PALATABILITY VARIATION BETWEEN THE SEX PHENOTYPES OF BLADDER SALTBUSH (*ATRIPLEX VESICARIA*)

by

Dionne Lee Maywald

Departments of
Environmental Science & Management
and
Botany

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SUMMARY

This study reports the first thorough investigation of palatability variation in *Atriplex vesicaria* Heward ex Benth. (bladder saltbush). The main aims of this research were to examine the idea that the sex phenotypes of this species differ in their palatability to sheep, and to characterise some of the temporal and spatial features of the phenomenon.

Intensive small-plot dietary trials were conducted in a chenopod community to determine whether sheep would selectively graze the sexes of bladder saltbush. The results showed that sheep preferentially grazed female saltbushes over male and bisexual ones, which supported previous research from New South Wales. This result was subsequently demonstrated at several spatial scales including a paddock dietary experiment, a series of cross-fence comparisons and in cafeteria trials.

The cafeteria trials showed that sheep avoid grazing male saltbushes due to a chemical deterrent. Sheep are able to detect and avoid male plants by sight using the male flower spike as a visual cue. In the absence of an obvious visual cue, sheep rely on an olfactory cue to detect male plants. The identification and characterisation of the chemical deterrent was beyond the scope of this study, and remains an area for further research.

Several detrimental effects of selective grazing were detected during this study. Grazing was shown to reduce the size and reproductive output of female shrubs. Furthermore, it was shown that sheep tend to return to shrubs which they have grazed previously, and thus keep them in a chronically reduced state.

In the semi-arid rangelands of South Australia, where bladder saltbush appears to be grazed year-round, physical protection will be required to maximise the survival and reproductive output of moderately to heavily grazed populations.

DECLARATION

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

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

21/1/98

Date

Dionne Lee Maywald

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CHAPTER 1
INTRODUCTION

PROJECT OVERVIEW

There is mounting evidence that the sex phenotypes of *Atriplex vesicaria* Heward ex Benth.[1] are not equally palatable to Merino sheep in the rangelands of southern Australia. The information to date has been largely anecdotal; however, the results of some studies support the notion that the female phenotype is preferentially grazed over the male. The aims of this project were to:

- Verify that the sex phenotypes of *A. vesicaria* vary in their palatability.
- Characterise some of the spatial and temporal contexts of the palatability variation.
- Attempt to elucidate the cues in *A. vesicaria* which influence the behaviour of sheep.
- Highlight some of the ecological implications of intraspecific variation in palatability, and how these may influence pastoral land management and monitoring.

It is well known that when animals are presented with a range of plant species, they do not graze them equally. In many systems, where animal behaviour is relatively consistent or where the context is well understood, the order of consumption of different species can often be

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[1] Nomenclature in this thesis follows Jessop & Toelken (1986) and Jessop (1993).

predicted according to the relative palatability and abundance of individual species (e.g. Leigh & Mulham 1964, 1966, 1967, Robards *et al.* 1967, Leigh 1974). At a finer scale, animals also selectively graze individual plants within a species, or plant parts on a single individual. Previous grazing trials have indicated that intraspecific variation in palatability occurs for several chenopod species in South Australia (Maywald 1993). One of these species is *Atriplex vesicaria*, which was chosen for this detailed study of palatability variation because:

- It is a widespread species throughout the chenopod shrublands of Australia.
- It is recognised as an important ecological and forage species.
- Its basic biology is generally understood and a large body of literature is associated with it.
- There is accumulating evidence that palatability variation occurs within the species.

LITERATURE REVIEW - THE AUSTRALIAN RANGELANDS

Description

Generally, the term 'rangeland' in Australia describes those areas where rainfall is insufficient in amount and/or reliability to support sustained crop production (Box & Perry 1971). Thus defined, about 75% of Australia (or 5.7 million km$^{2)}$ is arid or semi-arid rangeland (Perry 1977). Of this area, almost half is used for permanent, free-range livestock grazing on native vegetation (Wilson & Graetz 1979). Pastoral management is sedentary rather than nomadic, and apart from shearing, crutching, lamb marking, branding and culling, sheep and cattle are left to fend for themselves throughout the year (Williams 1980). The areas of the rangelands that are not used for pastoral purposes include Aboriginal lands, conservation reserves, mining leases and unoccupied desert (Maconochie 1996).

