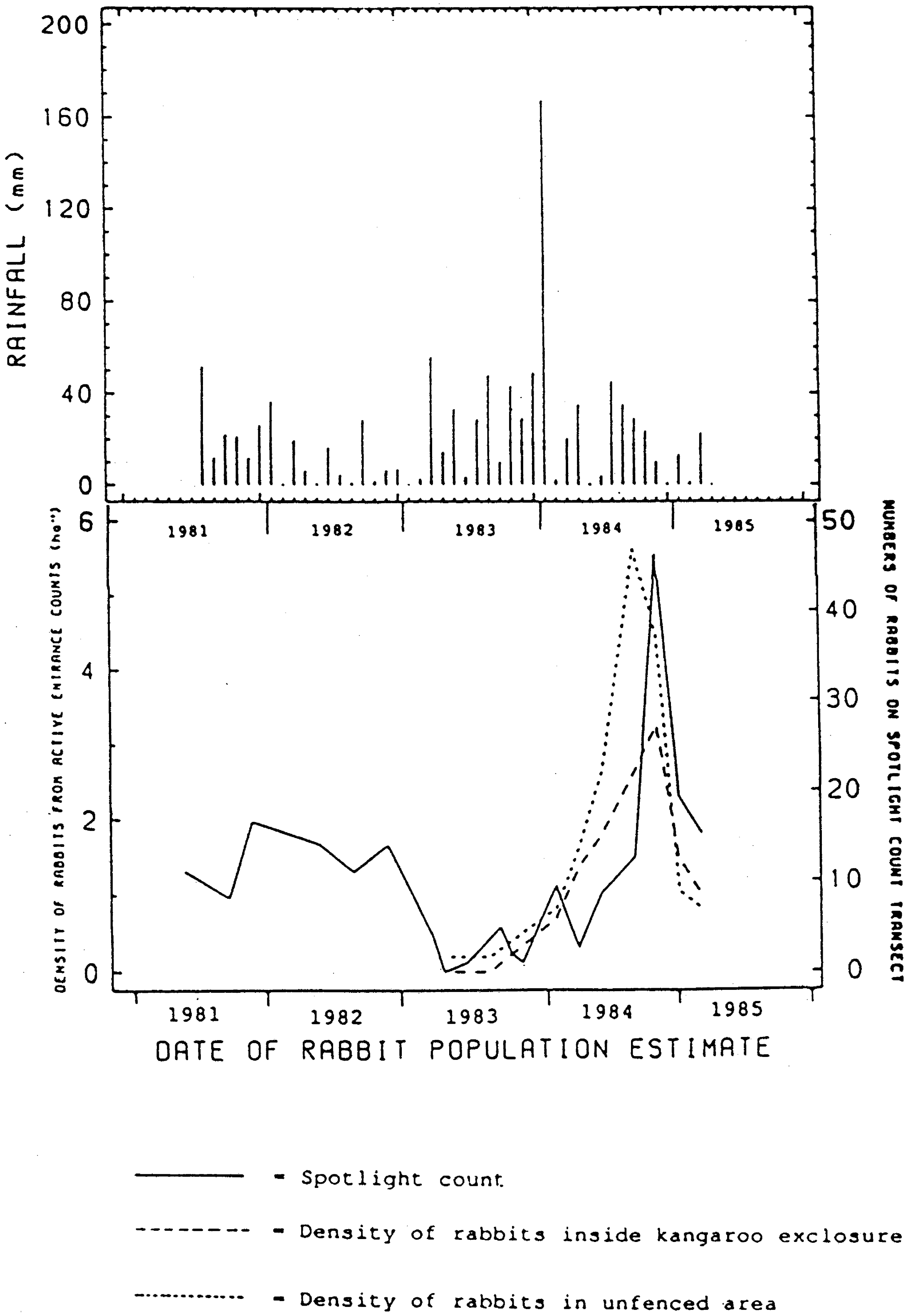


Fig.3.1.3 Number of sightings per unit area in each 10 yd annulus out from a warren at Calindary, N.S.W. in March 1973 and September 1974.

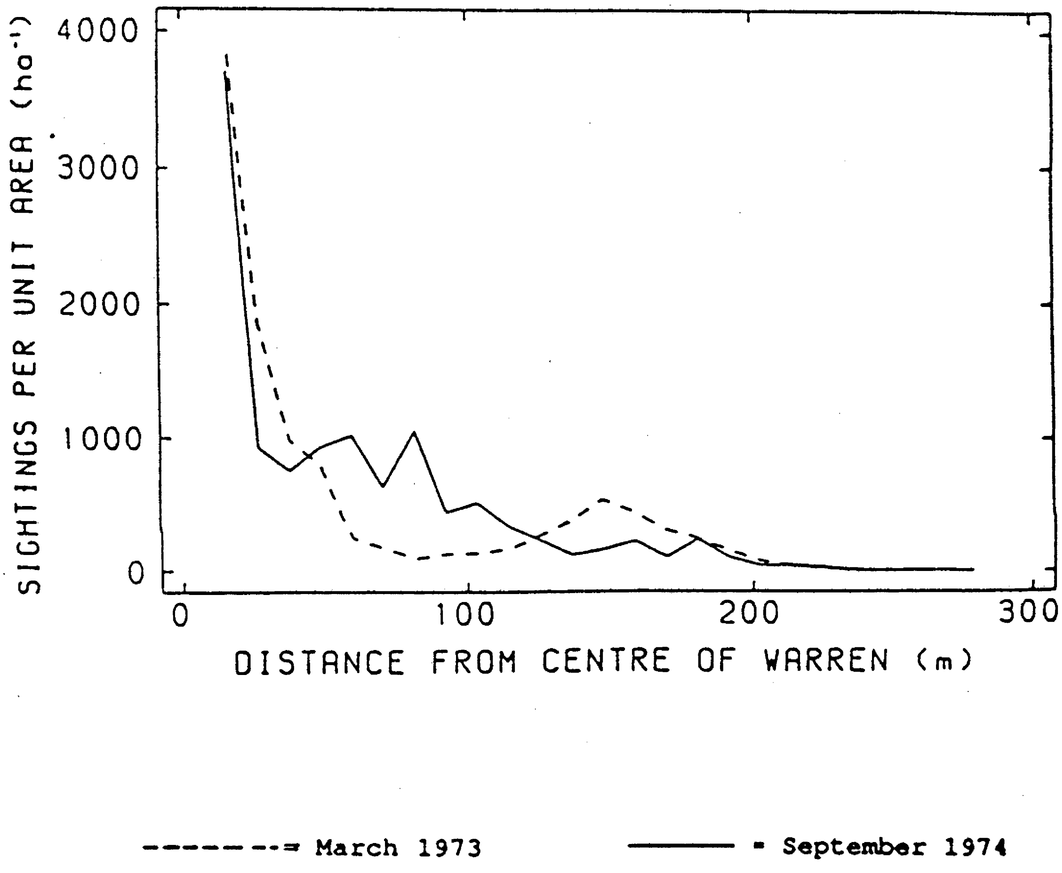
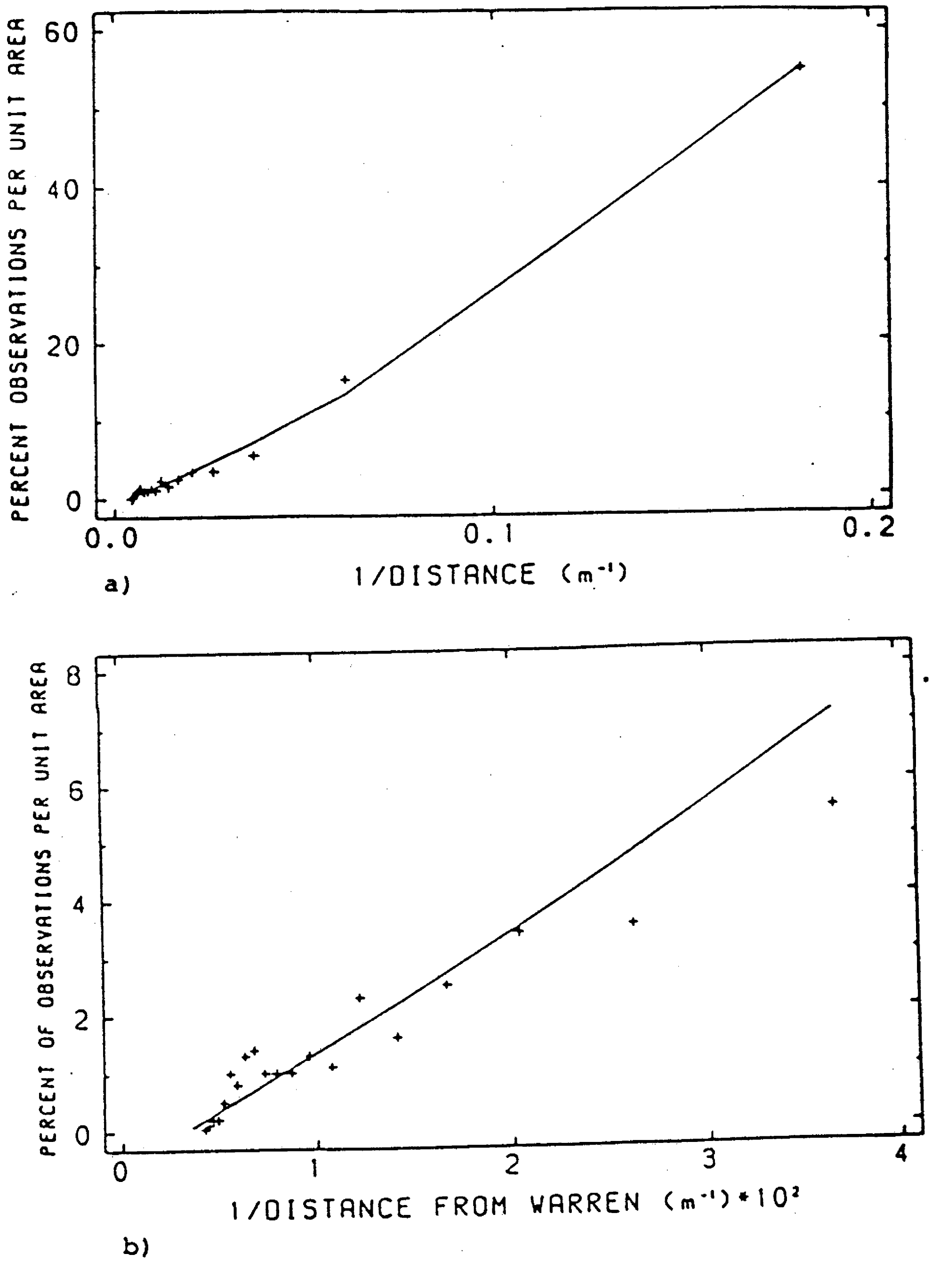


Fig.3.1.4 Percentage of sightings of rabbits per unit area.



a) Including area to 20 m from warren centre.

b) Excluding area to 20 m from warren centre.

+ - Real values ——— - Fitted values

2. Long term effects on vegetation

In the previous section I described a method of estimating the relative past grazing pressure of rabbits at any site. In this section I describe the results of an experiment designed to use grazing indices calculated in this manner to investigate the long term effects of rabbits on pasture species composition.

2.1 Methods

This experiment was carried out within a 500 m by 500 m kangaroo proof fence. The fence was made of 10 cm mesh joined to 2 m star pickets every 5 m. The fence thus kept kangaroos out but allowed rabbits to move in and out freely.

The fence was put up in an area of gently undulating sand dunes where rabbit warrens were numerous (Fig.3.2.1). The vegetation was sparse belah (*Casuarina cristata*) and rosewood (*Heterodendrum oleifolium*) with an understorey of bluebushes (*Maireana pyramidata*) which occurred in varying densities. The trees were more numerous on the sand dunes although they were not confined to these areas.

All the warrens, both inside the fence and in the surrounding area, were accurately mapped and the number of entrances on each warren was counted (Fig.3.2.2).

Ninety 0.25 m^2 circular, rabbit proof cages were constructed and pegged down at thirty sites within the exclosure. The sites for the cages were at regular intervals along the diagonals of the fenced area and along one of the bisectors of the area (Fig.3.2.2). This arrangement was chosen rather than a random one because I thought it more likely that I would obtain a range of different grazing pressure indices with regular sampling since the warrens are clumped (Fig.3.2.2). A grazing index was calculated for each of the sampling sites (see Part 3, section 1.2). Three cages were placed at each site. One was positioned beside a bluebush and two were placed at least one metre away from the nearest bluebush. The cages were used because, initially, the experiment was designed to measure short term effect as well as long term effect. Rabbit numbers were, however, too low for an offtake to be detected during the course of the experiment. Data for the cages and uncaged quadrats were subsequently pooled (see below).

The plant species present in each of the rabbit proof cages, and in ninety 0.25 m^2 circular quadrats positioned within 0.5 m of each of the cages, were recorded. The cages remained in position throughout the experiment. Initially, the uncaged quadrats were also permanently marked but I was unable to find many of the markers on the fourth sampling occasion (June 1984). This was because the pegs had been marked with yellow tape and this became impossible to detect amongst the vegetation at some sites. At that time I selected new locations for the quadrat positions which were lost. On the following sampling occasion (September 1984), however, the markers were even harder to find and I recorded species richness only inside the cages. From then on I placed the uncaged quadrats at new positions at each sampling time. On one occasion (October 1983) the vegetation was recorded at only ten sites due to a lack of time.

Three randomly positioned 200 cm^3 cylindrical soil samples were taken to a depth of 5 cm at each of the sampling sites and analysed for coarse sand, fine sand, silt and clay content using standard techniques (Black et al. 1965).

On the final sampling occasion, rabbit pellets were counted in sixteen randomly positioned 0.25 m^2 quadrats at each sample site. If a quadrat fell on a buck heap it was repositioned.

2.2 Results

Appendix 5 lists the total number of species found at each of the sampling sites in all quadrats at each sampling time. It also gives the grazing index associated with each site, the pellet density recorded and the values for each of the soil texture parameters measured.

2.3 Discussion

2.3.1 Relationship between grazing index and total species richness

The rabbit warrens at the study site have a tendency to be on sand dunes. Since this could confound any relationship between grazing index and species richness I first tested the possibility that grazing index was associated with soil texture by looking for correlations between grazing index and each of the four measures of soil texture. Grazing index was significantly correlated with fine sand ($r^2 = 0.21$; $P = 0.0097$) and silt ($r^2 = 0.18$; $P = 0.0183$) content of the soil. Coarse sand and clay showed no significant correlation with grazing index. There is thus a correlation between soil texture and grazing index. The relationship is sufficiently weak, however, to be ignored.

The effects of past grazing cannot, however, be separated from the possible effects of differential runnoff associated with the position of each sampling site relative to the sand dunes. The relationship between grazing index and position relative to dunes was tested by placing each site in one of three categories; on a dune crest, on the side of a dune or in a swale. The grazing indices were also divided into categories and the χ^2-value calculated (Table 3.2.1). The correlation was significant ($P < 0.05$) implying that it would be difficult to separate the effects of past grazing from those of location on the dune. Location of the sampling sites relative to dunes was not included in further analyses since I assumed that a relationship with grazing index would reflect a relationship with position on the dune also.

In order to test the hypothesis that grazing index is significantly correlated with species richness, I used the statistical package, GENSTAT, to test various multiple regression models using the the soil texture variables, pellet density and grazing index to predict species richness. In testing the models I combined results for all the quadrats, both inside and outside cages. This was done since there were no significant differences in mean species richness inside and outside the cages except on the last two sampling occasions when there were more species present inside the cages. By this time the cages had been in position for two years and the differences could have been due to seed build up inside the cages or to improved microhabitats although there may also have been a component of recent grazing pressure. Since all sites were given the same treatment (three caged and three uncaged quadrats), combining the results for all quadrats was valid for making comparisons between sites and gave more information on which to base conclusions.

I first calculated which of the variables could, on its own, account for most of the variance in the data. I then carried out a step-wise multiple regression, including the other variables in the model in order of the percentage reduction in deviance caused by each one. The significance of the first variable is tested by comparing the deviance value with the value of the χ^2 distribution. The significance of added variables is tested by comparing the reduction in deviance caused by adding the variable with the value of

χ^2 with one degree of freedom. If it is greater than this value then the added variable has caused a significant reduction in deviance.

The species richness data were first log transformed since a geometric relationship was expected. Since the data were counts, the error was assumed to be Poisson. The mean deviance of the null model is used to assess whether this is a valid assumption since, if the mean deviance is high then it is likely that there is a significant departure from randomness. This was not the case for any of the models hence the assumption of a Poisson distribution was valid.

At all sampling times except the first two (April 1984, June 1984), grazing index emerged as the most significant variable (Table 3.2.2). At the first sampling time, no variable was significant and at the second sampling time percentage of fine sand content was the most significant variable. At this time, however, grazing index was significantly correlated with species richness when fitted first ($r^2 = 0.15$, $P = 0.03$). At the last sampling time (March 1985), although grazing index was the most significant variable, it was only significant at $P < 0.1$ whereas all the others are significant at $P < 0.05$. At all times, no other variable, when added to the one variable model, significantly reduced the deviance. The measured data and the fitted models for the six times when grazing index was the most significantly correlated variable are shown in Fig.3.2.3.

The lack of a correlation between grazing index and species richness at the first sampling time is likely to be due to the low number of species present at that time (15 as compared with a mean of 32 ± 2 at the other sampling times). The correlation with fine sand content in June 1984 may be explained by the greater ability of fine grained soils to retain moisture. At this time, the soils were being wetted for the first time after a prolonged dry period (see Fig.2.2.1) hence the greater ability of the upper layers of fine grained soils to retain moisture may have allowed more species to germinate and establish. As the soils absorbed water to a greater depth, this would have become less important in determining species composition and seed bank may have become relatively more important.

These results show that grazing index can be used as a predictor of species richness. They cannot, however, distinguish between the effects of past grazing pressure and differences in runoff/runon characteristics between sites since the two variables are closely correlated. To assess the likely influence of past grazing pressure alone, the relationship between individual species frequencies and grazing index must be determined. If the species which decline with grazing index are those which would be expected to be most susceptible to rabbit grazing then there will be some reason to conclude that the decline in species richness with grazing index was caused by rabbit grazing.

2.3.2 Relationship between grazing index and individual species frequencies

Since there is overlap between the individuals present at each sampling time, I amalgamated the data for all sampling times. A species was recorded as present or absent in each of the quadrats over all sampling times. Each species, therefore, had an associated frequency out of six for each sampling site. A total of seventy-two species were recorded (Table 3.2.3).

In order to test for relationships between individual species frequency and grazing index, I used GENSTAT to carry out logistic regression analyses on the individual species frequency data, assuming binomial error (see Neter & Wasserman 1974, pages 329-338, for a full description of logistic (or logit) transformations and the reasons for considering their use before doing a regression analysis). This assumption was made because the data were in the form of proportions (counts out of six). In such cases, a normal regression would not be applicable since this assumes a normal distribution and proportionate data usually have a binomial distribution. Thirty-five species showed a significant correlation between their frequency and grazing index (Table 3.2.3). Of these, seven showed an increased frequency with increasing grazing index. Of the remaining thirty-seven species, thirteen occurred at a low number of sample sites (fewer than six). The lack of a significant correlation for these species may, in some cases, be due to inadequate sampling.

As has been mentioned, grazing index was correlated with the position of the site relative to a sand dune. A significant correlation between a species' frequency and grazing index can, therefore, be interpreted as either the result of differential past grazing pressures or the result of different runoff/runon characteristics of the different sites. The hypothesis that past grazing pressure has influenced individual species densities will be supported if the results of the logistic regressions are consistent with those that would be expected based on known palatability of the species to rabbit grazing and susceptibility to damage by grazing. To do this, I assigned a susceptibility score to each species. The score is based on six attributes. Five of the attributes will affect the species palatability to rabbits. These are:

1. the ability to remain green as conditions dry out;
2. an erect habit;
3. spinyness;
4. toxicity and
5. the ability to fix nitrogen.

The sixth attribute, seed size, relates to the likely magnitude of the effect of removal of a seed head on future densities of the species. This attribute was included since I thought that species with relatively large seeds would be likely to produce relatively few seeds (Werner & Plat 1976) hence would be less able to replenish seed banks when grazing pressure was low. Many other attributes of plant species, such as size of seed store and seed longevity, will influence the effect of grazing on densities. Too little is known about the ecology of individual species, however, to be able to make use of such attributes. I have, therefore, confined myself to using attributes for which I had information for most species. As a result, the susceptibility scores can give only a rough measure of real susceptibility.

The information on growth habit, spinyness, and seed size came from my observations of the plants in the field and by reference to Cunningham et el.(1981). Information on ability to remain green during dry periods came from my photographic monitoring of vegetation plots every three months for three years. During that time, only the sclerolaenas and *Brachycome ciliaris* remained green when other species dried out. All other species dried out quickly or over time periods similar to many other species. Only *Swainsona phacoides*, *Medicago minima* and *Trigonella suavissima* belong to genera which are capable of fixing nitrogen. Only *Babbagia acroptera* was classed as toxic since I had first hand evidence of its avoidance by rabbits (see Part 1, section 2). Other species may also be toxic but I had no evidence to support this for any other species.

Each species was given one point for each of the following attributes; staying green during dry periods, having an erect habit, producing relatively few, large seeds (>1mm), and being able to fix nitrogen. Each species had one point deducted from its score if it produced spines or prickles and was given a score of zero if it was toxic. Factors such as fibrousness were not included since little information is available on this.

Table 3.2.3 lists the points awarded to each species for each of the attributes and the final susceptibility scores.

In order to test the correlation between susceptibility score and the nature of the relationship between grazing index and species density, I constructed a matrix (Table 3.2.4a) tabulating the number of species which fall into the different categories of susceptibility score and categories of correlation with grazing index. The matrix excludes the species which occurred at fewer than six sites. These 'rare' species were analysed separately (see below).

A χ^2 test showed that there was a significant ($P<0.05$) correlation between susceptibility score and relationship with grazing index (Table 3.2.4b). The results are consistent with there being a correlation between susceptibility score and response to grazing index. The species which show a decline in frequency with increasing grazing index generally have a high susceptibility index (2 or 3) and the species which show a negative correlation with grazing index, generally have a low susceptibility index (0 or 1). It is, theoretically, possible that susceptibility score is correlated with 'preference' of plant species for different positions relative to dunes. There are no obvious reasons, however, for this to be so. These results, therefore, provide evidence that differential rabbit grazing pressures around rabbit warrens has led to changes in species composition of the pasture.

The species which occurred at fewer than six sites were not included in the above analysis. Since rabbit grazing may have been a factor in their rarity I decided to pool the data for all 'rare' species i.e. occurring at less than six sites, and test the correlation between their frequency and grazing index. In pooling the data I treated all rare species as one species. A logistic regression gives a significant correlation between frequency of rare species and grazing index (Table 3.2.5). It is, however, likely that some of the rare species are rare for reasons other than rabbit grazing. If this were the case then the species with the highest susceptibility would show the best correlation and the fastest decline with grazing index and those with the lowest would show the worst correlation with grazing index (Table 3.2.5). I grouped the rare species into four groups with susceptibility scores of 0,1,2, and 3. I then treated each group as if it were one species and tested each group for its correlation with grazing index. As predicted, there is an increase in the significance of the regression between frequency and grazing index as susceptibility score increases and also an increase in the steepness of the slope of the regression. The results for the rare species with a susceptibility index of 0 do not, however, fit into this pattern. These species show an unexpectedly good correlation between grazing index and frequency with a slope as steep as the one for the species with a susceptibility index of 2. This can be explained by the small number of species with a susceptibility score of 0 (4). Of these, one species occurs at one site only and one at two sites. The remaining two species occur at four sites and each shows a significant correlation with grazing index (Table 3.2.3). Thus only two species contribute to the results for this group. There is no apparent reason for their decline with grazing pressure.

These results provide further evidence that past rabbit grazing has decreased the densities of susceptible species and that the extent of the decrease in any area is related to the level of past grazing pressure. It is, therefore, possible that species richness would increase in rabbit grazed areas if rabbit numbers were to decrease. It is also possible that the changes are irreversible but since the vegetation periodically persists only as a seed store, it is possible that, at these times, the rabbit-affected species could recolonize. It seems unlikely that rabbits will have caused the extinction of many species since there will always remain areas which are too far away from warrens for rabbits to graze there. Tree regeneration will also be able to take place in these areas which would have to be at least 200 m away from the nearest warren. It seems likely that rabbits will reduce the quality of the pasture that is available to other grazers by their long term effect on the vegetation. This conclusion rests on the assumption that the species which are depleted by rabbits are, on average, more nutritious than the remaining species.

2.4 Conclusions

The results from this chapter provide evidence that rabbits have, over the years since they first arrived in the area, caused changes in the species composition of the ground layer vegetation. The magnitude of the changes has been proportional to the grazing pressure, as measured by grazing index.

Fewer plant species have benefitted from rabbit grazing than have been adversely affected by it. Although rabbit grazing decreases the species richness of pastures in this area, and may be responsible for the low densities of some species, it is unlikely that rabbits could have caused the extinction of many species since there will always be some areas which are too far away from a rabbit warren (more than 200-300 m) for rabbits to graze there.

If the characteristics which make a plant species susceptible to rabbit grazing are associated with a higher nutritional value, then rabbit grazing will reduce the nutritional value of pastures in this area for other grazers as well as for themselves.

Table 3.2.1 Number of sampling sites in each grazing index/dune position category.

		Grazing Index Class		
		1	2	3
Position Relative to Dune	1	1	3	10
	2	1	5	2
	3	6	2	0

$\chi^2 = 19.5$ c.f. $\chi^2_{(0.05,4)} = 9.5$

Grazing Index; class 1 = 4.4 - 7.6 rabbits ha^{-1},
class 2 = 1.0 - 4.39 rabbits ha^{-1},
class 3 = 0.02 - 0.99 rabbits ha-1
Position Relative to Dune;
class 1 = dune crest,
class 2 = dune side,
class 3 = interdune

Table 3.2.2 The significance of the regression models of best fit relating logarithm of species richness to grazing index, rabbit faecal pellet density and soil texture parameters.

Sampling time	Variable	Parameter estimate	t-statistic	df	Significance of variable
4/83	No variables significant				
6/83	constant	2.284	17.92		
	FS	0.0625	3.09	28	0.003
10/83	constant	3.072	27.00		
	GI	-0.1368	-2.91	10	0.003
6/84	constant	2.567	31.40		
	GI	-0.0683	-2.39	28	0.015
9/84	constant	2.782	37.49		
	GI	-0.0838	-3.16	28	0.001
11/84	constant	2.7412	36.43		
	GI	-0.0740	-2.79	28	0.004
1/85	constant	2.582	31.57		
	GI	-0.0795	-2.73	28	0.005
3/85	constant	2.3878	26.99		
	GI	-0.0521	-1.72	28	0.076

GI=grazing index, FS=fine sand.