The topography of the Australian rangelands is generally low and undulating and does not receive snow (Perry 1977). As a result of the subtle change between the seasons, some rangeland plants do not demonstrate marked seasonality in their growth and reproduction (Wilson & Graetz 1979). Instead, these processes often occur in response to rainfall, which is highly erratic and unpredictable. The soils of Australia's rangelands are very old and are highly weathered (Stafford Smith & Morton 1990). As a consequence, they are of poor structure and fertility compared to others throughout the world (Perry 1977, Stafford Smith & Morton 1990).

The Chenopod Shrublands

The chenopod shrublands (Figure 1.1) are recognised as an important resource base for animal production and are used for extensive pastoral operations in southern Australia (Crisp 1975, Jackson 1958, Hacker 1987). Dominated by species of *Atriplex, Maireana, Rhagodia* and *Sclerolaena,* these shrublands support a sheep pastoral industry whose main product

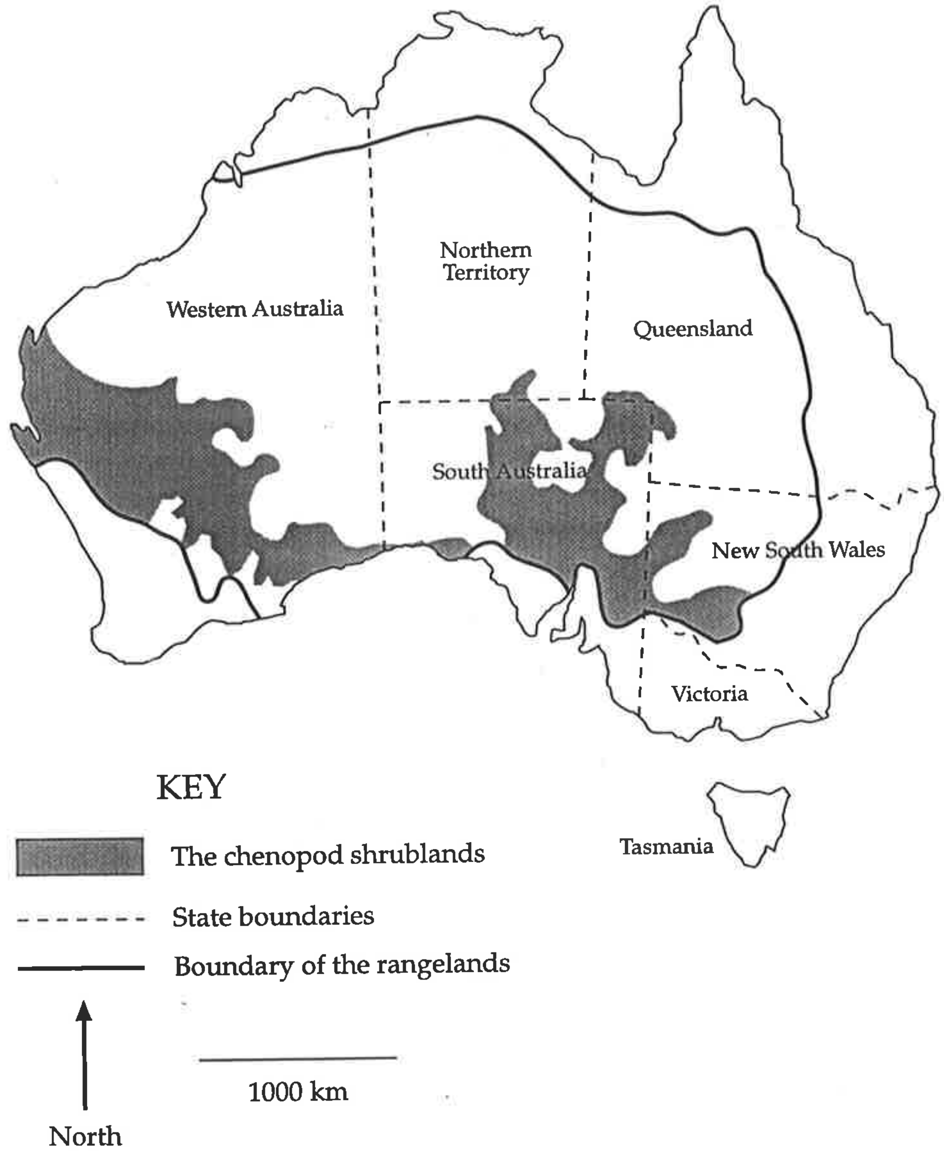

FIGURE 1.1. Location of the chenopod shrublands within the rangelands of Australia (after Wilson & Graetz 1979).

is wool (Graetz & Wilson 1984). Chenopod low shrubland associations cover about half a million hectares, or seven percent of Australia (Leigh 1994). This figure underestimates the true coverage of chenopod shrubs, as they also form the understorey in low woodland associations with various species of *Acacia, Casuarina, Eucalyptus, Myoporum* and *Alectryon* (Leigh 1972, Beadle 1981). Unlike some other parts of Australia and the world, these shrublands represent the climax vegetation and are not the result of woody plant invasion due to disturbance (Braunack & Walker 1985, Harrington 1986, Herbel 1986).

South Australia is a logical place to study chenopod shrublands because 87% of the state is rangeland and it contains the greatest area of chenopod shrubland in Australia (Perry 1967, Graetz & Wilson 1984, Leigh 1994). Furthermore, the geographical range of the chenopod shrublands in South Australia is thought to have been relatively unchanged by European settlement compared to other states (Oxley 1979).