Table 3.2.3 Regression statistics, number of occurrences and susceptibility scores for each species found within the experimental area.

Species	Number of occurrences	Slope of regression	Significance level	Susceptibility score						
				G	E	S	SEED	T	N	TOT
Acetosa vesicaria	1		ns		1		1			2
Actinoboli uliginosum	13	+	.01							0
Alternathera denticulata	6	+	.001							0
Atriplex sp.	10	-	.001	1	1		1			3
Alyssum linifolium	5		ns		1		1			2
Angianthus burkittii	2		ns							0
Asphodelus fistulosa	9	-	.01		1		1			2
Babbagia acroptera	1		ns	1	1			-2		0
Bassia decurrens	19	-	.001	1	1	-1	1			2
Bassia diacantha	6		ns	1	1	-1	1			2
Bassia brachyptera	4	-	.001	1	1		1			3
Boerhavia diffusa	30		ns				1			1
Brachycome ciliaris	13	-	.01	1	1		1			3
Brachycome leariloba	30		ns				1			1
Brassica tournefortii	1		ns		1		1			2
Calotis cuneifolia	2	-	.05	1	1		1			3
Calotis cymbacantha	18		ns		1	-1	1			1
Calotis hispidula	10		ns	1		-1				0
Calotis multicaulis	25		ns		1		1			2
Chenopodium melanocarpum	24	+	.001							0
Chloris truncata	3	-	.05		1		1			2
Convolvulus arvense	8	-	.001		1		1			2
Convolvulus erubescens	11	-	.001		1		1			2
Craspedia pleiocephala	28		ns		1					1
Crassula colorata	29		ns							0
Cucumis myriocarpus	4		ns				1			1
Cuphonotus humistratus	1		ns				1			1
Dactyloctenium radulans	6	-	.05		1		1			2
Daucus glochidiatus	26		ns		1	-1				0
Enneapogon avenaceus	30		ns		1					1
Eragrostis sp.	29		ns		1					1
Eragrostis dielsii	25		ns		1					1
Eriochlamys behrii	17	-	.001		1					1
Erodium botrys	9		ns		1	-1	1			1
Erodium cicutarium	2		ns		1	-1	1			1

continued overleaf ...

Table 3.2.3 continued

Species	Number of occurrences	Slope of regression	Significance level	Susceptibility score G	E	S	SEED	T	N	TOT
Euphorbia australis	12	+	.05	1						1
Euphorbia drummondii	4	-	.01	1						1
Goodenia cycloptera	21	-	.001		1		1			2
Harmsiodoxa brevipes	21	-	.01		1		1			2
Helipterum floribundum	9		ns		1					1
Helipterum jessenii	17	-	.001							0
Helipterum moschatum	30		ns							0
Helipterum pygmaeum	7		ns							0
Helipterum strictum	7	-	.05		1					1
Isoetopsis graminifolia	19		ns							0
Lepidium sp.	3		ns				1			1
Lophochloa cristata	24		ns							0
Lotus cruentis	2	-	.001		1		1		1	3
Medicago mimima	2	-	.001		1	-1	1		1	2
Millotia greevesii	4	-	.05							0
Myriocephalus rhizocephalus	4	-	.01							0
Omphalolappula concava	25	+	.01		1	-1				0
Phyllanthus sp.	2	-	.05	1			1			2
Pimelea simplex	2	ns			1		1			2
Plantago drummondii	29	-	.01		1		1			2
Portulaca oleracea	8	ns			1		1			2
Salsola kali	5	-	.05		1		1			2
Sclerolaena spp.	22	-	.001	1	1	-1	1			2
Sida spp.	4	ns			1		1			2
Solanum nigrum	1	ns			1		1			2
Stipa variabilis	26	-	.001		1		1			2
Swainsona phacoides	1	ns			1		1		1	3
Tetragonia tetragonioides	30	-	.001				1			1
Tragus australianus	19	ns			1	-1	1			1
Trianthema australis	11	ns			1		1			2
Tribulus terrestris	14	ns				-1				-1
Trigonella suavissima	1	-	.01		1		1		1	3
Triraphis mollis	23	+	.01		1					1
Vittadinia triloba	2	-	.01		1		1			2
Zygophyllum sp.	1	+	.01		1		1			2

G = Ability to remain green during dry periods
E = Erect habit
S = Spiney
SEED = Large seeds (>1mm long)
T = Toxic
N = Ability to fix nitrogen
TOT = Total susceptibility score

Table 3.2.4a. Number of species in each regression slope/susceptibility score category.

Slope of Regression of Species Frequency against Grazing Index		Susceptibility Score				
		-1	0	1	2	3
	-	0	1	3	10	2
	ns	1	7	10	4	0
	+	0	4	2	0	0

- = Species frequency decreases with grazing index,
ns = Species frequency shows no significant change with grazing index,
+ = Species frequency increases with grazing index.

Table 3.2.4b. Sign of difference between observed and expected values in cell and χ^2 values. Data for S.S. of -1 have been excluded since expected values for these cells would all have been less then one.

Slope of Regression of Species Frequency against Grazing Index		Susceptibility Score			
		0	1	2	3
	-	-2.69	-1.19	+4.41	+2.12
	ns	+0.22	+0.98	-1.18	-0.98
	+	+3.23	+0.004	-1.95	-0.28

Total $\chi^2 = 19.23$ c.f. $\chi^2_{(0.05,6)} = 12.59$

Table 3.2.5 The significance of logistic regression models relating grazing index to frequency of occurrence of rare species.

	RS	RS0	RS1	RS2	RS3
Coefficient of grazing index	-.49	-.44	-.22	-.37	-2.64
Change in deviance when grazing index added to null model	29.9	10.8	2.5	13.5	52.1
Significance level	<.001	<.01	ns	<.001	<.001

RS = All rare species included in analysis,
RS0 ... RS3 = Only rare species with a susceptibility score of 0 ... 3 included in analysis.

Fig.3.2.1 Location of study site.

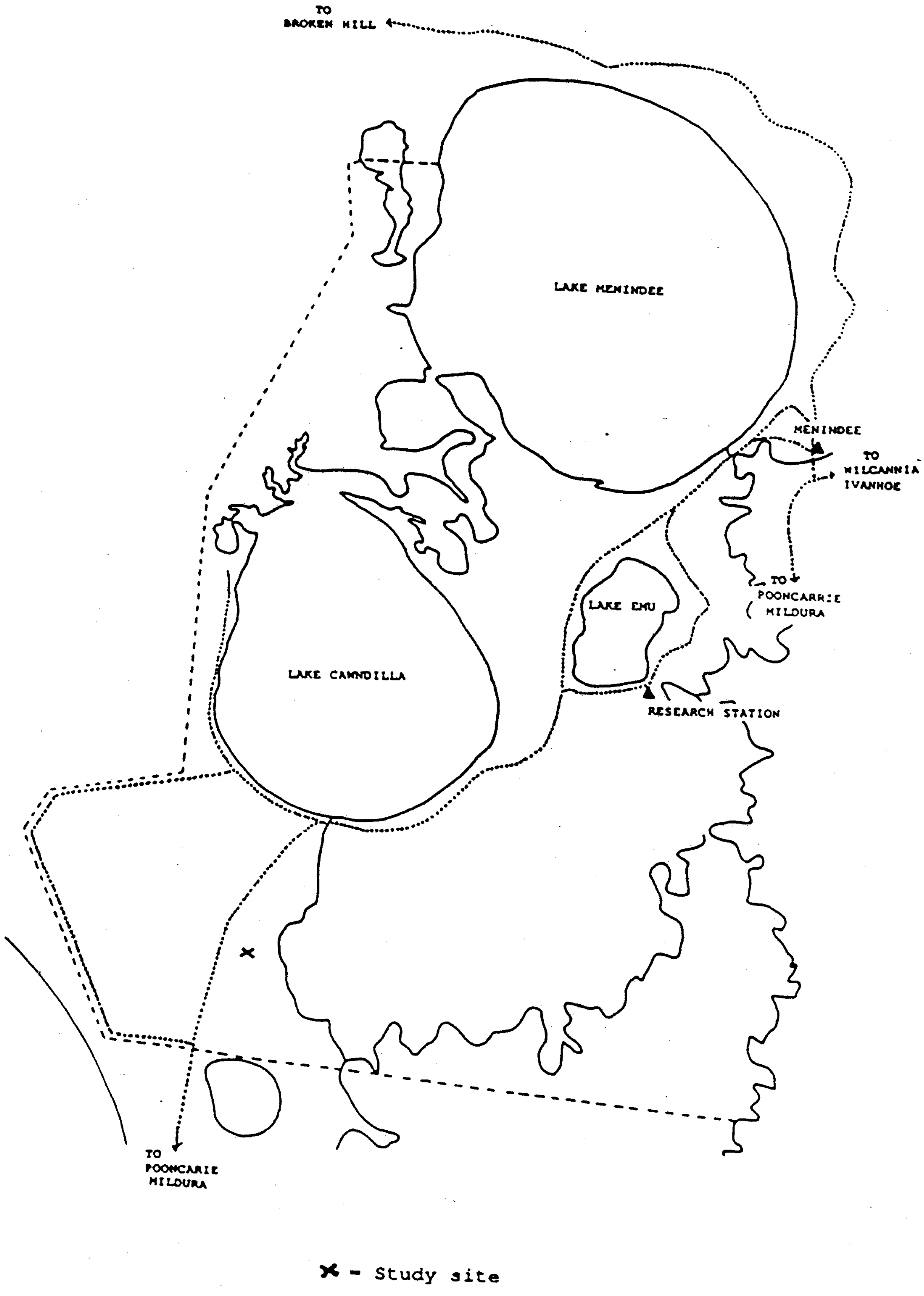


Fig.3.2.2 Location of rabbit warrens and vegetation sampling sites.

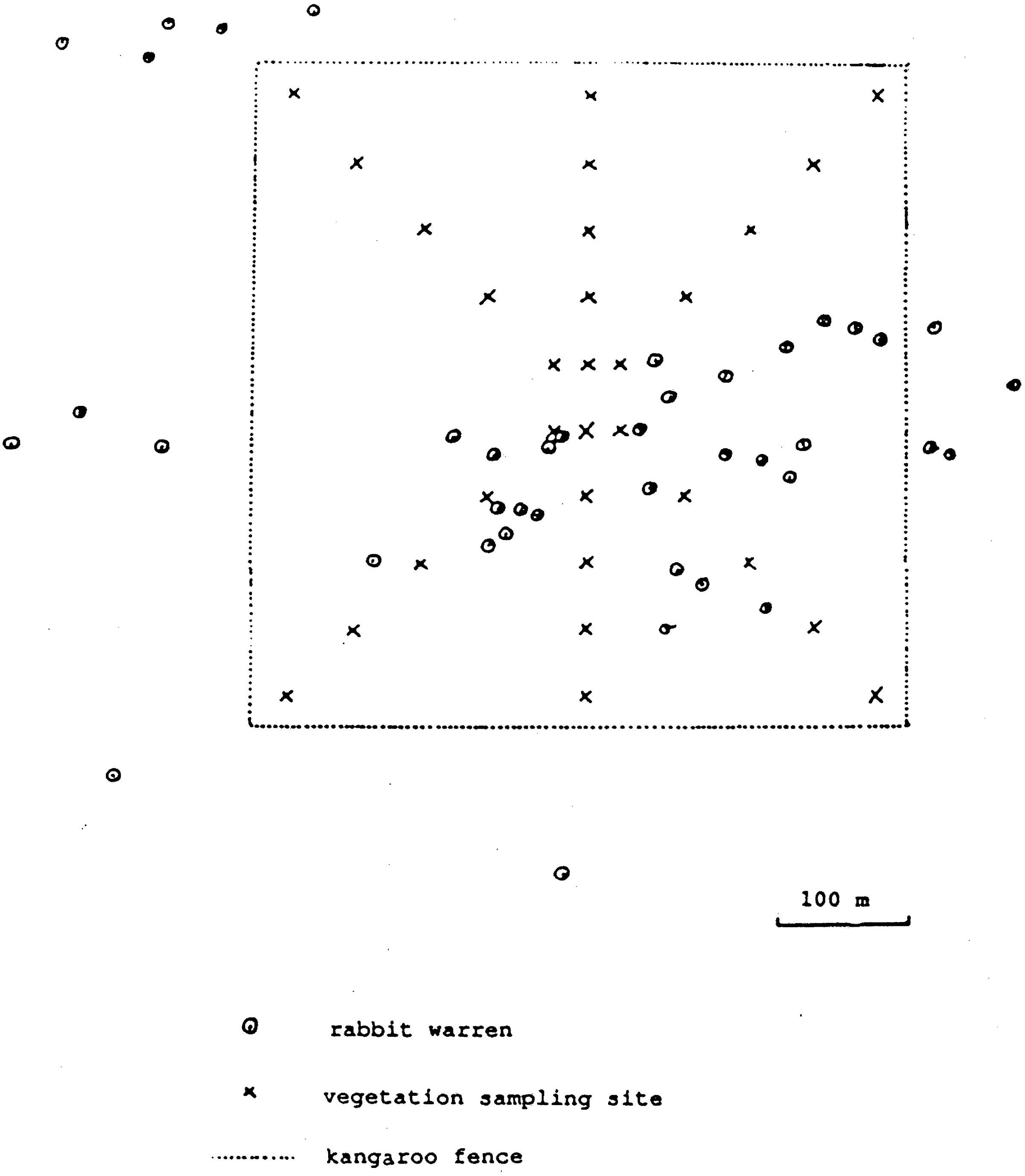
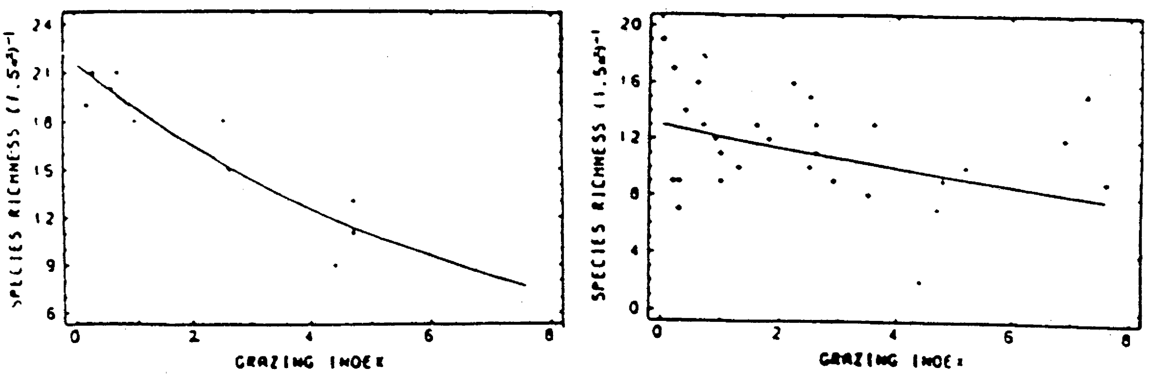
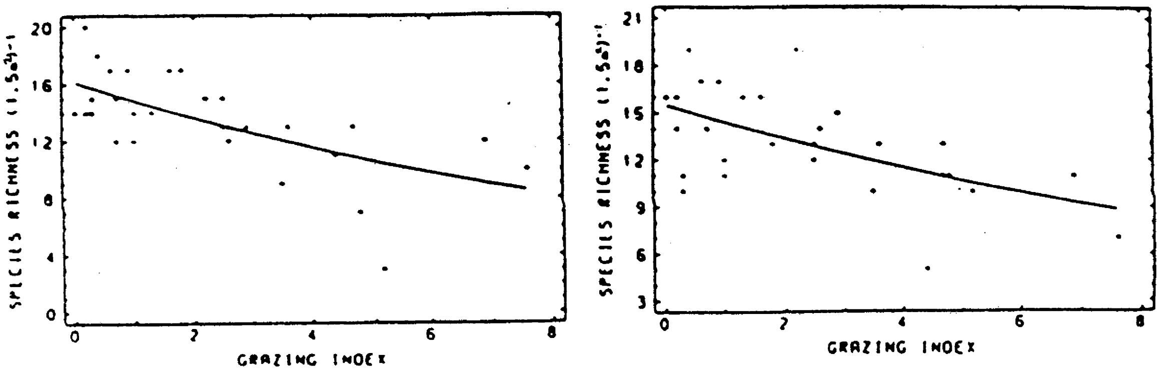


Fig.3.2.3 Measured and fitted values of species richness at different levels of grazing index.



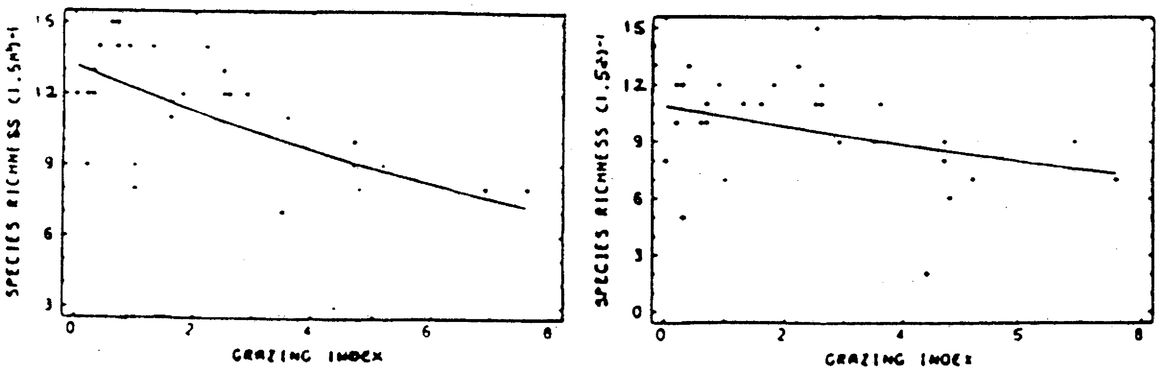
a) November 1983

b) June 1984



c) September 1984

d) November 1984



e) January 1985

f) March 1985

• = Measured values
—— = Fitted values

3. Effect of rabbits on vegetation close to warrens

The results of the grazing trials enabled me to draw conclusions about rabbit offtake and selectivity (Part 2, section 6). Predictions about the long term effects of rabbits on vegetation, based on these conclusions, were borne out by looking at vegetation changes along a gradient of past grazing pressure (Part 3, section 2). In this chapter, I describe an experiment designed to test predictions about the short term effect of rabbits on vegetation.

In order to detect a short term effect of rabbits, under natural conditions, I chose sampling sites where grazing pressure would be high. Since grazing pressure declines rapidly with distance from warrens (Part 3, section 1.2), I sampled vegetation close to two, large, well-used warrens. Even at peak rabbit densities, biomass changes at sites distant from warrens would have been too small to detect.

The results of the grazing gradient studies (Part 3, section 2) led to the prediction that vegetation close to warrens will be low in species susceptible to damage by rabbits. If susceptible species still exist in the seed bank close to warrens then protection from rabbit grazing would allow them to grow. This experiment allowed a test of these predictions.

Since palatability is a factor in susceptibility, it is likely that palatability will also be low close to warrens. If this is the case then offtake of any species will also be low. The predicted removal of any species can be calculated using the palatability indices and offtake model described in Part 2 and knowing the grazing pressure. This experiment was, therefore, designed to test predictions of offtake.

The gradients in vegetation with grazing index which are described in Part 3, section 2, might have been caused by differences in location relative to sand dune or proximity to trees rather than to differences in grazing pressure. In this experiment, I chose one warren which was in the open and one among trees. In air photographs of the area, the alignment of groups of trees in lines parallel to each other indicates their tendency to grow more densely on sand dunes. The locations of the two warrens in this experiment among different densities of trees (Fig.3.3.1) therefore enabled me to test whether location had affected the vegetation in this case. Similar vegetation types, or a higher number of species among trees, would provide some evidence that the gradients observed in Part 3,section 2 were not due to location.

The hypotheses to be tested were, therefore, as follows,

1. The vegetation close to the test warrens would consist largely of

non-susceptible species.

2. If seed banks of susceptible species are present, these species will be found growing more often in areas protected from rabbit grazing.

3. Offtake of individual species would be as predicted from the model described in Part 2.

4. The vegetation at both warren sites would be similar in species composition, despite differences in location relative to trees.

3.1 Methods

The information on warren entrances described in Part 3, section 1 was used to select two, large, well-used warrens within the kangaroo exclosure (Fig.3.3.1). In June 1984 fifteen 0.25 m^2 circular, rabbit- proof cages were set out in a circle round each warren at approximately 10 m from the warren centres. The exact location of each cage was determined randomly. Fifteen 0.25 m^2, circular quadrats were positioned within 0.5 m of each of the cages. Their positions were permanently marked with steel pegs.

In June, September and November of 1984 and in February and March of 1985 a list was made of all species present in the cages and quadrats. Where plants had been damaged and sharp edges remained, this was recorded as rabbit damage. The growth state of each species was also recorded as green, senescent or dead and with or without flowers or seeds.

At the second sampling time, the biomass of seven plant species was measured using the sampling technique described in Part 2, section 1. Measurements of four of those species were repeated at the third sampling time.

On each sampling occasion, rabbit numbers were estimated by the mark and recapture technique for warren 1 but this was not successful for warren 2 due to poor trap success and disturbance of traps by foxes. Rabbits were trapped and tagged with numbered chicken wing tags over two consecutive nights and were again trapped on a third night. Numbers of adult rabbits and kittens were estimated by standard mark and recapture analysis techniques (Caughley 1976). At low rabbit numbers this is only a very rough estimate but the estimates obtained in this way augmented the estimates made using number of active entrances (Part 3, section 1).

3.2 Results

The species present at the five sampling times, both inside and outside the cages, and at each of the two warrens, are given in Appendix 6, Table 6.1. The growth state of each species at each time and the presence of rabbit damage are given in Appendix 6, Table 6.2.

The biomasses measured in September and November 1984 are given in Appendix 6, Table 6.3.

The position of the two study warrens is given in Fig.3.3.1.

The estimates of rabbit numbers for the two warrens are given in Table 3.3.1.

3.3 Discussion

3.3.1 Susceptibility of species growing near the warrens

In order to test the hypothesis that the species growing around the warrens would be of low susceptibility, I compared the susceptibility scores (SS) of the species growing outside the cages with those of all the species measured at my sampling sites (Part 3, section 2). Table 3.3.2 lists the observed number of species found outside the cages at the warren sites. It also gives the numbers that would be expected if the proportions of species possessing each susceptiblity score were the same as those for the exclosure as a whole. A χ^2 test shows that the species growing around the warrens were, on average, significantly less susceptible to grazing than the species growing in the whole exclosure ($P = 0.024$).

Only three species (out of 22) had a susceptibility score of more than 1. *Phyllanthus* sp., *Plantago drummondii* and *Sclerolaena* spp. all had susceptibility scores of two. *Phyllanthus* sp. occured in only two quadrats. These three species may be protected by growth features which were not considered in the calculation of susceptibility score. Such features might be the basal meristems of *Plantago drummondii*, a high fibre content of the *Sclerolaena* spp. and possible toxicity of *Phyllanthus* sp.. *Phyllanthus* sp. ranked a very low palatability index in the second grazing trial (Table 3.3.3).

Three other species were recorded inside cages only. These were *Atriplex* sp. (SS=3), *Goodenia cycloptera* (SS=2) and *Stipa variabilis* (SS=2). From the start of the experiment i.e. before rabbits had had a chance to cause differences between caged and uncaged quadrats, *Stipa variabilis* was present only inside cages hence its absence outside was a function of sampling. The occurrence of the other two species indicates that their seeds persist in, or disperse into, even the most heavily grazed areas, although they grew in only one quadrat each.

3.3.2 Biomass removal

I constructed a model of rabbit offtake from the vegetation present round the warrens in September 1984 by using the palatability indices calculated for the second grazing trial which was carried out at roughly the same time. I assumed that the biomasses of each of the seven species measured in the fifteen uncaged quadrats at each warren represented the real biomass at this distance from the warrens. I then assumed that the average number of rabbits occupying each warren, between times 2 and 3, was six (Table 3.3.1) and calculated the effective grazing pressure due to this number of rabbits at 10 m from a warren. To do this I used the model of decline in rabbit use with distance from a warren which I derived in Part 3, section 1. The effective grazing pressure at 10 m was 7.3 rabbits ha^{-1}. I then calculated the change in biomass of each species which would be expected in two months assuming an offtake rate of 100 g $rabbit^{-1}d^{-1}$.

At both sites, the biomasses of all the species in the model declined by very small amounts (Table 3.3.4). Such differences would not have been detected by the sampling techniques which I was using. *Enneapogon avenaceus* is the only species which occurred in sufficient cages and quadrats to test this. For this species I tested for a cage effect by fitting a linear regression between the biomass at time 2 and the biomass at time 3. A significant deviation of the slope from unity would indicate growth or a decline in biomass. I then compared the slopes of the linear regressions fitted to the cage data with those fitted to the uncaged data. A significant difference would indicate a cage effect. A statistical comparison of the regressions (Sokal and Rolfe 1969, p.441) showed no significant differences at either warren for *Enneapogon avenaceus.*

The remaining species for which palatability indices were measured in grazing trial 2 were of low palatability (Table 3.3.3). The model, therefore, predicted no measurable cage effect for these species also. Between times 2 and 3 the presence/absence information shows no trends due to cageing (Table 3.3.3). This does not necessarily mean that there was no rabbit effect merely that monitoring of presence/absence was not sufficient to detect one. The evidence of rabbit damage to five species (Table 3.3.3) shows that some grazing did occur. Later differences between caged and uncaged quadrats are as likely to have been due to microclimatic effects as to cageing.

Since all the species present had low palatability indices (Table 3.3.3), I decided to investigate the case of a species with a high palatability index (such as *Convolvulus* sp.). I chose a palatability index value of 40 (somewhat more than 31.5, the palatability index of *Convolvulus erubescens*, and the highest index in the second grazing trial). I then calculated its change in biomass under rabbit grazing assuming that the rest of the pasture remained the same. I calculated the biomass changes at both high and low biomass of the imaginary species. The results, over two months, are given in Table 3.3.5. The imaginary species declined markedly. These results suggest that highly palatable plant species would be expected to show significant declines in abundance over two months. The proportionate decline in biomass would be greater for a species which was not plentiful.

3.3.3 Effect of location on species composition

The final hypothesis I tested was that the vegetation at both warrens would be the same despite one being near trees and one being out in the open. Of the 22 species which grew outside the cages, three species were not common to both warren sites. These were *Babbagia acroptera*, *Helipterum jessenii* and *Phyllanthus* sp.. All of these species are rare i.e. they occurred in only one quadrat at any time. Of the three species which came up only within cages, *Stipa variabilis* occurred at both warren sites whereas *Goodenia cycloptera* and *Atriplex* sp. occurred only at warren 2 (near trees, dune slope). The species composition at the two sites was therefore similar despite the different environments of the two warrens. The greater number of species found inside the cages at warren 2 (dune slope) is the opposite to the effect that would be expected if the gradients described in Part 3, section 2 were due to location.

This supports the conclusion that the vegetation gradients are not due to location but to rabbit grazing.

3.4 Conclusions

1. Only non-susceptible species grew close to both warrens. Despite this, there are limited seed banks of some susceptible species which might lead to these species returning to the pasture if rabbit grazing were removed.

2. For the species for which sufficient measurements of biomass were made, there was no detectable effect on biomass of protection from grazing. Neither was an effect of cageing on species frequency detected. These results are consistent with predictions of rabbit offtake of individual species made using the offake and selection model described in Part 2, section 2.

3. Two warrens in different environments do not have large differences in species composition although a few, more susceptible, species grew at the warren which was amongst trees (dune slope). This supports the conclusion that vegetation changes with grazing index are not caused by concomitant changes in topography.

Table 3.3.1 Estimates of numbers of rabbits occupying the two study warrens.

		June 1984	Sept 1984	Nov 1984	Jan 1985	Feb 1985
Number of active entrances	W1	9	9	13	3	4
	W2	4	8	11	6	8
Population estimated from the above	W1	5	5	8	2	3
	W2	3	5	7	4	5
Population estimate from trapping (Warren 1)	A	2	2*1	10	9	5*2
	K	4	12	10	0	0

W1 = Warren 1 W2 = Warren 2
A = Adults K = Kittens
*1 = Numbers of adults undetermined since only kittens trapped.
*2 = Numbers uncertain due to low retrap numbers.

Table 3.3.2 Observed and expected numbers of species with each susceptibility score occuring in uncaged quadrats.

Susceptibility Score	Expected Number	Observed Number
-1	0.3	0
0	5.1	10
1	6.4	9
2	8.1	3
3	2	0

$\chi^2 = 11.27$, c.f. $\chi^2_{(0.05,1)} = 3.84$

Table 3.3.3 Number of occurrences of each species at both sites on the second and third sampling times. Also palatability indices and species showing signs of damage by rabbits (*).

Species	CAGED Sept 1984	CAGED Nov 1984	OPEN Sept 1984	OPEN Nov 1984	P.I. Sept 1984
Atriplex sp.	1	1	0	0	
Boerhavia diffusa	0	3	1	2	6.0
Brachycome lineariloba	29	25	26	23	
Calotis hispidula	1	3	2	3	
Chenopodium melanocarpum	1	1	2	0	1.2
Craspedia pleiocephala	21	28	12	20	0.8
Crassula colorata	10	3	12	1	
Daucus glochidiatus	11	2	11	2	2.4
Enneapogon avenaceus *	25	27	28	27	2.0
Eragrostis dielsii *	2	4	5	3	1.0
Goodenia cycloptera	0	1	0	0	
Helipterum floribundum	1	7	3	5	4.1
Helipterum moschatum	24	22	20	20	0.8
Lophochloa cristata	12	10	11	8	5.3
Myriocephalus rhizocephalus	7	0	5	0	
Omphalolappula concava	20	3	17	6	
Phyllanthus sp.	0	0	1	1	0.3
Plantago drummondii *	13	10	12	10	2.3
Sclerolaena spp. *	9	9	6	8	1.0
Stipa variabilis	7	6	0	0	
Tetragonia tetragonioides	8	4	11	6	
Tragus australianus	1	0	0	0	
Triraphis mollis *	8	6	4	3	

Table 3.3.4 Predicted decline in biomass of seven species present at time 2, due to rabbit grazing alone.

Biomass (kg ha^{-1}) - Warren 1

Week	Cras	Enn	Era	Hel	Lop	Pla	Scl
0	15.9	628.0	4.1	40.8	3.2	2.4	217.0
1	15.9	623.9	4.0	40.7	3.1	2.4	216.3
2	15.9	619.8	4.0	40.6	3.1	2.4	215.6
3	15.8	615.6	3.9	40.5	3.0	2.3	214.8
4	15.7	611.5	3.9	40.3	3.0	2.3	214.1
5	15.7	607.4	3.8	40.2	2.9	2.3	213.4
6	15.7	603.3	3.8	40.1	2.9	2.3	212.7
7	15.6	599.2	3.8	40.0	2.8	2.3	211.9
8	15.6	595.1	3.7	39.9	2.8	2.2	211.2

Biomass (kg ha^{-1}) - Warren 2

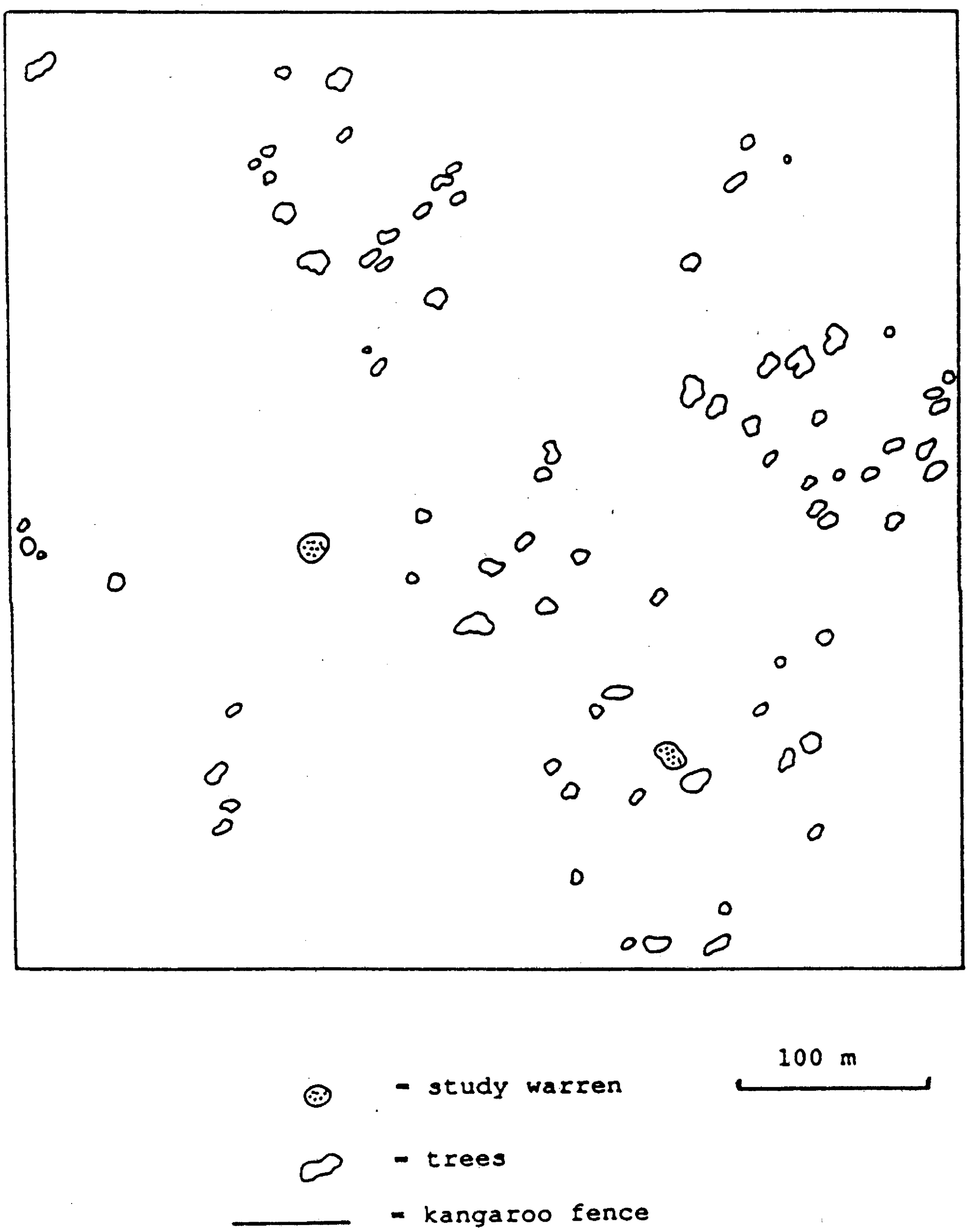
Week	Cras	Enn	Era	Hel	Lop	Pla	Scl
0	9.1	824.0	8.3	10.3	2.6	4.7	142.0
1	9.1	819.5	8.2	10.3	2.6	4.7	141.6
2	9.1	814.9	8.1	10.2	2.5	4.6	141.2
3	9.0	810.4	8.0	10.2	2.5	4.6	140.8
4	9.0	805.9	8.0	10.2	2.4	4.6	140.4
5	9.0	801.4	7.9	10.2	2.4	4.5	140.0
6	9.0	796.9	7.8	10.2	2.4	4.5	139.6
7	9.0	792.3	7.7	10.1	2.3	4.5	139.2
8	8.9	787.8	7.6	10.1	2.3	4.5	138.8

Table 3.3.5 Biomass decline of imaginary species with palatability index of 40 and different initial biomasses. Other species as at Warren 1.

Biomass (kg ha^{-1})

Week	SpX1	SpX2	SpX3
0	0.5	50.0	600.0
1	0.4	47.1	595.2
2	0.4	44.3	590.4
3	0.3	41.6	585.6
4	0.3	38.9	580.8
5	0.2	36.3	576.0
6	0.2	33.9	571.2
7	0.2	31.4	566.4
8	0.2	29.1	561.7

Fig.3.3.1 Location of study warrens and trees within kangaroo exclosure.



4. Effect on trees and shrubs

The grazing trials showed that rabbits tend to select for plants which remain green as others dry out. This means that tree and shrub seedlings are potentially at risk from rabbits during dry times. Lange and Graham (1983) found that Western Myall (*Acacia papyrocarpa*, Benth.) seedlings were selectively eaten by rabbits and Moore (1984) found that the rate of removal of planted seedlings was related to the distance from a rabbit warren. These results support the conclusion that rabbits can prevent the regeneration of trees whose seedlings possess no protection against rabbit grazing. Lange and Graham (1985) also found that seedlings which were 'protected' by tall grasses were less likely to be grazed by rabbits than those which were in the open. The conclusion that regeneration could take place in 'protected' areas is born out by my observations at my study site where *Pittosporum phylliraeoides* (native apricot) suckers sprouting round an adult had all grown up through a bluebush. When part of a seedling grew past the edge of the bush it almost invariably showed the sliced off edge which is characteristic of rabbit damage. Saplings and seedlings of the two commonest trees at Kinchega ; *Casuarina cristata* and *Heterodendrum oleifolium*, are seldom observed.

From the results of the grazing trials, I concluded that rabbits do not have a large effect on adult bluebushes. Since seedlings are more accessible and may have different salt, water and fibre contents than adults, this conclusion may not apply to seedlings.

In this chapter I describe an experiment designed to test the hypothesis that rabbits, under natural conditions, select for food with a high water content during dry times and that the rate of removal of such food is related to grazing index. I also describe an experiment designed to assess the effects of rabbits on naturally occurring bluebush seedlings. Lastly, I report on the results of a girth survey of *Casuarina cristata* and *Heterodendrum oleifolium* and draw some tentative conclusions about the effect of rabbits on these two species.

4.1 Methods

At each of the thirty vegetation sampling sites described in Part 3, section 2. I placed ten small (about 1 cm^3) pieces of carrot. Five were placed around each of the rabbit proof cages. This made it easy to locate the remaining carrot pieces the next day without actually marking the position of the carrot pieces. This was done on the 27th and 28th January 1985. The number of carrots remaining at each site was recorded the following morning. The vegetation at this time was dry (see rainfall record, Fig.3.1.2) but rabbit numbers were still relatively high (see Fig.3.1.2).

Bluebush seedling survival under rabbit grazing was monitored by tagging naturally regenerated seedlings occurring both inside, and close to, the rabbit proof cages at each of the vegetation monitoring sites. Bluebush seedlings were first seen at the study site in June 1984 and further seedlings were observed after this date. The seedlings monitored in this experiment were, therefore, no more than four months old since the first seedlings presumably germinated as a result of the high rainfall in January of 1984 (Fig.3.1.2=/). Small pieces of wire coated in coloured plastic were bent into a circle and placed over the seedlings. The tags were, therefore, at ground level so would have provided minimum interference to rabbits. A maximum of six seedlings was tagged within any cage or in the area near to any cage. At many sites fewer than five seedlings could be found in, or near to, cages. In these cases, all seedlings were tagged. The seedlings were first tagged on the 1st November 1984 and were monitored on the 25th January 1985. The number remaining in each cage or close to each cage was recorded and, where possible, fresh seedlings were tagged to replace the ones which had disappeared. The seedlings were again monitored on 17th March 1985.

The girth distributions of the populations of the two tree species growing within the kangaroo fence were determined by measuring the girth of all trunks about 10 cm above ground level. Many of these trees branch close to the ground hence the girth measurements had also to be made close to ground level.

4.2 Results

The number of carrots remaining at each of the sites on each day, together with the mean for both days, is given in Table 3.4.1. The grazing index for each site is also given.

The numbers of bluebush seedlings tagged, and subsequently recorded, both inside, and adjacent to, cages are given in Table 3.4.2.

The girth size distributions for the two tree species are shown in Fig.3.4.1.

4.3 Discussion

4.3.1 Selection for preferred food

On the first night that carrots were put out, at least one piece of carrot was removed from each site and on the second night, at least one piece of carrot was removed from all but one site (Table 3.4.1). The rabbits were, thus, rangeing widely. It is surprising, however, that the rabbits did not remove either all the carrots at a site or none at all. Their behaviour shows that they may have been able to detect the carrot pieces only within a small area since the carrot pieces were positioned up to three metres apart. If this were the case then the rate of disappearance should be related to the amount of time that rabbits spent in any one area. To test this I carried out regressions of the mean number of carrots left at each site against the grazing index associated with that site. The first attempt at the regression revealed that three sites (14,15 and 28) showed higher values for uneaten carrots than would be expected considering their high grazing indices. On inspection of the warren map (Fig.3.2.2) it was obvious that these sites were close to the warrens where I was trapping rabbits at the same time (see Part 3, section 3). Since this activity would almost certainly have upset the grazing behaviour of the rabbits in those warrens, I decided to exclude the three sites from the analysis.

I tested a linear, quadratic and exponential model of decline in carrots remaining with increasing grazing index. All three produced significant results but the exponential model gave the best fit ($r^2 = 0.38$, $P = 0.0007$) (Fig.3.4.2). The probability of a piece of carrot being eaten therefore increased with grazing index .

The rabbits were selecting for the carrot pieces since the proportion of carrot biomass removed was far greater than would be expected if the rabbits were eating the carrot pieces in proportion to their contribution to the biomass of the pasture. It seems, therefore, that rabbits are extremely good at finding some sorts of preferred food at such times. There is evidence that seedlings of at least some trees are attractive to rabbits (Lange and Graham 1983, Moore 1984). If rabbits are as able to find tree seedlings as carrot pieces then only a small proportion of seedlings would be expected to survive the times when rabbits are in relatively high numbers and are seeking such food. If tree seedlings remain accessible to rabbits for several years then the chance of them 'escaping' times of high rabbit numbers until they are too big to be affected, are small since it requires only two favourable years for rabbit numbers to reach peak levels (Part 3, section 1). Since tree seedlings also require favourable years to grow, the two events are likely to coincide. Seedlings will, however, have a higher probability of survival the further they are from rabbit warrens and at more than 200-300 metres they will most likely be unaffected by rabbits.

4.3.2 Removal of bluebush seedlings

Before looking at the immediate effect of rabbits on seedlings, I decided to test whether the density of bluebush seedlings was related to grazing index. Knowing that bluebush adults are little affected by rabbits, I did not expect to find a relationship since seed production should not be affected. The existence of a correlation would indicate either that regeneration is affected by position on a dune or that rabbits had had an effect on the seedlings prior to them being tagged. Even though the maximum number of seedlings tagged at any site was eighteen, I was able to look for such a relationship because, at most sites, there were less than eighteen seedlings and at many sites there were no seedlings. No correlation existed between seedling densities either inside or outside the cages and grazing index. This, therefore, provides evidence that seedling establishment is independent of grazing index.

In order to investigate the effect of the rabbit proof cages on the survival of seedlings, I carried out logistic regressions, using the statistical package GENSTAT, to look first for an effect of site on seedling establishment (i.e. were there significantly different numbers of seedlings at different sites?) and then for a cage effect. I also used a logistic regression to test for an effect of grazing index. Logistic regression analysis is the appropriate analysis in this case since the data are binomial (presence/absence) and because this technique implicitly weights the results for each quadrat according to the number of seedlings present at the start. I also looked for a subsidiary effect of presence adjacent to, or between, an adult bluebush.

When site was fitted to the null model of seedling survival, the deviance of the model was reduced from 44.3 to 15.4, ($P < 0.001$) for survival between the first and second sampling times and from 60.0 to 38.5 ($P < 0.001$) for survival between the second and third sampling times. Site, therefore, had a significant effect on seedling survival. When a cage factor was subsequently added to the models for the two time periods, the deviances were reduced by 15.45 ($P < 0.001$) and 13.4 ($P < 0.001$). Significantly more seedlings, therefore, survived inside cages than outside during both time intervals. Grazing index was not significantly correlated with seedling survival (P

> 0.999 for both time intervals). Location in relation to an adult bluebush had no effect on seedling survival (P = 0.18 and P = 0.13 for the first and second time intervals respectively).

These results show that seedlings growing inside cages had a greater chance of survival than those growing outside cages. Their survival, however, was not related to grazing index. Two possible causes of the cage effect are reduced grazing and/or disturbance by rabbits and improved microhabitat. Both these factors could apply to the cages. The seedlings which disappeared from the cages provide evidence that seedlings can die without the influence of rabbits.

If it is assumed that the reduced survival outside cages was caused by rabbits, then these results show that rabbits will not suppress bluebush regeneration completely. They may, however, reduce it by as much as 50% assuming that removal of some seedlings by rabbits does not increase the survival chances of the remaining seedlings. In order to be sure of these conclusions, however, the effect of microclimate would have to be separated from that of rabbits. The lack of a correlation between seedling survival and grazing index, and the fact that seedlings disappeared even inside cages, is evidence that rabbits alone may not have been responsible for the disappearance of seedlings outside cages.

4.3.3 Tree girth distributions

A population producing enough offspring to at least replace the present population must have the same number, or more, individuals in the young age classes than in the mature age classes unless pulsed recruitment is occurring. In interpreting the tree girth data for my study site, uncertainty arises in relating girth to age. The growth rates of arid zone trees have been little studied. Lange (1965) found that three *Callitris columellaris* trees growing near Woomera in central South Australia had produced approximately one growth ring per year. Apart from exceptional growth years, the mean growth ring width was 1.5 mm with a maximum of 3 mm. The mean growth rate was, therefore, about 1.5 mm increase in radius per year. The average rainfall at Lange's study site (<160 mm) is slightly lower than that at Kinchega (200 mm).

There are only two small trees (<40 cm girth) among the populations of both species of tree at my site (Fig.3.4.1). Assuming a growth rate of 1.5 mm per year, trees with a girth of 40 cm (radius = 63 mm) are about forty years old. Since both sheep and rabbits arrived in this area in the nineteenth century, the decline in recruitment is not likely to be due to either of these herbivores.

4.4 Conclusions

1. Rabbits, at moderate densities, can find and remove preferred food (carrot pieces) from a dry pasture even if the preferred food makes up only a small proportion of the total pasture biomass.

2. Rate of finding such preferred food increases with grazing index.

3. Cageing improved the survival of bluebush (*Maireana pyramidata*) seedlings in this study. There is insufficient evidence to distinguish between improved microhabitat and lack of rabbit grazing as the causal factor for the improved survival. A lack of correlation between grazing index and seedling survival and the death of some seedlings even inside cages suggests, however, that microhabitat was the more important.

4. Both *Casuarina cristata* and *Heterodendrum oleifolium* populations at my study site lack small individuals. The lack of regeneration spans at most the last forty years if growth rates are taken to be no less than 1.5 mm in radius per year. Since rabbits and sheep were present in the area long before 40 years ago, grazing is unlikely to account for this. There is, thus, no obvious evidence that rabbits or sheep have influenced regeneration.

Table 3.4.1. The number of carrot pieces remaining at each site on the mornings of 27th and 28th January.

Site	Grazing Index	Carrots remaining Day 1	Day 2	Mean
1	1.3	0	0	0
2	2.2	0	0	0
3	3.6	1	0	0.5
4	4.8	0	1	0.5
5	5.2	0	0	0
6	2.9	2	0	1
7	1.6	2	1	1.5
8	0.7	0	6	3
9	0.2	3	8	5.5
10	0.02	3	9	6
11	0.3	6	10	8
12	0.9	4	2	3
13	2.6	9	0	4.5
14 *	6.9	2	2	2
15 *	7.6	3	0	1.5
16	3.5	0	0	0
17	2.5	0	1	0.5
18	2.8	0	0	0
19	1.0	1	0	0.5
20	0.4	4	5	4
21	0.7	4	1	2.5
22	0.2	0	0	0
23	0.3	0	0	0
24	1.0	0	0	0
25	2.6	0	0	0
26	4.4	0	0	0
27	4.7	0	0	0
28 *	4.7	3	5	4
29	2.5	0	1	0.5
30	0.6	0	1	0.5

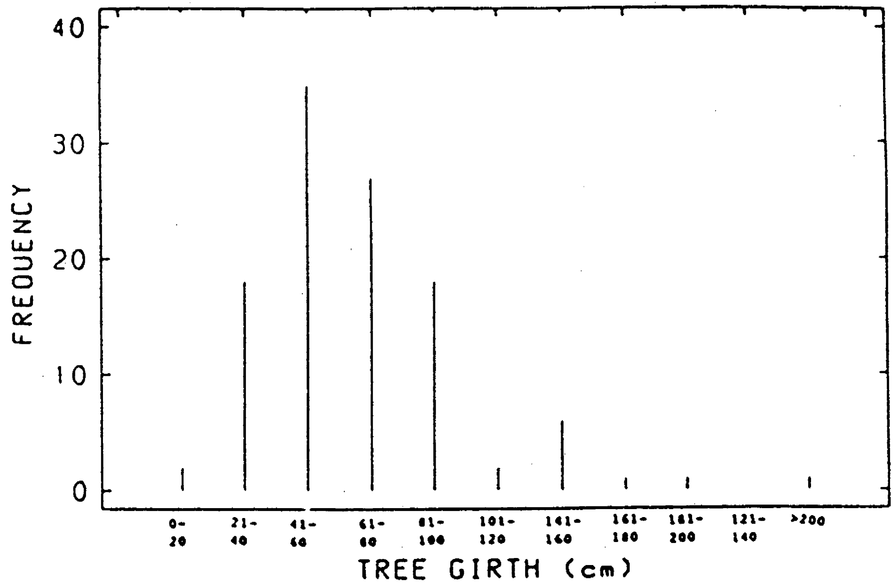
* = Excluded from analysis due to disturbance of site (see text).

Table 3.4.2. Numbers of bluebush seedlings tagged and subsequently recorded at each time.

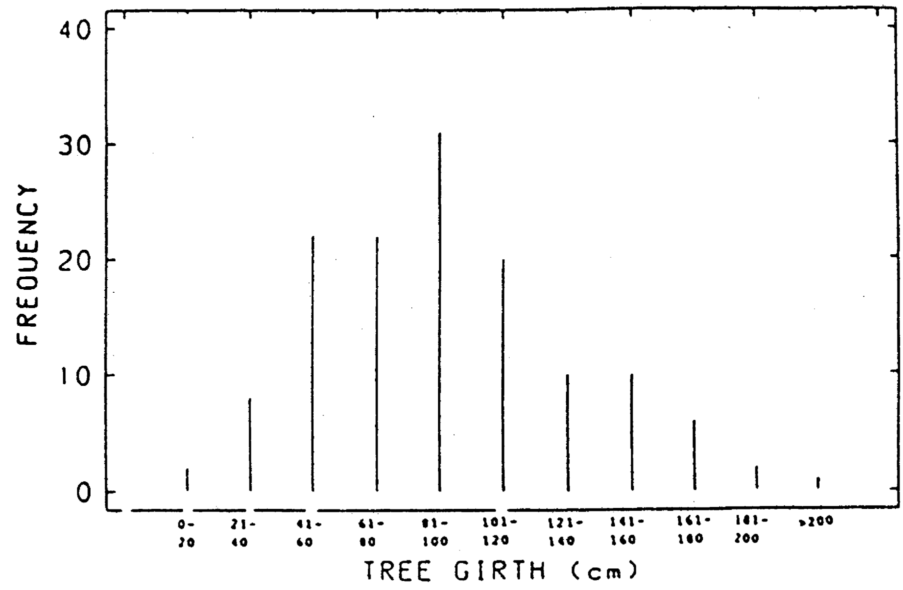
Site	Quadrat	1/11/84	25/1/85	17/3/85
1	BO	2	2	2
2	OC	1	1	0
2	BC	1	0*1	1
2	BO	5	2*3	2
6	OC	1	1	0
6	BO	3	3	0
6	BO	3	3	0
8	OC	1	1	1
8	BC	2	2	2
8	BO	6	4*2	6
9	OC	1	1	1
(2,2)	OO	3	1	0
(2,2)	OC	1	1	1
(2,2)	OO	3	1	0
(2,2)	BC	5	4*1	5
(2,2)	BO	5	0*5	4
(4,4)	BC	2	2	2
(4,4)	BO	6	6	5
(6,6)	BO	1	1	1
(7,7)	BO	3	3	3
(10,10)	BC	2	2	2
(10,10)	BO	2	2	1
(2,9)	BC	3	3	2
(2,9)	BO	3	3	1
(2,9)	OC	1	1	1
(5,6)	OC	1	1	1
(5,6)	BC	3	3	3
(5,6)	BO	3	3	3
(6,5)	BC	2	2	2
(6,5)	BO	5	0*1	0
(8,3)	BO	1	1	1
(9,2)	OO	1	0	0
(9,2)	BC	1	1	1
(9,2)	BO	1	0*1	0
(10,1)	BC	3	2	2

BC = cage next to bluebush, BO = open quadrat next to bluebush
OC = cage not next to bluebush, OO = open quadrat not next to bluebush.
0*1 = Zero seedlings remaining and one new one tagged.

Fig.3.4.1 Girth size distributions of *Heterodendrum oleifolium* and *Casuarina cristata* within the kangaroo exclosure.

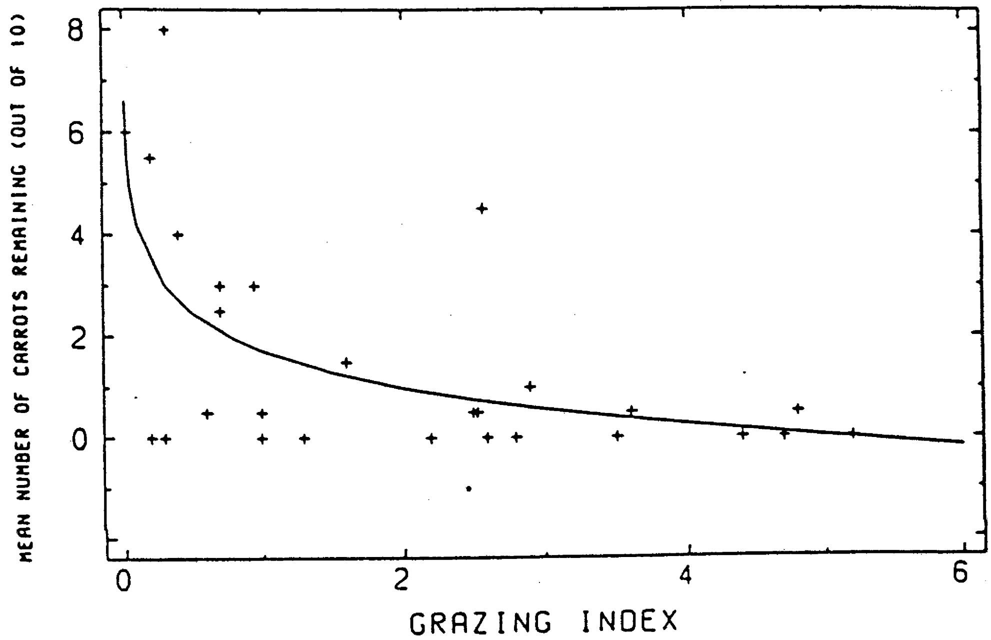


a) Heterodendrum oleifolium.



b) Casuarina cristata.

Fig.3.4.2 Relationship between number of carrots remaining and grazing index, excluding sites near warrens where rabbit trapping was in progress



Part 4

General discussion and conclusions

1. Introduction

The aim of this thesis, as outlined in the Part 1, was to assess the effects of rabbits on the vegetation of Kinchega National Park. The information gained was to be used to make predictions about the significance of rabbits to other components of the system. In particular it would be useful to managers to be able to make predictions about the effect of rabbits on the short and long term species composition of the pasture. It would also be useful to assess the degree to which rabbits can compete with other herbivores and with each other. Answering these questions would be helpful to both national park managers and graziers and may allow predictions to be made for areas other than Kinchega if sufficient process information is known.

The answers to some of the above questions are clearcut whereas those to others are dependent on the prevailing environmental conditions and on the magnitude of processes as yet unstudied. In this section I will summarize my conclusions regarding the effects of rabbits on the vegetation of Kinchega and will then discuss their use in answering the broader questions outlined above. This will lead to a statement of the areas in which information is lacking. The conclusions stated here rest on the assumptions discussed in the relevant sections. These will not be restated.

2. Effect on shrubs and trees

The evidence presented in this thesis (Part 2) shows that rabbits will have little effect on adult bluebushes (*Maireana pyramidata*). This conclusion is likely to be true for this species in any location where rabbits do not have access to water. It should not necessarily be extended to other species of chenopod shrub since *Maireana pyramidata* is considered to be one of the least palatable of the chenopod shrubs. The work reported on the effect on seedling bluebushes is not conclusive but suggests that rabbits will have an insignificant effect on regeneration of this species.

The tree girth data did not provide any evidence that rabbits have been affecting the regeneration of either *Heterodendrum oleifolium* or *Casuarina cristata*. The lack of saplings and seedlings of both these species is unexplained but need not be connected with rabbits. The rabbit's ability to find and eat highly palatable food when conditions are dry coupled with their preference for green feed at these times, is likely to lead to tree seedlings being at risk from rabbits. The lack of evidence for an effect of rabbits at my site should not, therefore, be considered as applying to other situations without further study.

3. Effect on ground layer vegetation

I concluded from the results of Part 2 that rabbits eat at least 100 g rabbit^{-1} d^{-1} dry weight and possibly up to about 180 g rabbit^{-1} d^{-1} when there is a green component in the pasture. The proportion of the diet which is made up of green material, is probably determined by the rabbit's need for a diet of >55% water and <40% fibre (Cooke 1974; 1982). Dry species, alone, cannot fulfill these requirements. Most species allow rabbits to maintain maximum offtake rates when green. The exceptions are the *Sclerolaena* spp. and toxic species. When *Sclerolaena* spp. are the only green plants available to rabbits, offtake per rabbit is below maximum. On such a diet, rabbits are likely to lose body condition and not breed. Numbers, therefore, will fall. When there is no green biomass of non-toxic species available, offtake will be very low and rabbits will lose condition quickly. At such times, rabbits numbers will fall rapidly as was recorded at the start of 1985 (Fig.3.1.2).

Rabbits can change the species composition of pastures in the short term since they graze selectively. Species most likely to be depleted are those which remain green as conditions become dry and are erect, non-spikey, non-toxic, and probably non-fibrous. An ability to fix nitrogen may also be a trait which leads to high palatability. If rainfall allows regrowth after defoliation then species with basal meristems will be able to resprout whereas those with aerial meristems will not. The latter, therefore, will be relatively more affected if conditions are suitable for regrowth.

There is evidence that, in the long term, rabbit grazing reduces species richness of pastures at Kinchega (Part 3, section 2). Species which are most susceptible to rabbit grazing are those which possess the traits listed above which make plants palatable to rabbits and which are least able to replenish seed banks when rabbit numbers are low. Such species are likely to be aerial seeders which produce few seeds.

The effect of rabbits declines with distance from rabbit warrens with the rate of decline being greatest near warrens. Areas outside rabbits' territories i.e. about 200 m from a warren, will suffer little effect of rabbits.

The influence of rabbits on species composition may have a long term effect on pasture biomass but too little is known about growth responses of individual arid zone species for predictions to be made in this regard. The rabbit's habit of digging up plant roots may cause a depletion of perennial species. Since these species respond more quickly to rainfalls than ephemerals, and can survive longer once conditions have dried out (Wellard 1987), this may affect the dynamics of pastures. I did not attempt to verify this hypothesis in this study.

4. Prediction of maximum short term effect on species composition

In order to assess the maximum effect of rabbits I have used the selection model $c_i/C = p_i{*}b_i/\Sigma p_i{*}b_i$ which was tested in Part 2, to make some predictions. I have assumed high rabbit densities and a pasture which would be subject to maximum offtake levels by individual rabbits and large differences between palatabilities of different pasture species. To do this, I chose to use the conditions of the second grazing trial since this trial contained many species possessing a wide range of palatabilities (Table 2.3.3). The presence of green vegetation also means that rabbits would be able to maintain condition and, if the pasture were growing, to breed. This conclusion is verified by the increasing rabbit numbers at the time of grazing trial 2 (Part 3, section 1.1). By the time that I ran the third grazing trial, rabbit numbers were declining hence any estimate of rabbit effect under similar conditions in the field would have to include an estimate of decline in grazing pressure with time. The green conditions of grazing trial 1 would not have remained long enough for rabbits to have a significant impact before conditions changed and when conditions are similar to those in grazing trial 4, rabbits will be at low densities. I, therefore, chose to use the conditions of grazing trial 2 to test the maximum potential impact of rabbits on vegetation. In running the model, I have assumed that palatabilities remained the same throughout. This rests on the assumption that green species remained green and dry ones remained dry. I have also assumed no growth. Such conditions would only occur if sufficient rainfall fell to prevent green plants from drying out but insufficient fell to allow growth. Although this is an unlikely event, it allows the prediction of a maximum rabbit effect. I ran the model at four different grazing pressures. Three of these are the predicted grazing pressures at 5, 10 and 20 metres from a warren with 30 entrances and 18 inhabitants (the maximum as calculated from Parer's (1982) equation). This was the size of the largest warren within my study area. The grazing pressures at these distances were equivalent to 55, 22 and 9 rabbits ha^{-1} as calculated using the relationship derived in Part 3, section 1. This assumes a circular territory with a radius of 240 metres which may be unrealistic for my study site (see Fig.3.2.2) where warrens were generally closer than 480 m. Most of them are, however, smaller than the 30 entrance warren used for the calculations of grazing pressure. Despite this, grazing pressures are likely to be higher than those stated above at the relevant distances from warrens since the mean maximum rabbit density at my study site was 5 rabbits ha^{-1} whereas the mean grazing pressure from a warren of 18 inhabitants with a 240 m radius circular territory, is 1.4 rabbits ha^{-1}. I have, therefore, also run the model at a grazing pressure of 100 rabbits ha^{-1}.

I set the initial biomasses to those of pen A in grazing trial 2 and used the model to calculate the biomasses of each species in the pasture after three months at the four grazing pressures. I assumed that rabbit offtake was 100 g rabbit^{-1} d^{-1} throughout. A higher offtake rate would have simulated the offtake in grazing trial 2 better but, since offtake would have been declining with time, an offtake rate of 100 g rabbit^{-1} d^{-1} was chosen as a reasonable approximation. It is possible, however, that a higher offtake would simulate reality better. The biomass did not reach the level at which offtake would have been less than 100 g rabbit^{-1} d^{-1} (Fig.2.6.1).

The resulting biomasses of each species after three months at the four grazing pressures are given in Table 4.4.1. The most palatable species showed marked declines in biomass especially at 100 and 55 rabbits ha^{-1}, however, no species completely disappeared except at these two highest grazing pressures. At these grazing pressures, the three most palatable species disappeared. At 9 rabbits ha^{-1}, most species suffered a reduction of less than 10%. The exceptions were *Convolvulus arvense*, *Convolvulus erubescens*, *Emex australis*, *Euphorbia drummondii*, *Sida* spp. and *Swainsona phacoides*. In the short term, therefore, rabbits will remove few species from the pasture except near large warrens and when rabbits are at high densities. High proportions of the most palatable species will, however, be removed at greater distances from warrens and this may influence pasture quality in the short term. The effect declines markedly with distance from warrens.It will become more significant for species which are also preferred by other herbivore species. If the affected species are the most nutritious, then rabbits could compete significantly with other herbivores by reducing pasture quality. Too little is known about the nutritional value of arid zone ground layer species to be able to say if the preferred species are also the most nutritious but it is likely that they are.

When rabbits are at low or moderate densities, they are unlikely to exert a large influence on pasture species composition within three months except close to warrens. Even a small effect, however, may influence seed set, hence long term species composition.

Table 4.4.1 Declines in the biomass of species present in the second grazing trial over three months as predicted by the offtake model for different grazing pressures. Biomasses in kg ha^{-1}. (X) = Week that biomass falls to zero.

Species	Initial biomass	Grazing pressure (rabbits ha^{-1}) 100	55	22	9	Percent Reduction at 9 r ha^{-1}
Boerhavia diffusa	9.8	0(10)	1.1	6.3	8.4	1.4
Calotis cymbacantha	41.8	0.15	16.6	34.3	39.1	6.4
Chenopodium melanocarpum	89.3	13.9	59.6	81.8	86.7	2.9
Convolvulus arvense	31.9	0(3)	0(9)	3.5	15.9	50.1
Convolvulus erubescens	17.9	0(3)	0(8)	1.4 8.	8.0	55.3
Craspedia pleiocephala	140	45.2	108	132	137	2.1
Daucus glochidiatus	21.0	0.2	9.1	17.6	19.8	5.7
Emex australianus	8.9	0(6)	0(12)	2.8	6.1	31.5
Enneapogon avenaceous	12.3	0.37	6.2	10.6	11.7	4.9
Eragrostis dielsii	33.1	7.6	23.9	30.8	32.3	2.4
Eragrostis sp.	30.1	0(12)	8.4	23.0	27.5	8.6
Euphorbia drummondii	9.0	0(9)	0.50	5.1	7.5	16.7
Helipterum floribundum	5.1	0(12)	1.2	3.8	4.6	9.8
Helipterum moschatum	83.5	24.4	63.3	78.6	81.8	2.0
Lophochloa cristata	18.3	0(11)	2.7	12.3	16.0	1.0
Phyllanthus sp.	8.7	5.9	7.9	8.5	8.6	1.1
Plantago drummondii	46.6	0.54	20.8	39.2	44.0	5.6
Salsola kali	42.5	11.3	31.6	39.8	41.6	2.1
Sclerolaena spp.	47.0	10.4	33.6	43.7	45.8	2.5

contd. overleaf

Species	Initial biomass	Grazing pressure (rabbits ha^{-1}) 100	55	22	9	Percent Reduction at 9 r ha^{-1}
Sida spp.	34.9	0(9)	1.8	19.6	28.8	17.5
Stipa variabilis	1.6	0.31	1.1	1.5	1.6	0.0
Swainsona phacoides	75.2	0(9)	4.5	43.2	62.6	16.7
Tetragonia tetragonioides	183	31.7	125	168	178.1	2.7
Total	992	152	527	808	913	7.96

5. Factors affecting the magnitude of intra- and inter-specific competition between herbivores

Figure 4.5.1 shows the major interactions which must be considered when attempting to build a dynamic model of an arid grazing system. Such a model would allow accurate prediction of the degree of competition between herbivores as well as prediction of the effects of herbivores on the other elements of the system. In this section I will discuss the state of our knowledge of the processes shown in Fig.4.5.1 and go on, in section 6, to make some predictions from a simple, static model.

5.1 Pasture growth and decay

Since competition between herbivores may, at times, be largely for plant biomass, rates of growth and dieback under different conditions must be known if the significance of a herbivore effect is to be assessed.

Rainfall over the previous 12 months can be used as an approximate predictor of plant biomass in chenopod shrublands (e.g. Wellard 1987; Noble 1977). Robertson (1987), using five years of data from Kinchega national park, found that adding a factor representing initial biomass improved the predictive value of the model since the rate of increase in biomass declined as initial biomass increased. Such a model can be made more realistic by using an index of soil moisture, rather than rainfall, to predict plant biomass. Noble and Crisp (1980) used a soil moisture index as a predictor of pasture biomass in an area of chenopod shrubland at Koonamore vegetation reserve in South Australia. The model was derived from 50 years of data and was based on the biomass of all the ground layer species. The vegetation at Koonamore is similar to that at Kinchega (Wellard 1987) hence this model may be an adequate predictor of plant biomass at Kinchega as well as at other arid zone sites. This needs to be tested.

5.2 Species composition and plant biomass

At Kinchega, species composition varies considerably (pers. obs.). It can range from a near monoculture of an ephemeral forb to a mixture of fifty species or more which may be dominated by ephemeral forbs or by more perennial grasses and *Sclerolaena* spp. (see Part 3, section 2). In order to avoid having to construct different empirical relationships between rainfall, or soil moisture, and plant biomass for each new area, or pasture type, of interest it is necessary to know the degree to which pastures differ in composition in time and space and to what extent these differences affect biomass production. The factors determining species composition are virtually unknown. Noble and Crisp (1980) were unable to predict species composition from the Koonamore records although they were able to accurately predict plant biomass. This suggests that species composition is relatively unimportant in prediction of plant biomass. Wellard (1987), however, found that perennial species grew and decayed more slowly than ephemeral species at Kinchega thus the ratio of perennial to ephemeral plants in the pasture would influence pasture biomass. It is possible that the vegetation at Koonamore was consistent in its proportions of these two components. Since grazing might affect this ratio, it is a factor which would have to be considered when making predictions of pasture biomass in grazed systems. Crisp (1975), found that temperature influenced the germination potential of most species at Koonamore but that there was large overlap between 'summer' and 'winter' species. Robertson (1987) considers that most species at Kinchega can germinate in any season but many of the perennial grasses will only germinate after a summer rainfall. The mulching effect of perennial species and their ability to resprout will also influence the magnitude of a response to a given rainfall.

5.3 Species composition and pasture quality

Species composition is also likely to influence the proportion of the pasture which remains green as well as pasture quality in general. This will influence herbivore condition. Little information is available on the nutritional value of arid zone pasture species.

5.4 Grazing and species composition

As was discussed in Part 1, section 1.5.5, grazing commonly reduces the proportion of palatable perennial species in a pasture. In the arid zone, perennial species are likely to disappear or behave like ephemerals under heavy grazing. This is because they decay more slowly than ephemerals (Wellard 1987) hence are grazed for longer when conditions are dry. The digging up of roots by rabbits may also reduce the quantities of perennials.

The influence of seed bank on species composition, and of grazing on seed bank, have been little studied although in Part 3, section 2, I provide some evidence that rabbits, probably through an effect on seed bank, have been able to change species composition.

The long-term effects of grazing by large herbivores on pasture species composition are difficult to study in the arid zone mostly because of the large natural changes in species composition. There is also a lack of areas which have never been grazed. Areas from which herbivores have only recently been excluded may lack the original seed bank hence may not be able to return to original pasture types. Exclosure studies show variable effects. Austin et al.(1981), working near Deniliquin in south western New South Wales, found exclosure for 20 years was beneficial to *Enteropogon acicularis* but had no effect on *Danthonia caespitosa.* Crisp (1975) found that, at Koonamore, indigenous annual herbs were favoured by protection and alien weeds were favoured by continuous grazing. By contrast, Leigh et al. (1979) studied the effect of sheep grazing at three different densities, over five years, on a property near Ivanhoe in western New South Wales. On comparison with sheep exclosures, they concluded that there had been few permanent differences in the composition of the pasture which had been caused by grazing. It is possible, however, that any changes would have taken longer than five years to become obvious.

5.5 Grazing and rates of growth and decay

Although we know how much biomass herbivores remove, we know little about the effect of grazing on rates of growth and decay. The effect of grazing on growth depends on the species being studied (see Belsky (1986) for a review of this subject) and on the grazing pressure. Grazing, by reducing transpirational losses or by maintaining the pasture in a juvenile state, may allow a pasture to stay green for longer. Newsome (1971) hypothesized that this effect could explain the apparent advantage to kangaroos in Central Australia of grazing in proximity to stock. Bosch (1984) found that *Enneapogon avenaceus*, in Central Australia, had highest total biomass production at intermediate levels of defoliation and that growth of defoliated plants was prolonged into dry periods in comparison with that of undefoliated plants. Any such effect would benefit rabbits. Grazing may also influence decay rates in the short term.

Grazing may have a long term effect on growth rates by influencing soil organic matter hence infiltration capacity. Crisp (1975) found that inside Koonamore vegetation reserve rooting depth was greater, and there was better infiltration, than outside the reserve. As a result, the total quantity of water available for plant growth was greater. This will affect both the species which can germinate and their growth and decay rates.

5.6 Herbivore population dynamics

Rabbit densities can be predicted using the information outlined in Part 1. Warren densities can also be used to estimate maximum rabbit densities for any site (Part 3, section 1).

Bayliss (1987), using seven years of population data from Kinchega, showed that the rate of increase in kangaroo populations can be related to amount of rainfall in the previous six months. The model has yet to be tested and testing may show that rainfall alone is sufficient to predict kangaroo densities at any site. Since kangaroo numbers declined only once during Bayliss' study, the data are unsuitable for predicting rates of decline since these will depend on all the factors shown in Fig.4.5.1 which determine pasture biomass and quality. Bayliss (1987) predicted kangaroo densities at Kinchega where they have access to water. Numbers are likely to decline faster where they do not have access to water.

Where rabbits <u>do</u> have access to water i.e. within about 200 m from water, they are likely to have a greater effect on both species composition and biomass than when they do not since numbers will remain high for longer. At Kinchega, at the start of the 1982/83 drought, rabbit populations remained high for longer in areas adjacent to water then in areas distant from water (pers. obs.). The rate of decline under such conditions will be determined mostly by predation and disease until the vegetation is entirely removed. Numbers will then fall rapidly. The effect on shrubs will also be much greater since bluebushes are eaten when water intake is high (see Part 2, section 2).

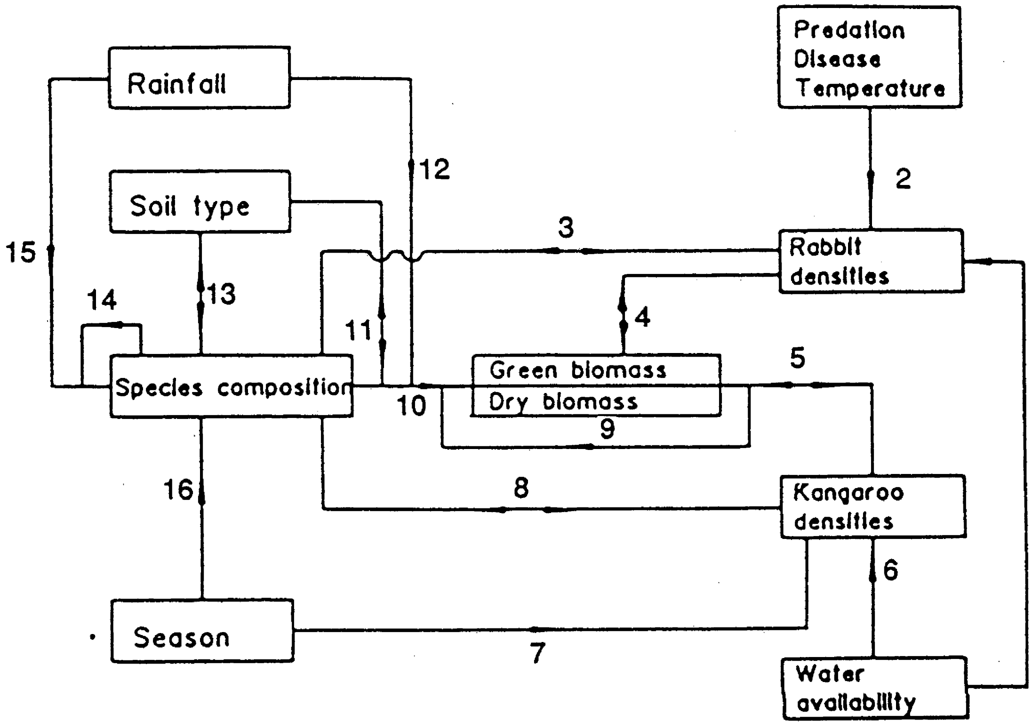
5.7 Pasture quality and competition

As has been stated in the previous section, the degree of competition which results from the selective grazing of rabbits cannot be assessed without more information about the nutritional value of different plant species. We do know, however, that rabbits without access to water need sufficient green feed such that their diet contains about 55 % water (Cooke 1974; 1982) and that they select for green vegetation. It follows, therefore, that when a pasture contains no green vegetation, rabbit numbers will fall rapidly.

Kangaroos and sheep do not have the same dietary water requirements as rabbits when they have access to free water. As a result, they can survive longer than rabbits once pastures are completely dry. The rate at which they lose condition will, however, depend on pasture quality. The total extent of competition between rabbits and other herbivores cannot, therefore, be evaluated since the effect of changes in species composition and depletion of green biomass on the condition of other herbivores, is unknown. Shepherd (1987) found that both red (*Macropus rufus*) and western grey (*Macropus fuliginosus*) kangaroos had lost condition, as measured by a kidney fat index, by the start of the 1982/83 drought at Kinchega. This index did not, however, indicate a further loss of condition until the last three months of the drought when pasture biomass was extremely low (about 9 kg ha^{-1} (Robertson 1987) at the end of the drought). Kangaroos, therefore, may lose condition quickly when there is a lack of green feed. Competition with rabbits for such material may, thus, be significant in determining the length of time that kangaroos can survive on dry feed. Alternatively, kangaroos may suffer more from the reduced biomass caused by rabbit grazing, since a reduction in biomass would reduce the time for which kangaroos would have access to dry feed.

It is also likely that kangaroos and sheep show intra- and inter- specific competition for the most nutritious components of the pasture. Leigh et al. (1979), found that sheep grazing a belah-rosewood woodland showed lower productivity per sheep as sheep grazing pressure was increased. They also found that sheep preferred green grasses and forbs when available. This has also been shown to be the case for kangaroos (Newsome 1971). It seems highly likely, therefore, that sheep and kangaroos will compete with rabbits for green vegetation during dry times.

Fig.4.5.1 Schematic representation of arid zone grazing system.



Key to Relationships

1.The effect of water availability on rabbit numbers is discussed in Part 1, section 1.3.6.

2.The effects of predation, disease and temperature on rabbit populations are discussed in Part 1, sections 1.3.3, 1.3.7 and 1.3.8.

3. Pasture species composition affects both pasture biomass and proportion of the pasture which remains green during dry periods. The latter is likely to affect rabbit numbers (see Part 1, section 1.3.2). Differences between different plant species in their nutritional value are also likely to affect rabbit condition hence also survival and reproductive success.

Evidence presented in this thesis supports the hypothesis that rabbit grazing can affect species composition.

4. Rabbits without access to water require green vegetation to maintain condition. Since rabbits eat green vegetation they reduce its biomass.

5. If there is insufficient pasture biomass, kangaroos will not be able to maintain adequate intake and will lose condition and breeding potential.

Kangaroos, by eating pasture, reduce its biomass.

6. Kangaroos require free water when conditions are dry but will travel several kilometres to reach it (Pridell 1987).

7. Grey kangaroos (*Macropus fuliginosus*) are seasonal breeders.

8. The quality of a pasture is affected by its species composition. Pasture quality will affect kangaroo condition. Kangaroos are selective feeders (Short pers. com.) hence will influence species composition of a pasture.

9. Standing green pasture biomass affects growth rates hence future biomass.

10. See 3 above.

11. Soils affect plant species composition and biomass through their water holding abilities and nutrient availabilities.

Plant species composition and biomass have long term effects on soils by influencing organic matter content hence also water holding capacity and nutrient content.

12. Rainfall is essential for plant growth and can be related to pasture biomass (Wellard 1987; Noble 1977).

13. As 11.

14. Species composition is likely to influence future species composition via seed bank and presence of perennial parts.

15. The amount and distribution of rainfall is likely to influence species composition via differing moisture requirements for seed germination of different plant species.

16. Temperature is likely to differentially influence germination and/or establishment of different pasture species.

6. Intra- and inter-specific competition: some predictions

In order to build a dynamic model of the system described above, more information would be required in the following five areas.

a. The determinants of species composition and its interactions with the other components of the system.

b. The effects of grazing on rates of growth and decay

c. The effects of grazing on pasture quality.

d. The important factors determining pasture quality for different herbivores.

e. The effects of declining pasture quality on herbivore condition and survival.

At present, it is only possible to make predictions regarding the extent of competition between rabbits and kangaroos if assumptions are made about the nature of the processes listed above.

I have chosen to calculate the potential for competition between rabbits and kangaroos when it will be at its greatest. This will be when both herbivore species are at high densities and when pasture biomass is low and not increasing. I have, therefore, chosen herbivore densities to be maximum, the vegetation to be at intermediate biomass and the proportion of green biomass to be similar to that in grazing trial 2 (i.e. 30%). Robertson (pers. com.) estimated an intermediate growth flush to be about 400-500 kg ha^{-1} so I have assumed a pasture biomass of 450 kg ha^{-1} which is about half that present in grazing trial 2.

Bayliss (1987) estimated kangaroo densities at Kinchega to have been about 0.6 ha^{-1} at the start of the 1982 drought. At this time kangaroo numbers were at the highest recorded for the park and were at densities similar to those of sheep outside the park (Bayliss 1985). I have used three levels of rabbit density, all of which are high, and compared them with the situation without rabbit grazing. The rabbit densities were set at 10, 20 and 35 ha^{-1}. The first density is higher than the maximum densities I calculated for my study sites of 5 and 8 ha^{-1}, but is possible for the area considering the approximate nature of the estimate. The density of 35 rabbits ha^{-1} is the maximum rabbit density recorded in arid Australia (Cooke unpubl.). I have assumed no rainfall, hence no growth, during the period of the calculations.

Decay was assumed to be at a rate of 0.64 % per day. Noble (1977) estimated that decay rates at Koonamore were at about 0.5 % per day without rain and 0.64 % per day on wet days. The rate used is equivalent to 10 % of the biomass being left after a year.

Green biomass was assumed to dry off at a rate of 1.3 % per day. This is equivalent to 10 % of the green biomass being left after six months. This rate is a conservative one since Noble (1977) estimated drying off to be at twice this rate. I have assumed that grazing has no effect on rates of decay or drying off. The effect on growth is not relevant since I have assumed no growth.

I have further assumed that rabbits eat 100 g rabbit^{-1} d^{-1}, that they eat only green biomass and that numbers fall to zero as soon as all the green biomass is removed. I have assumed an average offtake by kangaroos of 0.85 kg kangaroo^{-1} d^{-1} (Short 1987) and have run the model with two levels of selectivity for green biomass. These were no preference and a preference for green biomass ten times that for dry biomass. Kangaroos were taken to survive at initial densities until all the pasture biomass fell to zero.

Having thus defined the system, the survival times of rabbits and kangaroos are given in Table 4.6.1 and shown in Fig.4.6.1 together with the amount of green biomass which each of the two species will have consumed before numbers fall to zero.

The questions which can be asked of this model relate to the effect of varying rabbit density on:

1. rabbit survival;
2. kangaroo survival;
3. amount of green biomass eaten by rabbits;
4. amount of green biomass eaten by kangaroos;
5. the effect of kangaroo selectivity on the above.

6.1 Effect of rabbit density on rabbit survival

Figure 6.1a shows that the time rabbits survive falls rapidly with increases in density up to about 10 ha^{-1} but less rapidly thereafter. Increased selectivity for green forage by kangaroos reduces rabbit survival, especially at low densities of rabbits, but the effect is small.

6.2 Effect of rabbit density on kangaroo survival

Kangaroo survival time declines as rabbit densities increase but the increased survival time is not proportional to rabbit density. At 10 rabbits ha^{-1}, kangaroos survive 1.5 months less than if there are no rabbits but at higher rabbit densities, the reduced survival time of kangaroos is negligible. This decreasing effect is due to the earlier deaths of rabbits at higher densities.

If there are no rabbits then the model predicts that kangaroos survive longer if they do not select for green biomass. This is because the dry vegetation decays whereas the green biomass dries out and, as such, is still available. The kangaroos therefore have access to more biomass if they do not select. If there are rabbits, then kangaroos survive longer if they do select for green biomass since they then eat a proportion of the green biomass which would otherwise mostly be eaten by rabbits. Kangaroo selectivity, however, does not have a large effect on kangaroo survival times.

6.3 Effect of rabbit density on quantity of green biomass eaten by rabbits.

The higher the rabbit density, the larger the quantity of green biomass which they consume (Fig.4.6.1b). Amount consumed does not increase linearly, however, because, at higher rabbit densities, although they consume green biomass faster, they also die out sooner.

A kangaroo preference for green vegetation causes a decline in rabbit offtake but not a large one.

6.4 Effect of rabbit density on quantity of green biomass eaten by kangaroos.

The quantity of green biomass eaten by kangaroos declines rapidly as the density of rabbits increases. Even relatively low numbers of rabbits can greatly reduce the intake of high quality diet by kangaroos. Above 10 rabbits ha^{-1} there is little further effect of rabbit density on green biomass consumed by kangaroos.

Kangaroo selectivity has a large effect on the green biomass eaten by kangaroos, particularly when rabbit density is low. At higher rabbit densities, rabbits remove green biomass so quickly that kangaroo selectivity has less effect on the total amount of green biomass which they eat.

6.5 Conclusions from the model and discussion of assumptions

The model makes the assumption that kangaroo mortality is solely dependent on the availability of any biomass. This is unlikely to be true in view of the likely influence of pasture quality on kangaroo condition. If this assumption were true, however, the model predicts that rabbits do not shorten kangaroo survival by more than about 2 months (i.e. about 20%) even at very high density.

The effect of rabbits on kangaroo diet quality may be judged by the competition for green biomass. Without rabbits, kangaroos have access to larger quantities of green biomass. This may enable them to maintain better condition and to live longer as biomass declines or when it runs out. There is insufficient information at present to quantify this effect but the model predicts that a rise in rabbit density will have maximum effect on kangaroo diet quality at rabbit densities less than 10 rabbits ha^{-1}.

The rate of drying of the green vegetation used in the model may be lower than is likely in reality and be particularly low in comparison to rates of dry-off in summer. A faster rate of drying would lead to a smaller effect of rabbits on kangaroos and would mean that a combination of drying out and rabbits would remove all the green vegetation sooner.

In the model I assumed that rabbits eat only green vegetation and that all green vegetation provides a maintenance diet for rabbits. The grazing trials showed that rabbits will also eat some dry vegetation when there is a good supply of green vegetation. This would mean that they would live longer than the model predicts especially at densities where the removal of green vegetation by rabbits is of greater importance than is drying off, in depleting the total amounts of green biomass i.e. at higher rabbit densities. They would then have a larger effect on kangaroos. At low rabbit densities, this behaviour will have little effect on kangaroo, or rabbit, survival time since under these conditions, rabbits die out only shortly before the pasture would otherwise dry out completely. Total biomass removal by rabbits would, therefore, be increased only slightly, under low rabbit densities, if rabbits were also eating dry material.

As has been discussed in Part 4, section 3, rabbits are unlikely to be able to maintain condition on a diet of *Sclerolaena* spp., even when green, thus a more realistic model would show, not instantaneous die off of rabbits, but a slow decline when rabbits were eating only these species. Without this refinement the model provides an assessment of maximum rabbit effect.

The conclusions relating to competition with kangaroos can also be applied to sheep since, although an individual sheep eats more than a kangaroo, the total grazing pressure of kangaroos used in this model was similar to the grazing pressure of sheep outside Kinchega.

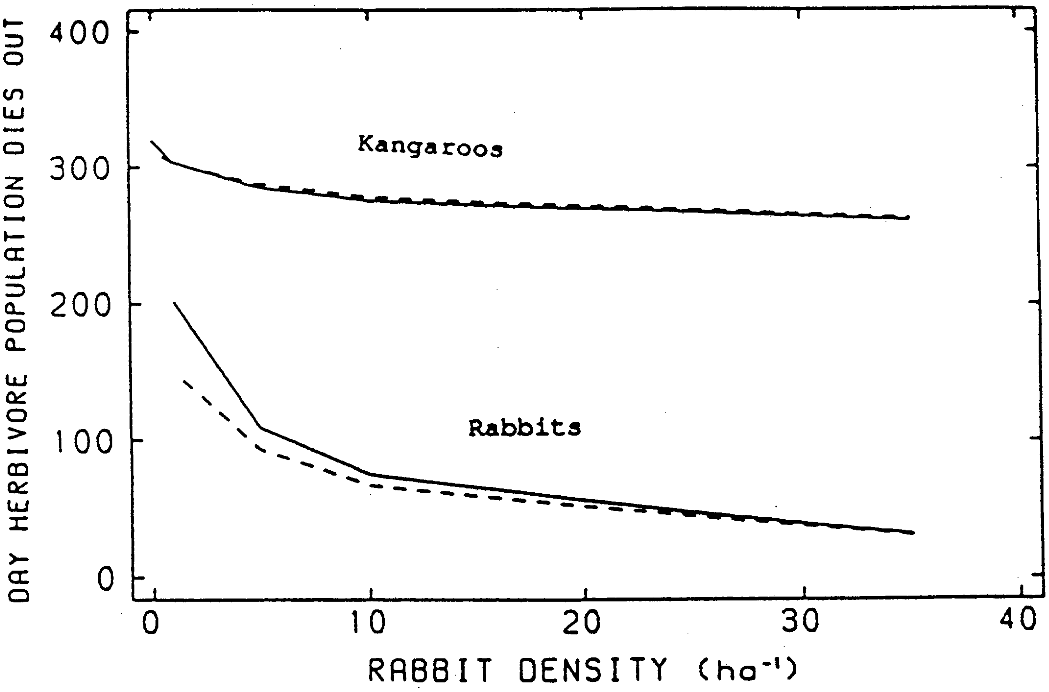
This model represents the most likely situation when rabbits will compete with other herbivores. It is also possible, however, that rabbits will compete with other herbivores for a new growth flush. If the new growth is from seed, and not from resprouting perennials, then it is likely that rabbits will be in low numbers since their food supply will have been low for some time. If the growth flush is from perennials as well as from seed, then it will be too rapid for rabbits to prevent it from occurring as was demonstrated in grazing trial 4 (Part 2, section 5). The only situation where rabbits may be able to compete for a new growth flush will be if there is a series of small growth flushes sufficient to allow rabbit numbers to increase but insufficient to 'escape' from the grazers. Such a series of small growth flushes is an unlikely event.

Table 4.6.1 Projected survival times of rabbits and kangaroos under different grazing regimes and amounts of green biomass eaten by the two herbivore species. Initial biomass = 450 kg ha^{-1}.

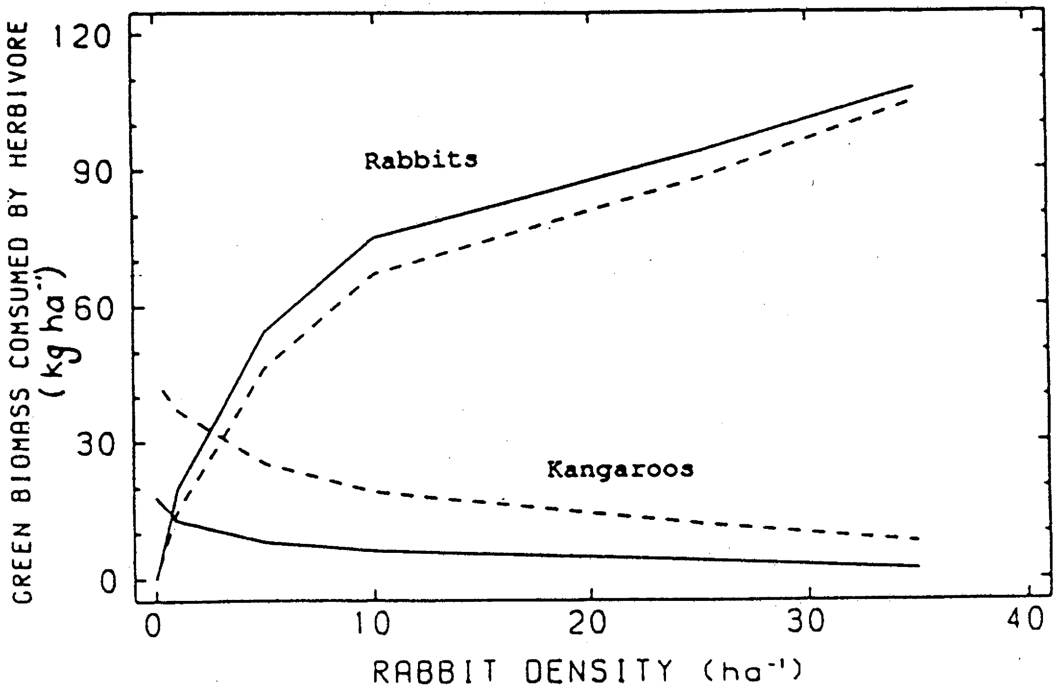
Rabbit density	0		10		20		35	
Kangaroo preference ratio	1	10	1	10	1	10	1	10
Day rabbit population falls to zero	-	-	75	67	47	44	31	30
Day kangaroo population falls to zero	320	312	275	278	267	269	261	263
Green biomass consumed by rabbits (kg ha^{-1})	0	0	75	67	94	88	108	105
Green biomass consumed by kangaroos (kg ha^{-1})	18	44	6	19	4	12	2	8

Fig.4.6.1 Predicted relationship between rabbit density and other components of the model described in section 6.

a) Survival time of rabbits and kangaroos.



b) Green biomass consumed by rabbits and kangaroos.



——— = Kangaroo preference value = 1
------- = Kangaroo preference value = 10

7. Conclusions

The effect of rabbits on the vegetation of Kinchega is described in detail in Parts 2 and 3. Rabbits were found to have little effect on adult bluebushes. There was no evidence that rabbits would prevent regeneration of bluebushes or of either of the two tree species present at the study site. Rabbits ate at least 100 g rabbit^{-1}d^{-1} dry weight if pastures contained a green component. Offtake as high as 180 g rabbit^{-1} d^{-1} was recorded on a mature pasture with a green component. Only *Sclerolaena* spp. and toxic species did not allow this maximum offtake when green. Rabbits selected for species which remained green as conditions dried out and were erect, non-toxic, and non-spiny. An ability to fix nitrogen may also have increased palatability and high fibre content may have decreased it. Evidence was found that rabbits, over the long term, have reduced pasture species richness by causing declines in frequency of occurrence of the most palatable species.

The models described in Part 4, sections 4 and 6 are an attempt to quantify the effects of rabbits on pasture biomass and species composition. They lead to the conclusion that rabbits can have a large effect on pasture species composition where grazing pressure is high such as close to warrens. This is likely to influence the condition of both rabbits and other herbivores. Competition with other herbivores, therefore, cannot be assessed solely in terms of the relative quantities of biomass which are eaten by the different species. The effects of rabbits on the nutritional quality of pastures must also be considered.

For a given decline in rabbit density, the amount of green feed available to other herbivores increases as rabbit density declines. If green biomass is taken to represent the highest quality component of the pasture then increases in density when rabbit numbers are low will have a greater relative effect on pasture quality than increases when numbers are high. The quantity of green biomass available to other herbivores decreases only minimally with increasing rabbit numbers at high rabbit densities (above about 10 rabbits ha^{-1}).

Even if other herbivore species suffer from rabbits only in terms of reduced total biomass, the necessity for rabbits to have green feed leads to the conclusion that increases in rabbit density at high rabbit densities (also above about 10 rabbits ha^{-1}) have minimal effect on kangaroo survival time.

The model described above provides a basis from which the cost-effectiveness of rabbit control could be assessed. It shows that rabbit control may have little effect on other herbivores if rabbit densities are not decreased to below about 10 rabbits ha^{-1}. Below this density, the benefit from rabbit control, for a given decline in rabbit density, is greater at low rabbit densities. It is, therefore, highly advantageous to control rabbits when they are in low numbers. The most effective time to control rabbits would, therefore, be when they are already in low numbers, such as during dry times. At such times, the rabbit's preference for food with a high water content and its well developed searching ability might be used to attract rabbits to poisoned bait.

The competition model is a simple one which would gain in the accuracy of its predictions if more information were available in the areas listed in section 6 and if this were incorporated into the model. Until this can be done, the predictions must remain tentative.

In terms of management for conservation purposes, rabbits probably have less effect on the biomass ratio of perennial to ephemeral vegetation than do large herbivores since rabbits die out sooner than larger herbivores during dry times and this is when the vegetative parts of perennials are most at risk from grazing. Since the quantity of perennials affects the moisture relations of the soil and the growth response to a given rainfall event, rabbits may be less able to influence the biomass dynamics of pastures than are the large herbivores. The effect of rabbits digging up roots may be similar to continued grazing but this was not investigated in this study. Decreased densities of large herbivores would allow rabbits to survive longer into dry periods. This might lead to increased rabbit densities at other times since larger populations of rabbits would survive droughts hence the breeding population at the start of the next breeding season would also be larger. It is possible, however, that, at lower densities of large herbivores, the vegetation would become taller and dry out more quickly. This would be disadvantageous to rabbits.

Since rabbits affect species composition, rabbit control might be considered as an option in conservation areas in order to encourage plant species which are sensitive to rabbit grazing and to increase species richness in arid areas such as Kinchega. It is possible that some species would not increase if rabbit grazing were depressed but seed banks of most species exist in areas outside the influence of warrens and the experience at Wyperfeldt National Park (Cochrane & McDonald 1966) showed that species susceptible to rabbits could increase if rabbits were removed.

Bibliography

Andrew M.H., Noble I.R. & Lange R.T. (1979) A non-destructive method for estimating the weight of forage on shrubs. Aust. Rangel. J. **1**(3), 225-31.

Austin M.P., Williams O.B. & Belbin L. (1981) Grassland dynamics under sheep grazing in an Australian Mediterranean type climate. Vegetatio **47**, 201-11.

Bayliss P. (1985) The population dynamics of red and western grey kangaroos in arid New South Wales, Australia. 1. Population trends and rainfall. J. Anim. Ecol. **54**, 111-25.

Bayliss P. (1987) Kangaroo dynamics. In: Kangaroos; their ecology and management in the sheep rangelands of Australia. (Caughley G.C.,Shepherd N.C., Short J.C. Eds.). C.U.P.

Black C.A., Evans D.D., Ensminger L.E. & White J.L. (1965) Methods of soil analysis. Part 1. Physical and mineralogical properties,including statistics of measurement and sampling. American Society of Agronomy. Madison, Wisconsin, U.S.A. No.9 in the series AGRONOMY. 777 pp.

Bosch O.J.H. (1984) Defoliation and its effect on *Enneapogon avenaceus* populations during the short growth periods in Central Australia. In: Working papers, Second international rangeland congress, Adelaide, Australia. Section 9.

Bowler J.M. (1982) Aridity in the late Tertiary and Quaternary of Australia. In: Evolution of the Flora and Fauna of Arid Australia.(Barker W.R., Greenslade P.J.M. Eds.). Peacock publications, Melbourne. pp. 35-45.

Campbell D.A. (1978) Pasture species zonation associated with rabbit dunghills on the Northern Tablelands of N.S.W. Dip. Sci. Agric. thesis. University of New England.

Caughley G. (1976) Analysis of vertebrate populations. A Wiley-Interscience publication. 234 pp.

Caughley G.C, Shepherd N.C. & Short J.C (Eds.) (1987) Kangaroos; their ecology and management in the sheep rangelands of Australia. C.U.P.

Cochrane G.R. & McDonald N.H.E (1966) A regeneration study in the Victorian mallee. Vic. Nat. **83**, 220-26.

Cooke B.D. (1974) Food and other resources of the wild rabbit. Ph.D. thesis. University of Adelaide. 131 pp.

Cooke B.D. (1977) Factors limiting the distribution of the wild rabbit in Australia. Proc. Ecol. Soc. Aust. **10**, 113-20.

Cooke B.D. (1981) Rabbit control and the conservation of native mallee vegetation on roadsides in South Austalia. Aust. Wild. Res. **8**, 627-36.

Cooke B.D. (1982) Reduction of food intake and other physiological responses to a restriction of drinking water in captive wild rabbits. Aust. Wild. Res. **9**, 247-52.

Crisp M.D. (1975) Long term change in arid zone vegetation at Koonamore, South Australia. Ph.D thesis, University of Adelaide.

Cunningham G.M., Mulham W.E., Milthorpe P.L. & Leigh J.H. (1981) Plants of Western New South Wales. N.S.W. Government Printing Office. 766 pp.

Daly J.C. (1981) Social organization and genetic structure in a rabbit population. In: Proceedings of the World Lagomorph conference held in Guelph, Ontario, August 1979 (K. Myers Ed.). pp. 90-97.

Dunnet G.M. (1957) A test of the recapture method of estimating the number of rabbits in a warren. C.S.I.R.O. Wild. Res. **2**, 90-100.

Dunsmore J.D. (1974) The rabbit in subalpine south-eastern Australia 1.Population structure and productivity. Aust. Wild. Res. 1, 1-16.

Farrow E.P. (1917) On the ecology of the vegetation of Breckland. III General effects of rabbits on the vegetation. J. Ecol. **5**(1) 1-18.

Fenner F. (1983) Biological control, as exemplified by smallpox eradication and myxomatosis. Proc. R. Soc. Lond. **B218**, 259-285.

Fenner F., Marshall I.D. & Woodroofe G.M. (1953) Studies in the epidemiology of infectious myxomatosis of rabbits. 1.Recovery of Australian wild rabbits from myxomatosis under field conditions. J. of Hyg. **51**, 15-242.

Foran B.D., Low W.A. & Strong B.W. (1985) The response of rabbit populations and vegetation to rabbit control on a calcareous shrubby grassland in Central Australia. Aust. Wild. Res. **12**, 237-47.

Friedel M.H. (1985) The population structure and density of Central Australian trees and shrubs, and relationships to range condition, rabbit abundance and soil. Aust. Rangel. J. 7(2), 130-39.

Fullagar P.J. (1981) Methods for studying the behaviour of rabbits in a 33-ha enclosure at Canberra and under natural conditions at Calindary in N.S.W. In: Proceedings of the World Lagomorph conference held in Guelph, Ontario, August 1979 (K. Myers Ed.). pp. 240-55.

Gibb J.A. (1977) Factors affecting population density of the wild rabbit and their relevance to small mammals. In: Evolutionary ecology. (B.Stonehouse, C.M. Perrins Eds.) The Macmillan Press, London. pp 33-46.

Gibb J.A., Ward G.D. & Ward C.P. (1969) An experiment in the control of a sparse population of wild rabbits in New Zealand. N.Z. J. Sci.**12**, 509-534.

Gillham M.E. (1955) Ecology of the Pembrokeshire Islands. III The Effect of grazing on the vegetation. J. Ecol. **43**, 172-206.

Grayson F.W.L. & Hassall M. (1985) Effect of rabbit grazing on population variables of *Chorthippus brunneus*. Oikos. **44**, 27-34.

Hayward J.S. (1961) The ability of the wild rabbit to survive conditions of water restriction. C.S.I.R.O. Wild. Res. **6**(2), 160-75.

Hughes R.L. & Rowley I. (1966) Breeding season of female wild rabbits in natural populations in the Riverina and Southern Tablelands districts of N.S.W. C.S.I.R.O. Wild. Res. **11**, 1-10.

Johnston T.N. (1969) The effect of sheep and rabbit grazing on regeneration of white cypress pine (*Callitris columellaris*). Aus. For. Res. **4**(2), 3-12.

King D.R. (1984) Rabbit kitten survival in the South West. W.A. Dept. Agr. J. Agr. 1, 9-11.

King D.R. & Wheeler S.H. (1985) The European rabbit in South-Western Australia. 1. Study sites and population dynamics. Aust. Wild. Res. **12** , 183-96.

Lange R.T. (1965) Growth ring characteristics in an arid zone conifer. Trans. Roy. Soc. Aust. **89**, 133-37.

Lange R.T. (1967) Nitrogen, Sodium and Potassium in foliage from some semi-arid and temperate zone shrubs. Aust. J. Biol. Sc. **20**, 1029-32.

Lange R.T. & Graham C.R. (1983) Rabbits and the failure of regeneration in Australian arid zone acacia. Aust. J. Ecol. **8**, 377-81.

Leigh J.H. (1972) Saltbush and other chenopod browse shrubs. In: The use of trees and shrubs in the dry country of Australia. (Ed. N.Hall). pp 284-98.

Leigh J.H., Wilson A.D. & Mulham W.E. (1979) A study of sheep grazing a belah (*Casuarina cristata*) - rosewood (*Heterodendrum oleifolium*) woodland in Western New South Wales. Aust. J. Agric. Res. **30**,1223-36.

Lloyd H.G. (1981) Biological observations on post-myxomatosis wild rabbit populations in Britain, 1955-79. In: Proceedings of the World Lagomorph conference held in Guelph, Ontario, August 1979 (K. Myers Ed.). pp. 623-32.

Martin J.T. (1977) The ecology of the wild rabbit at three locations in a semi-arid environment. M.Sc. thesis. University of Sydney.

McIntosh D.L. (1966) The digestibility of two roughages and the rates of passage of their residues by the red kangaroo, Megaleia rufa(Desmarest), and the merino sheep. C.S.I.R.O. Wild. Res. **11**, 125-35.

Moore A.D. (1984) The grazing of arid zone acacia seedlings by rabbits : a simulation model and the process of grazing at the level of the individual. B.Sc. (Hons) thesis. Uni. of Adelaide. 140 pp.

Myers K. (1961) Rabbit biology and behaviour and their bearing on control. In: Rabbit control symposium - Sydney 1960. pp 26-33.

Myers K. (1970) The rabbit in Australia. In: Proc. Adv.Study Inst. Dynamics Numbers Popul. pp 478-506.

Myers K. (1981) Proceedings of the World Lagomorph conference held in Guelph, Ontario, August 1979. University of Guelph, Canada. 983 pp.

Myers K. & Parker B.S. (1965) A study of the biology of the wild rabbit in climatically different regions in Eastern Australia. I. Patterns of distribution. C.S.I.R.O. Wild. Res. **10**, 1-32.

Myers K. & Parker B.S. (1975a) A study of the biology of the wild rabbit in climatically different regions in Eastern Australia. VI Changes in numbers and distribution related to climate and land systems in semi-arid North Western N.S.W. Aust. Wild. Res. **2**, 11-32.

Myers K. & Parker B.S. (1975b) Effect of severe drought on rabbit numbers and distribution in a refuge area in semi-arid North-Western New South Wales. Aust. Wild. Res. **2**, 103-20.

Myers K. & Poole W.E. (1962) A study of the biology of the wild rabbit in confined populations. III Reproduction. Aust J. Zool. **10**, 225-267.

Myers K. & Poole W.E. (1963) A study of the biology of the wild rabbit in confined populations. IV The effects of rabbit grazing on sown pastures. J. Ecol. **51**, 455-51.

Newsome A.E. (1971) Competition between wildlife and domestic livestock. Aust. Vet. J. **47**, 577-86.

Noble I.R. (1975) Computer simulations of sheep grazing in the arid zone. Ph.D. thesis, University of Adelaide.

Noble I.R. (1977) Long-term biomass dynamics in an arid chenopod shrub community at Koonamore, South Australia. Aus. J. Bot. **25**, 639-53.

Noble I.R. & Crisp M.D. (1980) Germination and growth models of short-lived grass and forb populations based on long term photo-point data at Koonamore, South Australia. Israel J. Bot. **28**, 195-210.

Noy-Meir I. (1973) Desert ecosystems: Environment and Producers. Ann. Rev. Ecol. Syst. **4**, 25-51.

Parer I. (1982a) Dispersal of the wild rabbit at Urana in New South Wales. Aust. Wild. Res. **9**, 427-41.

Parer I. (1982b) European rabbit (Australia). In: 'C.R.C.' handbook of census methods for terrestrial vertebrates. (David E. Davis Ed.).C.R.C. Press: Florida. pp 136-38.

Parer I & Libke J.A. (1985) Distribution of rabbit warrens in relation to soil type. Aust. Wild. Res. **12** , 387-405.

Parer I & Wood D.H. (1986) Further observations on the uses of warren entrances as an index of the number of rabbits (*Oryctolagus cuniculus*). Aust. Wild. Res. **13**,

Phillips W.M. (1953) The effect of rabbit grazing on a re-seeded pasture. J. Brit. Grass. Soc. **8**, 169-81.

Pielou E.C. (1969) An introduction to mathematical ecology. Wiley-Interscience, New York.

Poole W.E. (1960) Breeding of the wild rabbit (*Oryctolagus cuniculus*) in relation to the environment. C.S.I.R.O. Wild. Res. **5**, 21-43.

Priddel D. (1983) The movement of red and western grey kangaroos in Western New South Wales. Ph.D. thesis. University of Sydney.

Richards G.C. (1979) Variation in water turnover by wild rabbits in an arid environment due to season, age group and reproductive condition. Aust. Wild. Res. **6**, 289-96.

Robertson G. (1987) Plant dynamics. In: Kangaroos; their ecology and management in the sheep rangelands of Australia. (G.C Caughley, N.C. Shepherd & J.C Short Eds.). C.U.P.

Robertson G., Short J. & Wellard G. (1987) The environment of the Australian sheep rangelands. In: Kangaroos; their ecology and management in the sheep rangelands of Australia. (G.C Caughley, N.C. Shepherd & J.C Short Eds.). C.U.P.

Rogers P.M (1981) Ecology of the European wild rabbit in Mediterranean habitats. II. Distribution in the landscape of the Camargue, S.France. J. Appl. Ecol. **18**, 355-71.

Rogers P.M. & Myers K. (1979) Ecology of the European wild rabbit in Mediterranean habitats. 1. Distribution in the landscape of the Coto Donana, S.Spain. J. Appl. Ecol. **16**, 691-703.

Rolls E.C. (1969) They all ran wild. Angus and Robertson, Sydney.

Shepherd N. (1983) An investigation of some aspects of capture myopathy in the red kangaroo (*Macropus rufus*). Ph.D. thesis. University of Sydney.

Shepherd N. (1987) Condition and recruitment of kangaroos. In: Kangaroos; their ecology and management in the sheep rangelands of Australia. (G.C Caughley, N.C. Shepherd & J.C Short Eds.). C.U.P.

Short J. (1985) The functional response of kangaroos, sheep and rabbits in an arid grazing system. J. Appl. Ecol. **22**, 435-47.

Sokal R.R. & Rohlf F. (1969) Biometry. W.H. Freeman and Co. 776 pp.

Southern H.N. (1955) A Britain without rabbits ? Discovery 16, 186-89.

Stafford Smith M. (1984) Behavioural ecology of sheep in the Australian arid zone. Ph.D. thesis, A.N.U.

Stanley R.J. & Milthorpe P.L. (1977) The effects of climate and grazing by rabbits on survival and growth of black bluebush seedlings at Menindee in western N.S.W. In: Aust. Rangelands Soc. second conf., Broken Hill. July 8, 1977. pp 129-38.

Stodart E. & Myers K. (1966) The effects of different foods on confined populations of rabbits (*Oryctolagus cuniculus* (L.)). C.S.I.R.O. Wild. Res. **11**, 111-124.

Thomson H.V. (1951) Rabbits and other rodents. Ann. App. Biol. 38, 725-27.

Walter M.R., Martinet L., Moret B. & Thibault C. (1968) Regulation photoperiodique de l'activities sexuelle chez la lapine male et femelle. Arch. Anat. Histol. Embryol. **51** , 775-80.

Wellard G. (1987) The effect of weather on soil moisture and plant growth in the arid zone. In: Kangaroos; their ecology and management in the sheep rangelands of Australia. (G.C Caughley, N.C. Shepherd & J.C Short Eds.). C.U.P.

Werner P.A. & Plat W.J. (1976) Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). Am. Nat. **110**, 959-71.

Westoby M. (1980) Black-tailed jack rabbit diets in Curlew Valley, Northern Utah. J. Wild. Manage. **44**(4), 943-47.

Wheeler S.H. & King D.R. (1983) Rabbits without warrens. W.A J. Agr. **24**, 34-5.

Wheeler S.H. & King D.R. (1985) The European rabbit in south-western Australia. II Reproduction. Aust. Wild. Res. **12**, 197-212.

Wilson A.D. (1966) The value of *Atriplex* (saltbush) and *Kochia* (bluebush) species as food for sheep. Aust. J. Agric. Res. **17**, 147-53.

Wood D.H. & Lee A.K. (1985) An examination of sodium, potassium and osmotic concentrations in blood and urine of arid-zone rabbits in seasonal field conditions and in the laboratory. Aust. Wild. Res.**12**, 173-82.

Appendices

Appendix 1 - Calibration statistics for all grazing trials

Table 1.1 Characteristics of calibration curves for each species in grazing trial 1.

Species	n	r^2	P	D.P.	y-int.	C.F.
Asp	12	.72	.0006	O.K.	Y	.20
Atr	4			bunched		.35
Bab	6	.93	.0031	O.K.	N	.20
Boe	11	.86	.0001	O.K.	N	.30
Bra	7	.94	.0005	O.K.	N	.17
Che	1	insufficient points				.80
Con	4	no regression adequate				.32
Cra	6	.53	.0999	O.K.	N	.53
Dac	12	.90	.0000	O.K.	N	.33
Dau	4	no regression adequate				.14
Enn	8	.93	.0002	O.K.	N	.28
Era	6	.88	.0071	bunched	N	.14
Eupl	12	.94	.0000	O.K.	N	.12
Eupd	3	insufficient points				.16
Goo	8	.97	.0000	O.K.	N	.30
Hel	3	insufficient points				.34
Lot	3	insufficient points				.15
Pla	12	.98	.0000	O.K.	N	.30
Scl	12	.85	.0000	O.K.	N	.16
Sid	8	.89	.0017	O.K.	N	.09
Sti	2	insufficient points				.13
Tet	12	.87	.0000	O.K.	N	.24

n = number of individuals used for calibration curve, r^2 = fit of calibration curve, P = significance of calibration curve regression, D.F. = distribution of points, y-intercept = presence (Y) or absence (N) of a significant y-intercept ($P<0.05$), C.F. = conversion factor for converting number of hand held units into biomass.

Table 1.2 Comparison of initial and final conversion factors.

Species	Operator 1 Initial			Operator 1 Final			Operator 2 Initial			Operator 2 Final		
	C.F.	n	r^2	C.F.	n	r^2	C.F.	n	r^2	C.F.	n	r^2
Boe	.06	5	.96	.06	5	.87	.03	6	.99	.04	5	.91
Bras	Less than three points											
Cal	.18	9	.97	.17	9	.96	.18	8	.97	.24	9	.97
Che	.77	8	.82	1.4	9	.69	1.6	9	.87	1.8	9	.86
Cona	.19	3		.22	4	.96	.15	6	.98	.22	6	.84
Cone	.21	6	.93	.22	7	.71	.31	7	.91	.29	7	.79
Cra	.17	12	.73	.21	12	.74	.25	12	.77	.21	12	.73
Dau	.06	5	.46	.08	5	.46	.05	5	.51	.05	5	.88
Eme				Less than three points								
Enn	.43	6	.67	.45	6	.81	.34	5	.89	.33	5	.93
Erad				Less than three points								
Era	.36	8	.94	.49	9	.82	.56	11	.77	.44	11	.68
Eup	L.T. 3 points			.21	4	.53	.20	4	.15	.25	4	.39
Helf	.30	6	.85	.32	6	.93	.57	6	.92	.90	6	.72
Helm	.38	6	.91	.48	5	.96	.51	6	.96	.71	6	.92
Lop	.05	5	.51	.15	5	.50	.07	5	.59	.15	5	.98
Phy	.60	8	.96	.64	8	.98	.41	8	.80	.40	8	.78
Pla	.55	5	.96	.55	4	.97	.56	5	.60	1.02	4	.70
Sal	1.33	3	.99	1.26	4	.98	1.43	4	.97	1.26	4	.98
Scl	.70	8	.78	1.27	9	.78	.89	7	.78	.86	9	.79
Sid	.17	7	.98	.23	6	.91	.22	7	.78	.25	6	.84
Sti	.42	5	.63	.26	5	.81	.30	5	.92	.41	5	.61
Swa	.27	10	.83	.22	10	.93	.41	10	.80	.50	10	.87
Tet	.65	8	.50	.78	8	.54	.75	7	.51	1.92	8	.64

C.F. = Conversion factor, n = number of individuals used for calibration curve.

Table 1.3 Characteristics of calibration curves for grazing trial 2.

Species	Op.	n	r^2	P	D.P.	y-int.	C.F.
Boe	1	5	.95	.003	O.K.	Y	.06
"	2	6	.98	.000	O.K.	N	.03
Bra	1	8	.78	.004	O.K.	N	.54
"	2	8	.94	.000	O.K.	N	.57
Cal	1	9	.98	.000	O.K.	N	.18
"	2	9	.97	.000	O.K.	N	.20
Che	1	9	.78	.002	O.K.	N	1.03
"	2	9	.89	.000	O.K.	N	1.77
Cona	1	12	.92	.000	O.K.	N	.22
"	2	13	.87	.000	O.K.	N	.19
Cone	1	7	.86	.003	bunched	N	.22
"	2	7	.91	.001	O.K.	N	.31
Cra	1	12	.75	.000	O.K.	N	.19
"	2	12	.77	.000	O.K.	N	.23
Dau	1	5	.49	.188	O.K.	N	.07
"	2	5	.75	.055	O.K.	N	.05
Eme	1	9	.66	.008	O.K.	N	.94
"	2	9	.58	.016	O.K.	N	.89
Enn	1	8	.30	.161	O.K.	N	.51
"	2	6	.91	.004	O.K.	N	.37
Erad	1	5	.93	.007	bunched	N	.63
"	2	6	.95	.002	O.K.	N	.52
Era	1	10	.80	.001	bunched	N	.43
"	2	12	.69	.001	bunched	N	.48
Eup	1	9	.82	.001	O.K.	N	.17
"	2	9	.78	.002	O.K.	N	.18
Helf	1	6	.96	.001	O.K.	N	.32
"	2	6	.91	.004	O.K.	N	.71
Helm	1	9	.98	.000	O.K.	N	.41
"	2	9	.93	.000	O.K.	N	.68
Lopd	1	5	.51	.176	O.K.	N	.05
"	2	5	.60	.126	O.K.	N	.07
Lopg	1	5	.50	.181	O.K.	N	.15
"	2	5	.98	.000	O.K.	N	.15
Phy	1	8	.99	.000	bunched	N	.63
"	2	8	.79	.003	bunched	N	.41

contd. overleaf

Table 1.3 contd.

Species	Op.	n	r^2	P	D.P.	y-int.	C.F.
Pla	1	7	.98	.000	O.K.	N	.58
"	2	7	.71	.017	O.K.	N	.72
Sal	1	10	.93	.000	O.K.	N	1.28
"	2	10	.93	.000	O.K.	N	1.32
Scl	1	9	.87	.000	O.K.	N	1.07
"	2	9	.79	.002	O.K.	N	.85
Sid	1	7	.97	.000	O.K.	N	.20
"	2	7	.85	.004	O.K.	N	.24
Sti	1	9	.60	.014	O.K.	N	.33
"	2	9	.65	.008	O.K.	N	.32
Swa	1	10	.92	.000	bunched	N	.25
"	2	10	.89	.000	bunched	N	.46
Tet	1	8	.53	.041	O.K.	N	.72
"	2	8	.59	.029	O.K.	N	1.07

Op. = operator, n = number of individuals used for calibration curve, P = probability of significant regression being due to chance, D.P. = distribution of points, C.F. = conversion factor. O.K. = points spread out, Y = significant y-intercept, N = non-significant y-intercept. Lopd = dead *Lophochloa cristata*, Lopg = green *Lophochloa cristata*. Otherwise, species names abbreviated to first three letters of genus. If more than one species in one genus then first letter of species is also used.

Table 1.4 Characteristics of calibration curves used for grazing trial 3.

Species	Operator 1 Initial				Operator 1 Final				Operator 2 Initial				Operator 2 Final			
	n	r^2	y	C.F.	n	r^2	y	C.F.	n	r^2	y	C.F.	n	r^2	y	C.F.
Asp	6	.83	N	.12	5	.82	N	.26	6	.43	Y	.09	6	.80	N	.09
Con	7	.30	Y	.31	7	.54	Y	.35								
Cra	9	.77	N	.76	9	.89	Y	.11	8	.85	N	.15	9	.94	Y	.17
Dac	11	.76	N	.16	12	.66	N	.21	12	.49	N	.11	12	.49	N	.11
Enn	11	.76	Y	.16	12	.79	Y	1.8	11	.46	N	1.6	12	.60	Y	1.6
Erad	6	.42	Y	.15	6	.88	N	.23	6	.22	Y	.21	6	.78	N	.24
Erag	9	.85	Y	.42	11	.95	N	.49	7	.97	N	.87	11	.96	N	1.1
Goo	7	.08	Y	.20					8	.25	Y	.19				
Hel	7	.93	Y	.18	7	.97	N	.20	7	.98	N	.13	7	.98	N	.15
Scl1	5	.97	N	1.1	5	.99	N	1.6	5	.98	N	.70	5	.99	N	.64
Scl2	9	.89	N	1.3	5	.95	N	1.3	9	.98	N	.85	5	.89	N	.72
Scl3	Less than 3 points															
Sid	7	.95	N	.21	8	.89	Y	.25	7	.85	N	.30	8	.87	N	.28
Sti	6	.89	N	5.2	5	.90	N	4.5	5	.98	N	7.2	5	.86	N	7.4
Swa	5	.53	Y	.26	4	.81	N	.45	6	.40	Y	.44	4	.90	N	.55
Tri	6	.29	Y	1.0	4	.71	Y	1.6	5	.41	Y	1.2	4	.97	N	1.4

n = number of individuals used for calibration curve, y = presence (Y) or absence (N) of a significant y-intercept D.P. = distribution of points, C.F. = conversion factor.

Table 1.5 Characteristics of calibration curves for grazing trial 4.

Species	Initial					Final				
	n	r^2	P	y-int	C.F.	n	r^2	P	y-int	C.F.
Cra	5	N.R.A.			.12					
Dau	7	N.R.A.			.08					
Era	11	N.R.A.			.53	10	.62	.281	N	.28
Enn	14	.38	.019	N	2.0	14	.82	.000	N	2.2
Scld	11	.90	.000	N	.85	11	.96	.000	N	.98
Sclg	11	.83	.001	N	.17	8	.59	.043	N	.16
Sti	9	.59	.005	N	2.6	9	.55	.033	N	2.8

N.R.A. = No regression adequate, n = number of individuals used in calibration curve, P = probability that significant regression occurred by chance, y-int = Presence (Y) or absence (N) of a significnat y-intercept. C.F. = conversion factor.

Appendix 2 - Biomasses of each species and total biomass in all quadrats in each grazing trial.

Table 2.1 Biomass of each species in all quadrats in grazing trial 1 ($g(3m^2)^{-1}$).

PEN A

RDYS	ASP	ATR	BAB	BOE	BRA	CON	CRA	DAC	DAU	ENN	ERA	EUP1
0	10.10	0.700	3.200	11.85	1.700	3.520	0.265	21.78	1.470	2.240	2.310	17.22
3	3.20	0.700	3.200	11.55	1.700	0.160	0.000	14.44	0.560	2.520	1.120	14.04
6	1.10	0.700	2.950	8.70	0.255	0.000	0.000	11.72	0.280	1.820	1.190	16.20
9	0.55	0.788	3.050	10.50	0.000	0.000	0.000	11.96	0.000	1.680	0.630	17.16
12	0.05	0.350	3.350	7.05	0.000	0.000	0.000	11.05	0.000	1.540	0.455	16.38
15	0.05	0.000	2.950	5.85	0.000	0.000	0.000	9.57	0.000	1.400	0.490	14.64
18	0.10	0.000	3.450	4.50	0.000	0.000	0.000	8.91	0.000	1.120	0.525	15.24
21	0.00	0.000	2.850	0.75	0.000	0.000	0.000	8.17	0.000	0.700	0.245	12.24
24	0.00	0.000	2.800	0.30	0.000	0.000	0.000	7.75	0.000	0.840	0.105	10.14
27	0.00	0.000	2.050	0.00	0.000	0.000	0.000	6.27	0.000	0.490	0.175	8.76
30	0.00	0.000	1.400	0.00	0.000	0.000	0.000	7.26	0.000	0.140	0.175	6.84
33	0.00	0.000	0.150	0.00	0.000	0.000	0.000	7.67	0.000	0.140	0.105	8.34

RDYS	EUP2	GOO	HEL	LOT	PLA	SCL	SID	STI	TET	TOT
0	1.080	2.550	1.275	0.300	29.25	40.48	0.270	0.195	58.92	210.7
3	0.600	2.250	0.340	0.450	27.00	23.28	0.270	0.000	55.92	163.3
6	0.000	0.750	0.085	0.000	14.25	14.24	0.045	0.000	56.64	130.9
9	0.080	0.450	0.000	0.000	6.38	11.92	0.045	0.000	58.08	123.3
12	0.000	0.375	0.000	0.000	3.15	9.44	0.000	0.000	69.48	122.7
15	0.000	0.075	0.000	0.000	1.20	3.32	0.000	0.000	54.72	94.3
18	0.000	0.000	0.000	0.000	0.52	1.68	0.000	0.000	50.52	86.6
21	0.000	0.000	0.000	0.000	0.00	0.35	0.000	0.000	37.44	62.7
24	0.000	0.000	0.000	0.000	0.00	0.00	0.000	0.000	28.92	50.9
27	0.000	0.000	0.000	0.000	0.00	0.00	0.000	0.000	17.76	35.5
30	0.000	0.000	0.000	0.000	0.00	0.00	0.000	0.000	10.50	26.3
33	0.000	0.000	0.000	0.000	0.00	0.00	0.000	0.000	2.88	19.3

PEN B

RDYS	ASP	ATR	BAB	BOE	BRA	CHE	CRA	DAC	DAU	ENN	ERA
0	4.150	1.837	1.600	18.15	2.125	1.600	0.530	21.61	0.350	4.270	0.455
3	0.550	1.663	1.100	19.05	1.572	2.000	0.265	12.38	0.140	4.200	0.420
6	0.400	1.663	1.600	19.95	0.085	1.600	0.132	9.40	0.420	2.660	0.350
9	0.000	0.613	1.400	16.20	0.000	0.000	0.000	6.52	1.400	1.890	0.245
17	0.000	0.438	0.900	15.90	0.000	1.600	0.000	8.58	1.120	1.960	0.140
23	0.000	0.175	0.850	4.50	0.000	1.200	0.000	8.25	0.280	1.400	0.000
29	0.000	0.175	1.300	0.30	0.000	0.000	0.000	9.57	0.560	0.910	0.070

RDYS	EUP1	EUP2	GOO	HEL	LOT	PLA	SCL	SID	TET	TOT
0	12.600	2.160	0.525	0.340	0.075	19.05	26.00	0.225	46.32	164.0
3	14.940	1.200	0.150	0.170	0.112	14.40	14.24	0.157	43.08	131.8
6	15.240	0.960	0.075	0.170	0.038	12.82	13.84	0.225	58.68	140.3
9	10.860	0.080	0.000	0.170	0.075	8.10	7.52	0.000	47.76	102.8
17	12.720	0.000	0.000	0.000	0.000	0.90	4.00	0.000	51.00	99.3
23	12.180	0.000	0.000	0.000	0.000	0.15	1.28	0.000	32.76	63.0
29	8.460	0.000	0.000	0.000	0.000	0.00	0.40	0.000	24.18	45.9

Species name denoted by first three letters of genus.
RDYS - Rabbit days. TOT - Total biomass in all quadrats.

Table 2.2 Biomass of each species in all quadrats in grazing trial 2 $(g(3m^2)^{-1})$.

Pen A

RDYS	BOE	CAL	CHE	CONA	CONE	CRA	DAU	EME	ENN	EDI	ERA	EUP
0	2.948	12.54	26.79	9.561	5.376	41.98	6.285	2.665	3.702	9.937	9.018	2.690
3	2.453	10.27	27.62	3.162	1.843	41.37	4.463	2.010	2.891	9.463	7.120	1.857
6	1.974	9.85	21.82	1.299	0.530	42.58	4.132	2.688	2.765	6.141	6.361	1.241
9	0.581	9.53	16.67	0.109	0.000	42.82	1.907	0.234	2.334	6.011	5.056	0.662
12	0.117	7.36	16.58	0.000	0.000	35.14	2.225	0.000	2.690	4.113	5.830	0.265
15	0.169	6.87	14.08	0.000	0.000	36.77	2.596	0.000	1.932	4.745	3.142	0.131
18	0.121	4.98	13.94	0.000	0.000	34.84	1.563	0.000	2.207	4.745	2.019	0.000
21	0.104	4.52	11.87	0.000	0.000	33.56	1.501	0.000	1.828	3.796	2.232	0.000
24	0.035	2.86	12.09	0.000	0.000	33.90	0.918	0.000	1.360	4.113	0.896	0.000
27	0.000	2.61	13.49	0.000	0.000	26.76	0.724	0.000	1.041	3.164	0.213	0.000
30	0.000	2.14	10.18	0.000	0.000	24.97	0.459	0.000	0.914	3.480	0.364	0.000
33	0.000	0.20	7.60	0.000	0.000	18.96	0.477	0.000	0.446	2.847	0.213	0.000
36	0.000	1.14	7.73	0.000	0.000	18.61	0.547	0.000	0.431	0.316	0.425	0.000
39	0.000	1.14	3.76	0.000	0.000	17.25	0.212	0.000	0.305	0.949	0.000	0.000
42	0.000	0.84	0.70	0.000	0.000	13.96	0.185	0.000	0.216	1.265	0.000	0.000
45	0.000	0.41	0.00	0.000	0.000	11.67	0.106	0.000	0.178	1.107	0.000	0.000
48	0.000	0.56	0.96	0.000	0.000	13.34	0.106	0.000	0.394	2.214	0.000	0.000

RDYS	HELF	HELM	LOP	PHY	PLA	SAL	SCL	SID	STI	SWA	TET	TOT
0	1.536	25.06	5.486	2.601	13.98	12.76	14.10	10.48	0.481	22.57	54.97	297.5
3	2.049	20.31	3.128	5.696	12.75	11.80	14.75	9.18	0.321	13.19	43.33	251.0
6	1.536	18.33	1.793	2.241	10.98	14.04	15.93	7.93	0.321	10.04	44.68	229.2
9	1.536	15.94	1.524	2.037	11.53	11.48	13.14	5.78	0.481	4.59	36.36	190.3
12	1.024	12.89	1.029	3.463	9.39	8.29	10.36	1.64	0.321	2.02	25.61	150.4
15	0.512	12.20	1.063	2.648	5.04	9.57	10.46	0.36	0.321	1.14	25.25	139.0
18	0.354	12.17	0.987	2.648	4.57	9.57	10.35	0.24	0.000	0.00	22.47	127.8
21	0.079	13.19	0.364	2.444	3.63	9.57	9.83	0.24	0.321	0.00	21.12	120.2
24	0.159	11.22	0.288	2.648	0.65	5.74	9.08	0.00	0.160	0.00	18.35	104.5
27	0.000	10.61	0.259	2.241	0.00	0.00	8.39	0.00	0.160	0.00	17.18	86.8
30	0.000	9.69	0.250	2.241	0.00	0.00	5.88	0.00	0.000	0.00	15.93	76.5
33	0.000	9.42	0.218	2.444	0.00	0.00	4.06	0.00	0.000	0.00	13.96	60.8
36	0.000	8.42	0.096	0.815	0.00	0.00	0.42	0.00	0.000	0.00	17.00	56.0
39	0.000	7.33	0.134	0.102	0.00	0.00	0.42	0.00	0.000	0.00	12.88	44.5
42	0.000	5.80	0.121	0.000	0.00	0.00	0.42	0.00	0.000	0.00	10.38	33.9
45	0.000	4.81	0.084	0.000	0.00	0.00	0.00	0.00	0.000	0.00	9.13	27.5
48	0.000	5.69	0.025	0.102	0.00	0.00	0.63	0.00	0.000	0.00	10.55	34.6

Pen B

RDYS	BOE	CAL	CHE	CONA	CONE	CRA	DAU	EME	ENN	EDI	ERA	EUP
0	1.069	12.34	28.51	9.225	9.328	43.25	5.872	4.021	2.587	5.844	4.523	2.288
3	0.568	9.14	21.29	2.889	2.313	37.89	4.592	4.488	3.449	2.104	3.309	1.050
6	0.035	10.17	23.58	1.163	1.337	38.22	3.921	0.468	2.601	3.843	3.066	0.215
9	0.134	8.32	18.80	0.000	0.000	33.14	2.702	0.468	1.799	4.160	2.611	0.172
12	0.000	8.61	16.87	0.000	0.000	32.17	2.667	0.000	2.081	3.527	1.503	0.045
15	0.000	6.48	19.16	0.000	0.000	32.33	2.349	0.234	3.122	3.602	1.715	0.000
18	0.009	3.64	17.68	0.000	0.000	26.03	2.278	0.468	2.587	2.578	1.472	0.000
21	0.017	3.99	16.13	0.000	0.000	27.86	1.509	0.234	2.156	2.736	1.017	0.000
24	0.000	3.02	18.64	0.000	0.000	25.71	1.042	0.234	1.368	1.471	1.411	0.000
27	0.000	4.98	17.46	0.000	0.000	19.78	0.759	0.000	1.368	1.526	0.486	0.000
30	0.000	0.82	18.04	0.000	0.000	19.55	0.883	0.000	0.558	1.526	1.032	0.000
33	0.000	1.33	16.28	0.000	0.000	19.34	0.265	0.000	0.595	1.526	0.000	0.000
36	0.000	0.00	20.19	0.000	0.000	16.37	0.419	0.000	0.089	0.949	0.213	0.000
39	0.000	0.10	13.92	0.000	0.000	15.63	0.335	0.000	0.089	0.894	0.000	0.000
42	0.000	0.10	10.17	0.000	0.000	13.98	0.000	0.000	0.000	0.894	0.000	0.000
45	0.000	0.31	13.41	0.000	0.000	11.60	0.053	0.000	0.126	1.210	0.000	0.000
48	0.000	0.20	13.04	0.000	0.000	11.94	0.053	0.000	0.342	1.210	0.000	0.000

RDYS	HELF	HELM	LOP	PHY	PLA	SAL	SCL	SID	STI	SWA	TET	TOT
0	7.298	4.273	5.930	1.944	6.162	54.39	11.51	2.595	0.411	18.31	56.77	298.4
3	5.711	4.278	3.156	1.944	1.884	53.86	9.60	2.731	0.493	12.14	44.32	233.2
6	6.029	3.727	2.017	1.426	2.465	48.03	12.15	2.019	0.493	10.04	44.95	222.0
9	7.139	2.014	1.896	1.426	2.645	41.57	12.15	0.119	0.164	3.54	37.62	182.6
12	5.077	4.000	1.474	1.630	1.048	44.14	9.59	0.594	0.493	0.25	17.36	153.1
15	3.808	4.171	1.818	1.833	1.594	31.22	10.55	0.237	0.493	0.13	26.77	151.6
18	3.490	3.833	1.481	1.630	0.506	33.81	10.22	0.237	0.082	0.00	24.44	136.5
21	3.667	4.755	0.519	1.426	0.471	35.35	11.19	0.000	0.000	0.00	21.48	134.5
24	2.257	3.662	0.468	1.426	0.000	31.73	8.97	0.000	0.000	0.00	18.79	120.2
27	2.697	3.181	0.339	0.815	0.000	7.10	8.52	0.000	0.000	0.00	17.27	86.3
30	2.221	2.634	0.293	0.713	0.000	0.00	7.56	0.000	0.000	0.00	15.30	71.1
33	1.269	2.634	0.289	0.407	0.000	0.00	4.79	0.000	0.000	0.00	15.65	64.4
36	1.269	2.463	0.440	0.611	0.000	0.00	0.85	0.000	0.000	0.00	15.47	59.3
39	0.952	2.292	0.264	0.306	0.000	0.00	0.42	0.000	0.000	0.00	12.88	48.1
42	1.269	2.120	0.256	0.509	0.000	0.00	0.42	0.000	0.000	0.00	9.84	39.6
45	0.952	2.463	0.298	0.306	0.000	0.00	0.00	0.000	0.000	0.00	10.02	40.7
48	1.269	2.292	0.100	0.306	0.000	0.00	0.00	0.000	0.000	0.00	7.34	38.1

Species name denoted by first three letters of genus. Where more then one species occurs in one genus, first letter of species name is also used.
RDYS - Rabbit days, TOT - total biomass in all quadrats.

Table 2.3 Biomass of each species in all quadrats in grazing trial 3 $(g(3m^2)^{-1})$.

Pen A

RDYS	CON	CRA	DAU	ENN	ERAD	ERAG	GOO	HELM	SCL1	SCL2	SCL3
0	3.640	2.670	7.967	304.79	18.59	24.17	0.201	0.290	25.253	2.786	4.000
2	0.662	3.145	4.670	273.53	26.50	26.00	0.402	0.096	23.546	6.976	6.667
6	0.000	3.099	3.205	246.96	23.36	14.82	0.000	0.192	18.428	3.171	4.667
10	0.000	2.035	5.128	239.15	17.66	12.09	0.000	0.096	21.499	3.171	4.333
14	0.000	1.480	2.472	267.28	19.52	9.12	0.000	0.096	16.721	1.903	5.333
17	0.000	1.434	2.930	265.72	14.06	7.52	0.000	0.000	16.380	4.439	5.667
18	0.000	0.925	2.106	284.47	13.71	8.21	0.000	0.000	25.253	1.268	7.000

RDYS	SID	STI	SWA	TRI	TOT
0	4.277	94.60	42.22	1.361	536.8
2	2.601	72.77	30.14	3.971	481.7
6	1.503	82.47	8.81	5.559	416.2
10	1.503	67.92	3.73	3.971	382.3
14	1.272	67.92	1.81	4.765	399.7
17	0.694	89.75	1.35	4.765	414.7
18	0.231	72.77	0.23	3.971	420.1

Pen B

RDYS	ASP	CRA	DAU	ENN	ERAD	ERAG	GOO	HEM	SCL1	SCL2	SCL3
0	0.330	12.11	2.363	131.99	2.691	12.62	0.192	1.110	8.749	2.367	12.000
3	0.330	7.25	1.939	201.22	1.223	16.99	0.192	1.249	14.806	3.155	6.667
6	0.330	4.09	2.424	187.05	0.856	9.71	0.192	0.763	6.057	2.761	6.667
9	0.047	3.78	2.182	177.33	1.101	6.79	0.192	0.694	10.768	0.394	8.667
12	0.094	2.39	1.515	198.38	0.245	12.62	0.192	0.798	13.460	1.183	8.667
15	0.000	2.16	2.000	153.85	0.734	11.65	0.192	0.555	10.768	1.578	10.667
18	0.000	1.54	1.333	124.70	0.612	10.68	0.000	0.347	10.768	1.183	10.667
22	0.000	0.77	0.545	112.55	0.245	5.82	0.000	0.555	7.403	0.789	6.000
26	0.000	1.00	0.727	110.93	0.489	4.85	0.000	0.347	8.749	0.000	6.667

RDYS	SID	SWA	TRI	TOT
0	7.71	24.30	63.96	269.9
3	11.20	29.21	25.86	321.3
6	14.84	18.84	34.02	288.6
9	11.93	14.47	22.45	260.8
12	11.64	7.10	25.18	283.5
15	2.62	0.00	18.37	215.1
18	0.00	0.00	19.73	181.6
22	0.00	0.00	11.57	146.3
26	0.00	0.00	16.33	150.1

Table 2.4 Biomass of each species in all quadrats in grazing trial 4 (g(4·5m)$^{-1}$).

Pen B

RDYS	CRA	DAU	ERA	ENN	S1G	S1D	S2G	S2D	STI	TOT
0	0.585	1.272	31.42	326.61	5.148	31.08	0.624	2.285	76.30	475.3
2	0.351	0.583	38.96	335.07	1.560	31.53	0.000	10.968	63.58	482.6
4	0.058	0.318	42.02	327.67	0.702	17.37	0.000	9.140	67.82	465.1
7	0.058	0.265	38.35	317.10	0.780	15.99	0.000	7.769	57.93	438.3
10	0.058	0.212	38.35	298.07	0.312	13.25	0.000	6.855	59.35	416.5
13	0.058	0.106	44.88	295.96	0.000	10.05	0.000	6.855	63.59	421.5
16	0.058	0.106	37.94	290.68	0.000	10.51	0.000	6.398	57.93	403.6
19	0.000	0.159	42.02	266.36	0.156	8.23	0.000	6.855	56.52	380.3
22	0.000	0.000	27.74	263.19	0.000	8.23	0.000	5.484	59.35	364.0
25	0.000	0.053	33.46	252.62	0.000	7.31	0.000	6.398	45.22	345.1
28	0.000	0.106	31.42	263.19	0.000	6.86	0.000	4.570	48.04	354.2
31	0.000	0.000	27.74	258.97	0.000	5.03	0.000	4.113	43.80	339.7
34	0.000	0.000	30.19	252.62	0.000	5.94	0.000	3.656	40.98	333.4
37	0.000	0.000	33.05	247.34	0.000	3.20	0.000	4.570	36.74	324.9

Species name denoted by first three letters of genus.
S1D - Sclerolaena sp.1 (dead), S1G - Sclerolaena sp.1 (green)
S2D - Sclerolaena sp.2 (dead), S2G - Sclerolaena sp.2 (green)
RDYS - Rabbit days, TOT - Total biomass in all quadrats.

Appendix 3 - Initial biomasses of each species in each quadrat in all grazing trials.

Table 3.1 Initial biomass of each species and total biomass in each quadrat in grazing trial 1 (g(0.25m^2)$^{-1}$).

PEN A

QUAD	ASP	ATR	BAB	BOE	BRA	CON	CRA	DAC	DAU	ENN	ERB	EUP1
1	0.800	0.175	0.000	0.000	0.000	0.000	0.000	1.650	0.280	0.000	0.000	0.300
2	0.000	0.000	1.100	0.600	0.000	0.000	0.000	1.320	0.000	0.280	0.350	1.080
3	1.100	0.000	0.200	1.200	0.680	1.920	0.000	1.980	0.070	0.000	0.000	2.280
4	1.800	0.000	0.200	1.500	0.170	0.320	0.000	0.990	0.000	0.000	0.420	3.060
5	0.900	0.000	0.500	0.750	0.425	1.280	0.000	0.165	0.140	0.000	0.910	1.260
6	0.500	0.000	0.300	0.300	0.000	0.000	0.000	1.650	0.140	1.120	0.000	0.480
7	1.500	0.000	0.700	2.700	0.000	0.000	0.000	3.630	0.140	0.000	0.210	1.560
8	0.600	0.000	0.100	0.600	0.170	0.000	0.000	0.330	0.700	0.000	0.000	0.420
9	0.400	0.000	0.050	1.500	0.170	0.000	0.000	1.980	0.000	0.560	0.000	3.000
10	1.100	0.000	0.000	0.000	0.000	0.000	0.265	1.980	0.000	0.000	0.000	0.840
11	0.900	0.000	0.000	2.400	0.000	0.000	0.000	4.620	0.000	0.280	0.280	2.100
12	0.500	0.525	0.050	0.300	0.085	0.000	0.000	1.485	0.000	0.000	0.140	0.840

QUAD	EUP2	GOO	HEL	LOT	PLA	SCL	SID	STI	TET	TOT
1	0.320	0.000	0.000	0.000	2.10	0.880	0.000	0.0000	3.36	9.86
2	0.000	0.000	0.000	0.000	0.90	1.760	0.225	0.0000	8.88	16.50
3	0.480	0.150	0.000	0.000	3.00	4.160	0.000	0.0000	2.28	19.50
4	0.080	0.300	0.000	0.000	3.00	2.560	0.000	0.0000	1.92	16.32
5	0.000	0.000	0.000	0.150	0.75	2.240	0.000	0.0000	7.92	17.39
6	0.000	0.000	1.020	0.000	0.15	3.760	0.000	0.0000	14.64	24.06
7	0.000	0.000	0.000	0.000	0.00	5.600	0.000	0.0650	5.16	21.26
8	0.000	0.000	0.000	0.000	0.60	7.520	0.045	0.0650	3.36	14.51
9	0.000	0.000	0.000	0.000	2.55	3.200	0.000	0.0650	0.84	14.31
10	0.040	1.800	0.085	0.150	13.50	3.360	0.000	0.0000	0.24	23.36
11	0.160	0.300	0.000	0.000	2.25	2.080	0.000	0.0000	0.72	16.09
12	0.000	0.000	0.170	0.000	0.45	3.360	0.000	0.0000	9.60	17.50

PEN B

QUAD	ASP	ATR	BAB	BOE	BRA	CHE	CRA	DAC	DAUC	ENN	ERA	EU1P
1	0.300	0.000	0.000	1.800	0.510	0.000	0.000	1.155	0.140	0.840	0.000	1.200
2	0.500	0.000	0.100	1.200	0.000	0.000	0.000	2.970	0.070	0.140	0.000	1.140
3	0.200	0.525	0.000	0.300	0.680	0.000	0.000	1.485	0.000	0.560	0.000	1.680
4	0.100	0.175	0.300	0.300	0.000	0.000	0.000	1.650	0.000	0.000	0.210	0.900
5	0.500	0.000	0.100	1.500	0.340	0.000	0.000	2.475	0.000	0.140	0.000	1.320
6	0.300	0.087	1.100	1.050	0.340	0.000	0.000	3.135	0.000	1.540	0.035	0.780
7	0.500	0.000	0.000	5.700	0.085	0.800	0.000	0.825	0.000	0.420	0.000	1.080
8	0.800	0.000	0.000	0.900	0.000	0.000	0.000	1.155	0.000	0.000	0.000	0.960
9	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.660	0.000	0.140	0.000	0.480
10	0.400	0.350	0.000	0.300	0.000	0.000	0.530	2.310	0.000	0.070	0.000	0.540
11	0.200	0.000	0.000	0.900	0.000	0.800	0.000	0.825	0.000	0.420	0.210	2.520
12	0.300	0.700	0.000	4.200	0.170	0.000	0.000	2.970	0.140	0.000	0.000	0.000

QUAD	EUP2	GOO	HEL	LOT	PLA	SCL	SID	TET	TOT
1	0.000	0.000	0.000	0.0000	1.950	1.840	0.000	4.200	13.94
2	0.000	0.000	0.000	0.0000	0.150	3.520	0.000	6.480	16.27
3	0.160	0.000	0.000	0.0000	0.450	1.600	0.135	3.960	11.73
4	0.080	0.300	0.000	0.0000	0.300	2.880	0.000	5.040	12.24
5	0.000	0.150	0.000	0.0000	0.150	3.680	0.000	5.520	15.88
6	0.480	0.000	0.000	0.0000	2.250	0.960	0.000	4.560	16.62
7	0.000	0.000	0.000	0.0000	2.550	0.400	0.000	2.400	14.76
8	0.480	0.000	0.000	0.0000	0.000	3.200	0.000	2.880	10.38
9	0.000	0.075	0.000	0.0750	0.300	1.600	0.090	0.240	3.71
10	0.640	0.000	0.340	0.0000	9.000	0.320	0.000	0.000	14.80
11	0.000	0.000	0.000	0.0000	1.950	2.560	0.000	5.520	15.91
12	0.320	0.000	0.000	0.0000	0.000	3.440	0.000	5.520	17.76

Species names denoted by first three letters of genus.
QUAD - quadrat number, TOT - Total biomass of all species.

Table 3.2 Initial biomass of each species, and total biomass, in each quadrat in grazing trial 2 ($g(0.25m^2)^{-1}$).

PEN A

QUAD	BOE	CAL	CHE	CONA	CONE	CRA	DAU	EME	ENN	ERAD	ERA	EUP
1	0.032	1.058	1.545	0.109	0.000	3.245	1.271	0.000	0.253	2.531	1.701	0.000
2	0.000	0.000	5.148	0.000	0.000	3.818	1.130	0.000	0.000	0.000	0.000	0.000
3	0.000	0.000	2.574	2.624	0.000	6.681	0.282	0.000	1.011	0.316	0.213	0.000
4	0.389	0.882	1.545	1.312	0.000	3.436	0.988	0.000	0.758	0.633	0.425	0.258
5	0.065	0.000	0.257	0.000	0.000	4.295	0.565	0.000	0.000	2.531	1.701	0.258
6	0.032	3.528	1.545	0.328	0.000	7.636	0.141	0.000	0.253	3.796	2.551	0.431
7	0.694	0.820	0.886	4.034	2.458	0.464	0.026	0.888	0.535	0.000	0.243	0.268
8	0.555	1.947	0.886	0.480	0.922	5.331	0.371	0.000	0.000	0.000	0.971	0.625
9	0.347	0.000	7.974	0.000	0.000	2.202	1.166	0.000	0.357	0.000	0.121	0.000
10	0.191	2.050	0.000	0.000	0.307	2.318	0.053	0.000	0.535	0.000	0.121	0.045
11	0.017	0.205	4.430	0.672	0.614	2.550	0.000	0.000	0.000	0.000	0.000	0.179
12	0.625	2.050	0.000	0.000	1.075	0.000	0.292	1.776	0.000	0.130	0.971	0.625

QUAD	HELF	HELM	LOP	PHY	PLA	SAL	SCL	SID	STI	SWA	TET	TOT
1	0.476	0.407	1.455	0.000	0.000	0.00	3.215	0.814	0.000	4.298	1.79	24.48
2	0.000	4.074	1.532	0.000	2.904	0.00	1.072	0.000	0.000	1.770	3.22	24.76
3	0.000	0.407	0.306	0.000	2.904	0.00	3.751	0.000	0.000	1.517	11.44	35.04
4	0.000	5.093	0.613	0.000	0.145	0.00	0.000	2.239	0.000	5.309	0.00	24.83
5	0.000	4.685	0.153	0.000	0.000	12.76	1.607	0.000	0.000	1.264	9.65	39.79
6	0.000	2.852	0.000	0.157	1.162	0.00	1.072	1.018	0.000	1.770	0.36	28.89
7	1.061	0.000	0.000	1.222	2.167	0.00	1.269	0.000	0.160	2.062	0.00	19.26
8	0.000	1.713	0.450	0.815	1.445	0.00	0.423	1.069	0.000	1.146	1.61	20.80
9	0.000	3.083	0.600	0.407	1.083	0.00	0.846	2.019	0.321	0.917	12.91	34.38
10	0.000	0.685	0.000	0.000	1.806	0.00	0.000	2.138	0.000	0.000	0.00	10.25
11	0.000	0.685	0.300	0.000	0.361	0.00	0.846	0.000	0.000	1.375	13.45	25.72
12	0.000	1.370	0.075	0.000	0.000	0.00	0.000	1.188	0.000	1.146	0.54	11.90

PENB

QUAD	BOE	CAL	CHE	CONA	CONE	CRA	DAU	EME	ENN	ERAD	ERA	EUP
1	0.065	0.000	6.178	0.437	0.000	3.627	1.553	0.000	0.000	3.796	1.701	0.000
2	0.000	1.676	1.545	0.219	0.000	3.245	0.035	0.000	0.253	0.633	0.000	0.000
3	0.032	0.000	2.059	0.000	0.446	3.054	0.176	0.000	0.506	0.000	0.000	0.172
4	0.000	0.000	1.030	0.000	0.000	2.004	0.071	0.000	0.000	0.000	0.213	0.431
5	0.000	0.000	0.000	1.094	3.343	3.627	0.071	0.468	0.758	0.633	0.000	0.000
6	0.000	0.000	6.178	0.656	2.006	3.818	0.706	0.000	0.000	0.000	0.425	0.345
7	0.069	5.330	3.544	0.480	0.614	2.782	0.000	0.000	0.000	0.000	0.000	0.268
8	0.243	1.640	0.886	2.305	1.843	1.391	0.663	2.665	0.357	0.000	0.728	0.804
9	0.104	3.075	1.772	0.000	0.000	8.577	0.159	0.000	0.000	0.000	0.486	0.000
10	0.139	0.000	1.772	3.266	0.000	4.404	1.166	0.000	0.178	0.000	0.728	0.000
11	0.208	0.615	0.000	0.768	0.768	3.477	0.583	0.888	0.357	0.000	0.000	0.268
12	0.208	0.000	3.544	0.000	0.307	3.245	0.689	0.000	0.178	0.783	0.243	0.000

QUAD	HELF	HELM	LOP	PHY	PLA	SAL	SCL	SID	STI	SWA	TET	TOT
1	0.000	0.204	0.766	0.314	1.162	2.55	1.607	0.000	0.000	1.517	6.434	32.01
2	0.000	0.102	0.383	0.000	0.000	0.32	1.072	0.000	0.329	1.011	0.715	11.81
3	7.298	0.000	0.153	0.000	2.033	10.85	0.000	0.000	0.000	5.309	1.787	34.38
4	0.000	0.102	1.149	0.000	0.000	25.52	0.536	0.102	0.082	1.770	3.575	36.66
5	0.000	0.000	0.536	0.000	0.581	0.00	0.000	0.000	0.000	0.000	9.294	21.19
6	0.000	0.611	0.766	0.000	0.581	0.00	3.215	0.000	0.000	4.803	4.289	28.45
7	0.000	0.000	0.150	0.000	0.361	0.00	0.846	0.119	0.000	0.458	9.686	24.77
8	0.000	1.370	0.300	0.204	0.000	7.25	0.423	0.000	0.000	0.917	0.000	24.05
9	0.000	0.685	0.150	0.000	0.361	0.00	1.692	0.712	0.000	0.229	7.533	25.54
10	0.000	0.171	1.051	0.000	0.000	5.27	0.423	0.237	0.000	1.375	5.919	26.30
11	0.000	0.343	0.300	0.815	0.000	2.64	0.423	0.712	0.000	0.458	1.076	14.76
12	0.000	0.685	0.225	0.611	1.083	0.00	1.269	0.712	0.000	0.458	6.457	20.72

Species name denoted by first three letters of genus.
QUAD - Quadrat number, TOT - Total biomass of all species.

Table 3.3 Initial biomass of each species and total biomass in each quadrat in grazing trial 3 ($g(0.25m^2)^{-1}$).

PEN A

QUAD	CON	CRA	DAU	ENN	ERAD	ERAG	GOO	HEL	SCL1	SCL2	SCL3	SID
1	0.000	0.276	0.641	48.45	0.000	0.000	0.000	0.000	12.28	0.310	0.000	0.000
2	0.000	0.460	1.282	23.45	2.324	1.824	0.000	0.000	3.41	1.858	0.000	0.000
3	0.000	0.368	0.549	39.08	0.465	0.912	0.000	0.000	0.00	0.000	0.000	0.347
4	0.000	0.644	1.099	43.77	0.697	2.280	0.000	0.193	0.00	0.000	0.000	0.000
5	0.000	0.184	1.831	15.63	3.022	3.192	0.100	0.000	0.00	0.619	4.000	0.231
6	1.985	0.046	0.000	10.94	5.113	7.753	0.000	0.000	8.19	0.000	0.000	0.000
7	1.655	0.000	0.000	26.57	0.000	0.000	0.100	0.097	0.00	0.000	0.000	1.387
8	0.000	0.000	0.183	0.00	0.000	0.000	0.000	0.000	0.00	0.000	0.000	0.231
9	0.000	0.046	1.648	26.57	2.789	4.561	0.000	0.000	0.68	0.000	0.000	1.387
10	0.000	0.000	0.000	45.33	0.000	0.000	0.000	0.000	0.00	0.000	0.000	0.462
11	0.000	0.368	0.733	6.25	4.184	3.648	0.000	0.000	0.00	0.000	0.000	0.000
12	0.000	0.276	0.000	18.76	0.000	0.000	0.000	0.000	0.68	0.000	0.000	0.231

QUAD	STI	SWA	TRI	TOT
1	0.00	2.709	0.000	64.68
2	21.83	0.677	0.000	57.11
3	0.00	1.355	0.000	43.07
4	0.00	7.225	0.000	55.90
5	0.00	0.903	0.000	29.71
6	0.00	6.322	0.000	40.35
7	53.36	2.709	0.000	85.88
8	0.00	6.322	0.000	6.74
9	19.40	7.676	0.000	64.77
10	0.00	0.903	0.000	46.69
11	0.00	0.000	0.680	15.87
12	0.00	5.418	0.680	26.05

PEN B

QUAD	ASP	CRA	DAU	ENN	ERAD	ERAG	GOO	HEL	SCL1	SCL2	SCL3	SIB
1	0.0000	2.776	0.121	6.48	0.000	5.824	0.000	0.000	6.730	1.183	0.000	0.000
2	0.0000	0.000	0.061	16.19	0.734	0.971	0.000	0.000	2.019	0.000	0.000	0.000
3	0.0942	1.542	0.121	34.01	0.000	0.000	0.192	0.000	0.000	0.000	0.000	0.000
4	0.0000	0.308	0.000	0.00	0.000	0.000	0.000	0.000	0.000	0.000	0.000	6.402
5	0.0471	0.771	0.000	11.34	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6	0.0000	0.463	0.000	0.81	0.978	5.824	0.000	0.000	0.000	0.000	0.000	0.000
7	0.0000	0.231	0.121	3.24	0.000	0.000	0.000	0.139	0.000	0.789	0.000	0.437
8	0.0000	1.542	0.364	21.05	0.978	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9	0.0000	0.771	0.364	0.00	0.000	0.000	0.000	0.278	0.000	0.000	2.667	0.582
10	0.0942	2.468	0.242	19.43	0.000	0.000	0.000	0.416	0.000	0.000	9.333	0.000
11	0.0942	0.463	0.364	19.43	0.000	0.000	0.000	0.139	0.000	0.394	0.000	0.000
12	0.0000	0.771	0.606	0.00	0.000	0.000	0.000	0.139	0.000	0.000	0.000	0.291

QUAD	SWA	TRI	TOT
1	3.276	0.00	26.39
2	1.092	0.00	21.07
3	0.000	0.00	35.96
4	2.184	0.00	8.89
5	0.546	0.00	12.70
6	1.638	17.69	27.40
7	0.273	0.00	5.23
8	3.822	0.00	27.76
9	5.460	40.83	50.95
10	0.546	0.00	32.53
11	2.730	5.44	29.06
12	2.730	0.00	4.54

Species names denoted by first three letters of genus. Where more than one species occurs in one genus, first letter of species is also used.
QUAD - Quadrat number, TOT - Total biomass of all species.

Table 3.4 Initial biomass of each species and total biomass in each quadrat in grazing trial 4 ($g(0.25m^2)^{-1}$).

QUAD	CRA	DAU	ERA	ENN	SCL1G	SCL1D	SCL2G	SCL2D	STI	TOT
1	0.000	0.159	0.816	40.17	0.156	9.140	0.000	0.000	0.00	50.44
2	0.000	0.212	7.344	14.80	0.156	0.914	0.000	0.914	19.78	44.12
3	0.117	0.106	0.816	48.62	0.000	0.914	0.000	0.000	0.00	50.58
4	0.000	0.106	0.000	42.28	0.624	3.656	0.000	1.371	0.00	48.04
5	0.000	0.000	0.000	0.00	0.000	0.000	0.000	0.000	0.00	0.00
6	0.000	0.053	1.632	0.00	2.028	0.000	0.000	0.000	0.00	3.71
7	0.000	0.000	9.792	2.11	0.624	0.000	0.000	0.000	0.00	12.53
8	0.000	0.265	5.712	14.80	0.000	0.000	0.624	0.000	0.00	21.40
9	0.058	0.159	0.816	25.37	0.156	0.000	0.000	0.000	0.00	26.56
10	0.000	0.106	0.000	23.25	0.000	0.000	0.000	0.000	8.48	31.84
11	0.000	0.000	0.000	4.23	0.000	0.000	0.000	0.000	0.00	4.23
12	0.000	0.000	0.000	10.57	0.000	0.000	0.000	0.000	31.09	41.66
13	0.000	0.000	2.448	0.00	0.000	0.000	0.000	0.000	5.65	8.10
14	0.000	0.000	0.000	35.94	0.000	0.000	0.000	0.000	11.30	47.24
15	0.000	0.000	0.000	12.68	0.312	6.398	0.000	0.000	0.00	19.39
16	0.410	0.000	0.000	40.17	0.000	0.000	0.000	0.000	0.00	40.58
17	0.000	0.106	2.040	1.06	0.078	0.000	0.000	0.000	0.00	3.28
18	0.000	0.000	0.000	8.46	0.000	0.000	0.000	0.000	0.00	8.46

Species name denoted by first three letters of genus.
SCL1D = Sclerolaena sp.1 (dead), SCL1G = Sclerolaena sp.1 (green)
SCL2D = Sclerolaena sp.1 (dead), SCL2D = Sclerolaena sp.2 (green).
QUAD = Quadrat number, TOT = Total biomass of all speies.

Appendix 4 - Derivation of caclulation of grazing pressure at a given distance from the warren.

Applies to a circular territory with a radius of 240 m.

Definitions:

TOBS = Total number of rabbit observations (from data of Fullagar and Davey (see Part 3, chapter 1).
DOBS = Number of observation in anulus at distance, D.
RAB = Number of rabbits using warren.
D = Distance from warren at which grazing pressure is to be calculated.
DGP = Grazing pressure at distance, D.
AREA = Total territory area.
DAREA = Area of annulus at distance, D.

Assuming $\mathrm{TOBS} \equiv \mathrm{RAB}$

Then $\mathrm{TOBS/AREA} \equiv \mathrm{RAB/AREA}$

And $\mathrm{DGP/(RAB/AREA)} = \mathrm{(DOBS/DAREA)/(TOBS/AREA)}$

Removing AREA $\mathrm{DGP} = \mathrm{(DOBS/(DAREA\ .\ TOBS))\ .\ RAB}$

i.e DGP = Value of regression equation at distance, D multiplied by number of rabbits in warren.

Appendix 5 - Total numbers of species present at each sampling site at each sampling time. Also values of grazing index, pellet density and soil texture parameters associated with each site.

SITE	S43	S63	S103	S64	S94	S114	S15	S35	GI	PD	CS	FS	SLT	CLY
1	4.	13.	****	10.	14.	16.	14.	11.	1.300	4.70	28.33	54.670	5.670	11.670
2	6.	16.	****	16.	15.	19.	14.	13.	2.200	14.20	27.67	58.000	5.330	8.670
3	8.	15.	****	13.	13.	13.	11.	11.	3.600	7.00	23.67	56.670	7.330	11.330
4	3.	9.	****	9.	7.	11.	8.	6.	4.800	9.20	29.67	58.000	3.330	9.000
5	4.	8.	****	10.	3.	10.	9.	7.	5.200	17.40	24.17	60.670	4.330	10.170
6	5.	13.	****	9.	13.	15.	12.	9.	2.900	29.00	23.00	57.500	7.000	12.500
7	5.	19.	****	13.	17.	16.	11.	11.	1.600	9.20	27.00	57.330	5.670	9.670
8	6.	12.	****	13.	15.	14.	15.	11.	0.700	12.30	27.00	57.330	5.000	10.300
9	8.	21.	****	9.	14.	14.	9.	10.	0.200	12.00	22.33	51.330	11.000	13.670
10	3.	16.	****	19.	14.	16.	12.	8.	0.020	7.70	31.00	55.330	5.330	9.000
11	3.	10.	****	7.	14.	11.	13.	12.	0.300	6.50	25.67	57.000	7.000	9.670
12	4.	15.	****	12.	17.	17.	14.	12.	0.900	10.60	30.67	54.670	3.670	10.000
13	6.	14.	****	11.	12.	14.	12.	12.	2.600	16.10	29.00	59.670	3.000	7.670
14	11.	17.	****	12.	12.	11.	8.	9.	6.900	14.90	31.33	58.330	2.330	7.330
15	7.	13.	****	9.	10.	7.	8.	7.	7.600	19.40	30.00	56.000	4.000	10.300
16	7.	17.	****	8.	9.	10.	7.	9.	3.500	11.20	25.00	56.330	5.670	11.000
17	5.	11.	****	15.	13.	12.	12.	15.	2.500	6.40	29.67	54.330	6.670	9.330
18	7.	20.	****	12.	17.	13.	12.	12.	1.800	6.40	19.67	53.000	11.670	14.000
19	3.	13.	****	11.	14.	12.	8.	7.	1.000	5.70	30.00	55.670	5.330	9.330
20	7.	14.	****	14.	18.	19.	14.	13.	0.400	6.00	31.00	53.670	8.670	12.670
21	13.	17.	21.	13.	12.	14.	14.	10.	0.700	14.00	35.33	51.330	4.000	8.330
22	2.	16.	19.	17.	20.	16.	12.	12.	0.200	4.75	29.00	55.670	6.330	9.330
23	13.	21.	21.	9.	15.	10.	12.	5.	0.300	5.90	24.33	53.670	8.000	13.000
24	5.	18.	18.	9.	12.	11.	9.	7.	1.000	2.30	27.67	54.000	5.330	12.000
25	5.	10.	15.	13.	13.	14.	12.	11.	2.600	13.80	29.00	55.000	5.670	9.670
26	1.	0.	9.	2.	11.	5.	3.	2.	4.400	12.60	35.00	54.660	2.000	7.670
27	4.	11.	11.	7.	13.	11.	10.	8.	4.700	11.20	24.67	59.000	5.000	10.670
28	6.	14.	13.	7.	13.	13.	9.	9.	4.700	18.00	23.00	61.000	4.330	10.330
29	2.	11.	18.	10.	15.	13.	13.	11.	2.500	12.80	28.67	57.670	3.330	10.330
30	10.	15.	20.	16.	17.	17.	15.	10.	0.600	12.40	27.00	60.670	2.330	8.330

SITE = Sampling site number, GI = Grazing Index, PD = Pellet density (/0.25m^2), CS, FS, SLT, CLY = Percentage of coarse sand, fine sand, silt and clay respectively.

S43-S35 = Sampling times e.g. S43 = April 1983, S35 = March 1985.

Appendix 6 - Presence, growth state and biomass of species recorded close to warrens (see Part 3, chapter 3)

Table 6.1 Number of occurrences of each species inside and outside cages at each site on each of the sampling occasions.

	CAGED										OPEN									
Species	June 1984		Sept 1984		Nov 1984		Jan 1985		Feb 1985		June 1984		Sept 1984		Nov 1984		Jan 1985		Feb 1985	
	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2
Atriplex Sp.				1		1														
Babbagia acroptera											1						1		1	
Boerhavia diffusa	3	2			1	2					4	2	1		1	1				
Brachycome lineariloba	3	5	15	14	14	11	15	12	14	14	11	7	13	13	12	11	13	12	12	9
Calotis hispidula				1	3			3	1	2				2	1	2				
Chenopodium melanocarpum		1	1		1		1	1	1			1	2							
Craspedia pleiocephala			13	8	14	14	12	8	13	8			9	8	11	9	7	4	8	3
Crassula colorata			1	9		3							2	10		1				
Daucus glochidiatus	2		9	2	2		2		6	1	1		9	2	1	1			2	
Enneapogon avenaceus.	14	13	14	11	15	12	15	14	15	14	15	14	15	13	14	13	15	14	15	13
Eragrostis dielsii	1	4	1	1	1	3		3	1	3	4	3	2	3	1	2	4	3	1	2
Goodenia cycloptera						1														
Helipterum floribundum				1		7		1						3	1	4				
Helipterum jessenii														1						
Helipterum moschatum			15	9	13	9	11	9	11	6			12	8	12	8	2	2	6	1
Lophochloa cristata			8	4	4	6	4	6	6	4			6	5	3	5		4	3	
Myrio-cephalus rhizocephalus			5	2							4	1								
Omphalo-lappula concava	1		9	11		3	2	5	3	5		2	8	9	2	4		2		1
Phyllanthus sp.											1		1		1					
Plantago drummondii	4		6	7	5	5	3	6	7	6	1	2	7	5	6	4	5	5	5	6
Sclerolaena spp.	5	4	5	4	6	3	5	4	6	4	2	3	2	4	4	4	2	4	3	3
Stipa variabilis	3	4	3	5	2	4	3	3	3	4										
Tetragonia tetragonioides	4	4	6	2	2	2		2	1	1	10	6	4	7	4	2		3		
Tragus australianus		1		1			2					1								
Triraphis mollis	6	4	4	4	3	3	3	4	3	1	5	3	2	2	1	2		2		1

W1 - Warren 1, W1 - Warren 2

Table 6.2 Growth state of each species at each sampling time and its palatability at time 2.

Spieces	June 1984	Sept 1984	P.I.	Nov 1984	Jan 1985	Mar 1985
Atriplex sp.		G				G
Babbagia acroptera	G				G	G
Boerhavia diffusa	G	G	6.0	G		
Brachycome lineariloba	G	G/FS		D/S	D/S	D/S
Calotis hispidula		G		D/F	D/S	
Chenopodium melanocarpum	G		1.2	D/S	D/S	D/S
Craspedia pleiocephala		G/F	0.8	D/F	D/S	D/S
Crassula		G/S		D/S		
Daucus glochidiatus	G	G/S	2.4	D/S	D/S	D/S
Enneapogon avenaceus	D,G/S	G/S	2.0	S/S	D/S	D/S*
Eragrostis dielsii	D,G/S*	G/S*	1.0	G*	D/S*	D/S*
Goodenia cycloptera				D/S		
Helipterum floribundum		G/S	4.1	D/F	D/S	
Helipterum jessenii		G				
Helipterum moschatum		G/F	0.8	D/F	D/S	D/S
Lophochloa cristata		G/S	5.3	D/S	D/S	D/S
Omphalo-lappula concava	G/S	G/S		D/S	D/S	D/S
Phyllanthus sp.	G	G/S	0.3	G/S		
Plantago drummondii	G/F	G/F*	2.3	D/S	D/S	D/S
Portulaca oleracea	G					
Sclerolaena spp.	G/S*	G/S*	1.0	G/S*	G*	D/S*
Stipa variabilis	D,G/S	G/S	S,D/S	D/S	D/S	
Tetragonia tetragonioides	G	G/S		D/S	D/S	
Tragus australianus		D/S		D/S		
Triraphis mollis	D,G/S	G/S	D/S	D/S*	D/S	
Myriocephalus	G/S	G/S				

G,S,D/F,S - green,senescent,dead/flowering,seeding

* - evidence of rabbit damage, P.I. - Palatability index

Table 6.3 Biomasses of each species measured at times 2 and 3 in each caged and open and quadrat (g $(0.25m^2)^{-1}$).

Warren 1

Caged

	September 1984								November 1984							
Quad	Bra	Cra	Enn	Era	Hel	Lop	Pla	Scl	Bra	Cra	Enn	Era	Hel	Lop	Pla	Scl
1	2.2	1.5	31	0	0.7	0.1	0	0	1	1.5	31	0	0.2	0	1	0
2	2.7	0.2	18	0	0.3	0	0	0	1	0.2	16	0	0.3	1	0	0
3	1.1	0.6	13	0	0.5	0.4	0	0	1	0.5	13	0.3	0.3	0	0	0
4	1.1	0.5	24	0	0.6	0	0.8	0	1	0.6	18	0	0.1	1	1	0
5	2.6	0.8	13	0	1.5	0	0	0	1	0.4	22	0	1.5	1	1	0
6	3.7	0.0	11	0	0	0	0.1	0	1	0	4.8	0	0	0	0	0
7	1.7	0.1	28	0	0.2	0	0	0.3	0	0.1	36	0	0	0	0	0.6
8	0.5	0.7	17	0	0.4	0	1.7	0.4	1	1.0	13	0	0.2	1	1	0.4
9	1.9	0.1	0	0	0.1	0	0.1	41	1	0.1	0	0	0.1	0	0	59
10	0.6	0.7	10	0	0.2	0.3	0	0.5	1	0.5	14	0	0.1	0	0	2.6
11	1.4	0.1	11	0	0	0	0	0	1	0.1	16	0	0	0	0	0
12	2.2	0.1	7	0	0.1	0	0	0	1	0	8.0	0	0	0	0	0
13	0.7	0.4	10	0	0.7	0	0	0	1	0.2	9.1	0	0.5	0	0	1.9
14	0.6	0.1	23	0	0.9	.2	0.3	5.7	1	0	22	0	0	0	0	55
15	0.6	0.5	27	0	1.6	0	0	0	1	0.2	44	0	1.0	0	1	0

Warren 1

Open

Quad	Bra	Cra	Enn	Era	Hel	Lop	Pla	Scl	Bra	Cra	Enn	Era	Hel	Lop	Pla	Scl
1	1.1	0.2	24	0	0.6	0.1	0.2	0	1	1.6	29	0	0.3	0	1	0
2	0.9	011	24	0	3.7	0.4	0	0	1	0.2	31	0	0	0	0	0
3	1.0	0.3	14	0.2	0.3	0.2	0	0	1	0.5	13	0	0.1	0	0	0
4	1.2	0.4	27	0	2.2	0.1	0.1	0	1	0.6	22	0	1.6	1	1	0
5	1.4	2.1	22	0	2.7	0	0.2	0	1	0.4	6.4	0	1.3	0	1	0
6	1.1	1.8	20	0	0	0	0	0	1	0	24	0	0	1	1	0
7	2.2	0.4	14	0	0.6	0.3	0	0	1	0.1	14	0	0.3	01	0	0
8	3.4	0.4	17	0	0.4	0.2	0.2	0	1	1.0	18	0	0.2	0	1	0
9	1.3	0	2	0	0	0	0	16	1	0.1	0.8	0	0	0	0	15
10	1.2	0	7	0	0.1	0	0	0	1	0.5	7.3	0	0	0	0	0
11	0.2	0.1	6	0	0.2	0	0	0	0	0.1	4.8	0	0	0	0	0
12	0.7	0.1	17	1.4	0.1	0	0	0	0	0	5.5	0	0	0	0	0
13	1.4	0.1	10	0	2.6	0	0	0	1	0.2	8.0	0	0.4	1	0	0
14	0	0.1	3	0	0	0	0.1	66	0	0	5.5	0	0	0	0	88
15	0.6	0	30	0	1.7	0	0.1	0	1	0.2	24	0	0.4	0	1	2.0

contd. overleaf

Table 6.3 contd.

Warren 2

Caged

	September 1984								November 1984							
Quad	Bra	Cra	Enn	Era	Hel	Lop	Pla	Scl	Bra	Cra	Enn	Era	Hel	Lop	Pla	Scl
1	0.7	0.4	64	0	0.2	0	0	0	1	0.1	43	0	0.2	0	0	0
2	0.4	0.3	33	0	0.1	0.1	0.8	0	1	0.1	69	0	0.2	1	1	0
3	1.3	2.8	28	0	0	0	0	0	1	1.0	19	0	0.4	0	0	0
4	3.1	0.1	18	0	0.1	0	0.1	0	1	0	25	0.2	0	1	1	0
5	2.8	0	30	0	0	0	0	0	1	0	19	0	0	0	0	0
6	0	0.6	0	0	0.7	0.5	0.4	0	0	0.7	15	0	0.6	1	0	0
7	7.1	0	22	0	0.2	0	0	0	0	0	10	1.0	0	0	0	0
8	2.6	0.1	16	0	0	0	0	0	1	0	22	0	0	1	0	0
9	3.7	0.1	33	0	0	0.1	0	1.3	1	0.1	19	0	0	0	0	0
10	6.3	0	30	0	0	0	0	5.6	0	0	36	0	0.1	1	0	12
11	0.1	0	0	0	0.3	0	0.1	46	0	0	0	0	0.1	0	0	39
12	2.2	0.2	0	0	0	0	0.1	17	1	0.1	0	0	0	0	0	53
13	4.6	0	15	0	0	0	0	0	1	o	7.2	0	0	0	0	0
14	1.5	0.4	14	0	0.1	0.1	0	0	1	0.3	22	0	0.1	1	1	0
15	2.4	1.0	50	0.2	1.6	0	0.3	0	1	0.3	26	0	0.6	1	1	0

Warren 2

Open

	September 1984								November 1984							
Quad	Bra	Cra	Enn	Era	Hel	Lop	Pla	Scl	Bra	Cra	Enn	Era	Hel	Lop	Pla	Scl
1	0.2	0.2	22	0	0	0.1	0.3	0	0	0	36	0	0	0	1	0
2	1.0	0.7	48	0	0.7	0.3	0.4	0	1	0.1	35	0	0.1	1	1	0
3	0.8	0.6	20	0	0	0	0	0	1	0	15	0	0.1	0	0	0
4	3.1	0	20	0	0.3	0	0.2	0	1	0	10	0	0	0	0	0
5	1.1	0	28	0	0	0	0	0	1	0	31	0	0	0	0	0
6	0	0	2.9	1.5	0.5	0.1	0	0	0	0	0	3.0	0.1	1	1	0
7	5.5	0	17	1.5	0.1	0	0	0.7	1	0	13	1.8	0	0	0	0
8	1.7	0	22	0	0	0	0	0	1	0	13	0	0.1	0	0	0
9	3.7	0	20	0	0	0	0	0.7	1	0	27	0	0	1	0	1.6
10	4.9	0	38	0	0.2	0.2	0	0	1	0	19	0	0	1	0	0
11	0	0	0	0	0	0	0	41	0	0	0	0	0	0	0	59
12	0.2	0	4.9	0	0	0	0	11	1	0	1.6	0	0	0	0	28
13	3.9	0.6	16	0.1	0	0	0	0	1	0.1	0	0	0	0	0	0
14	0.9	0.8	20	0	2.0	0.3	0.6	0	0	0.1	13	0	0.7	1	1	0
15	3.1	0.5	31	0	0.1	0	0	0	1	0.1	45	0	0	1	1	0

Quad - quadrat no. Bra - Brachycome lineariloba Cra - Craspedia pleiocephala Enn - Enneapogon avenaceous Era - Eragrostis dielsii Hel - Helipterum moschatum Lop - Lophochloa cristata Pla - Plantago drummondii Scl - Sclerolaena spp.

Where only 0 or 1 is recorded, 0 - absent, 1 - present.

Appendix 7 - Analysis of variance for regressions carried out on biomass data for grazing trials 1 to 3 (see part 2, sections 2 to 4).

1. Biomass data for grazing trials 1-3.

RD1A	T1A	RD1B	T1B	RD2A	T2A	RD2B	T2B	RD3B	T3B
0	210.7	0	164.0	0	297.5	0	298.4	0	269.9
3	163.3	3	131.8	3	251.0	3	233.2	3	321.3
6	130.9	6	140.3	6	229.2	6	222.0	6	288.6
9	123.3	9	102.8	9	190.3	9	182.6	9	260.8
12	122.7	17	99.3	12	150.4	12	153.1	12	283.5
15	94.3	23	63.0	15	139.0	15	151.6	15	215.1
18	86.6	29	45.9	18	127.8	18	136.5	18	181.6
21	62.7			21	120.2	21	134.5	22	146.3
24	50.9			24	104.5	24	120.2	26	150.1
27	35.5			27	86.8	27	86.3		
30	26.3			30	76.5	30	71.1		
33	19.3			33	60.8	33	64.4		
				36	56.0	36	59.3		
				39	44.5	39	48.1		
				42	33.9	42	39.6		
				45	27.5	45	40.7		
				48	34.6	48	38.1		

RDXY = Rabbit days, grazing trial X, pen Y.
TXY = Total biomass (g(3m^2)$^{-1}$), grazing trial X, Pen Y.

2. Results of analyses of variance

2.1 Grazing trial 1, pen A, including last 2 data points.

```
 Regression:  X is RD1A   Y is T1A       12 rows used

Origin  Y = B * X :  B =  2.5809     SD =  1.5043      T=   1.716  DF  11
Linear  Y = B0 + B1 * X :   B0                   B1
                        181.49               -5.3099
S.D. & T               6.9872    25.975    0.35867     14.804
R Squ =  0.9564   Prob =  0.0000

Quadratic  Y = B0 + B1 * X + B2 * X**2 :
                    B0                  B1                    B2
                 194.71              -7.9536              0.80112E-01
S.D. & T                          1.0768    7.386     0.31441E-01  2.548
F Test on quad term   6.4922     DF  1,   9  Prob = 0.0303
R Squ (uncorr) 0.9747  Prob = 0.0000    R Squ (corrected) 0.9690
QUAD  regression is adequate
```

```
ANOVA table from linear regression of T1A  against RD1A (   12 observations)
Source of var.        SS            df     Mean Square
---------------------------------------------------------
Regression :     36287.          1        36287.
    Error   :      1656.         10          166.
---------------------------------------------------------
    Total   :    37943.          11

 F-statistic =  219.17       DF = 1,    10
```

```
 ANOVA table from quadratic regression of T1A  against RD1A (   12 observations)
Source of var.        SS            df     Mean Square
---------------------------------------------------------
Regression :     36981.          2        18490.
    Error   :       962.          9          107.
---------------------------------------------------------
     Total   :    37943.          11

 F-statistic =  173.02       DF = 2,    9
```

2.2 Grazing trial 1, Pen A, excluding last 2 data points.

```
 Regression:  X is RD1A   Y is T1A      10 rows used

Origin  Y = B * X :  B =  4.0263     SD =  2.0922      T=    1.924  DF    9
Linear  Y = B0 + B1 * X :    B0                        B1
                           185.63                  -5.7436
S.D. & T                7.4915   24.779    0.46776      12.279
R Squ =  0.9496   Prob =  0.0000

Quadratic  Y = B0 + B1 * X + B2 * X**2 :
                    B0                  B1                        B2
                 195.37               -8.1789              0.90193E-01
S.D. & T                          1.5814     5.172      0.56384E-01   1.600
F Test on quad term   2.5587     DF  1,   7  Prob = 0.1515
R Squ (uncorr) 0.9631  Prob = 0.0000   R Squ (corrected) 0.9526
LIN.  regression is adequate
```

```
ANOVA table from linear regression of T1A  against RD1A (   10 observations)
Source of var.        SS            df     Mean Square
---------------------------------------------------------
Regression :     24495.          1        24495.
    Error   :      1300.          8          162.
---------------------------------------------------------
     Total   :     25794.          9

 F-statistic =  150.77       DF = 1,    8
```

```
 ANOVA table from quadratic regression of T1A  against RD1A (   10 observations)
Source of var.        SS          df     Mean Square
-------------------------------------------------------
Regression :    24843.        2       12421.
    Error   :      952.        7         136.
-------------------------------------------------------
     Total  :    25794.        9

 F-statistic =  91.353       DF = 2,    7
```

2.3 Grazing trial 1, pen B

```
Regression:  X is RD1B   Y is T1B       7 rows used

Origin  Y = B * X :  B =  3.7146      SD =  2.4791      T=   1.498  DF    6
Linear  Y = B0 + B1 * X :   B0                        B1
                          153.62                  -3.7725
S.D. & T              7.1393    21.517     0.44708       8.438
R Squ =  0.9344   Prob =  0.0007
Quadratic  Y = B0 + B1 * X + B2 * X**2 :
                       B0                  B1                        B2
                    156.41             -4.5546                0.27171E-01
S.D. & T                             1.9227    2.369       0.64598E-01  0.421
F Test on quad term  0.17695      DF  1,   4  Prob = 0.6944
R Squ (uncorr) 0.9372  Prob = 0.0024    R Squ (corrected) 0.9057
LIN.  regression is adequate

 ANOVA table from linear regression of T1B  against RD1B (    7 observations)
Source of var.        SS          df     Mean Square
-------------------------------------------------------
Regression :    10015.        1       10015.
    Error   :      703.        5         141.
-------------------------------------------------------
     Total  :    10719.        6

 F-statistic =  71.203       DF = 1,    5

 ANOVA table from quadratic regression of T1B  against RD1B (    7 observations)
Source of var.        SS          df     Mean Square
-------------------------------------------------------
Regression :    10045.        2        5023.
    Error   :      673.        4         168.
-------------------------------------------------------
     Total  :    10719.        6

 F-statistic =  29.830       DF = 2,    4
```

2.4 Grazing trial 2, pen A

```
Regression:  X is RD2A   Y is T2A       17 rows used

Origin  Y = B * X :  B =  2.2120     SD =  1.1468      T=   1.929  DF   16
Linear  Y = B0 + B1 * X :   B0                      B1
                          243.30                 -5.1607
S.D. & T                11.298   21.535     0.40146   12.855
R Squ =  0.9168   Prob =  0.0000
Quadratic  Y = B0 + B1 * X + B2 * X**2 :
                B0                    B1                    B2
             282.70                -10.414               0.10944
S.D. & T                  0.61806    16.849    0.12423E-01   8.809
F Test on quad term   77.599      DF  1,  14  Prob = 0.0000
R Squ (uncorr) 0.9873  Prob = 0.0000    R Squ (corrected) 0.9855
QUAD  regression is adequate

ANOVA table from linear regression of T2A  against RD2A (   17 observations)
Source of var.        SS           df       Mean Square
-----------------------------------------------------------
Regression :      97796.          1         97796.
     Error   :       8877.         15           592.
-----------------------------------------------------------
     Total   :   106673.          16

F-statistic =   165.25        DF = 1,    15

ANOVA table from quadratic regression of T2A  against RD2A (   17 observations)
Source of var.        SS           df       Mean Square
-----------------------------------------------------------
Regression :     105316.          2        52658.
    Error   :        1357.        14             97.
-----------------------------------------------------------
     Total   :      106673.        16

 F-statistic =   543.36        DF = 2,    14
```

2.5 Grazing trial 2, pen B

```
Regression:  X is RD2A   Y is T2B       17 rows used
Origin  Y = B * X :  B =  2.3674     SD =  1.1305      T=   2.094  DF   16
Linear  Y = B0 + B1 * X :   B0                      B1
                          240.23                 -4.9123
S.D. & T                10.573   22.722     0.37568   13.075
R Squ =  0.9193   Prob =  0.0000
Quadratic  Y = B0 + B1 * X + B2 * X**2 :
                        B0                    B1                    B2
                     274.40                -9.4688             0.94929E-01
S.D. & T                              0.77175   12.269    0.15513E-01   6.119
F Test on quad term   37.448      DF  1,  14  Prob = 0.0000
R Squ (uncorr) 0.9781  Prob = 0.0000    R Squ (corrected) 0.9749
QUAD  regression is adequate
```

```
ANOVA table from linear regression of T2B  against RD2A (   17 observations)
Source of var.        SS          df      Mean Square
-------------------------------------------------------
Regression :     88606.          1       88606.
    Error  :      7774.         15         518.
-------------------------------------------------------
    Total  :     96380.         16
F-statistic =  170.97       DF = 1,   15
```

```
ANOVA table from quadratic regression of T2B  against RD2A (   17 observations)
Source of var.        SS          df      Mean Square
-------------------------------------------------------
Regression :     94265.          2       47132.
    Error  :      2115.         14         151.
-------------------------------------------------------
    Total  :     96380.         16
 F-statistic =  311.92       DF = 2,   14
```

2.6 Grazing trial 3, pen B.

```
Regression:  X is RD3B   Y is T3B       9 rows used
Origin  Y = B * X :  B =  11.148      SD =  4.2429      T=   2.627  DF    8
Linear  Y = B0 + B1 * X :   B0                      B1
                         317.15                 -6.6409
S.D. & T              17.545    18.076     1.1832      5.613
R Squ =  0.8182   Prob =  0.0009
Quadratic  Y = B0 + B1 * X + B2 * X**2 :
                        B0                      B1                      B2
                   299.29                  -1.9439                 -0.18222
S.D. & T                                 4.0640   0.478        0.15126   1.205
F Test on quad term   1.4513      DF  1,  6  Prob = 0.2737    R Squ (uncorr) 0.8536
Prob = 0.0013    R Squ (corrected) 0.8048
LIN.  regression is adequate
```

```
ANOVA table from linear regression of T3B  against RD3B (    9 observations)
Source of var.        SS          df      Mean Square
-------------------------------------------------------
Regression :     26902.          1       26902.
    Error  :      5978.          7         854.
-------------------------------------------------------
    Total  :     32879.          8
 F-statistic =  31.503      DF = 1,    7
```

```
ANOVA table from quadratic regression of T3B  against RD3B (    9 observations)
Source of var.        SS          df      Mean Square
-------------------------------------------------------
Regression :     28066.          2       14033.
    Error  :      4813.          6         802.
-------------------------------------------------------
    Total  :     32879.          8
 F-statistic =  17.493      DF = 2,    6
```