The Genus Atriplex

Members of the genus *Atriplex* (Family Chenopodiaceae) are found on all continents (Osmond *et al.* 1980). The genus is recognised as an important source of species for game habitat, revegetation and animal production throughout the world (Carter 1986, Khalil *et al.* 1986, Potter *et al.* 1986, Garza & Fulbright 1988, Stringi *et al.* 1994). Australia exhibits one of the highest levels of endemism for the genus and is regarded as an important centre of diversification (Osmond *et al.* 1980). *A. vesicaria* is endemic to

Australia and is the most widespread of the 61 species in the country (Parr-Smith 1982, Wilson 1984). It is found in a discontinuous arc from the coastal areas of Western Australia, through much of South Australia and into central New South Wales (Figure 1.2, Oxley 1979). Small areas also occur in the Northern Territory and northern Victoria (Oxley 1979).

LITERATURE REVIEW - *ATRIPLEX VESICARIA*

Taxonomy and Description

Atriplex vesicaria Heward ex Benth. was first described in 1817 from a specimen collected at Molle's Plain in New South Wales (Wilson 1984). Its common name is bladder saltbush or perennial saltbush (Cunningham *et al.* 1992). The term bladder saltbush will be used in this thesis.

Bladder saltbush can exhibit an erect or decumbent habit and can grow to about one metre in height (Wilson 1984). Male and female flowers are mostly carried on separate plants; however, a minority of plants do carry flowers of both sexes (Bisalputra 1960). Thus, according to the conventions of Westergaard (1958), bladder saltbush is considered to be subdioecious. The male flowers are borne in terminal spikes whilst the female flowers are found in the axils of the upper leaves (Wilson 1984). Bladder saltbush exhibits several morphological variants (Parr-Smith & Calder 1979, Parr-Smith 1982). Most of the distinguishing characteristics of these are related to the fruiting body borne on the female; however, growth habit and leaf dimensions are also used to distinguish between

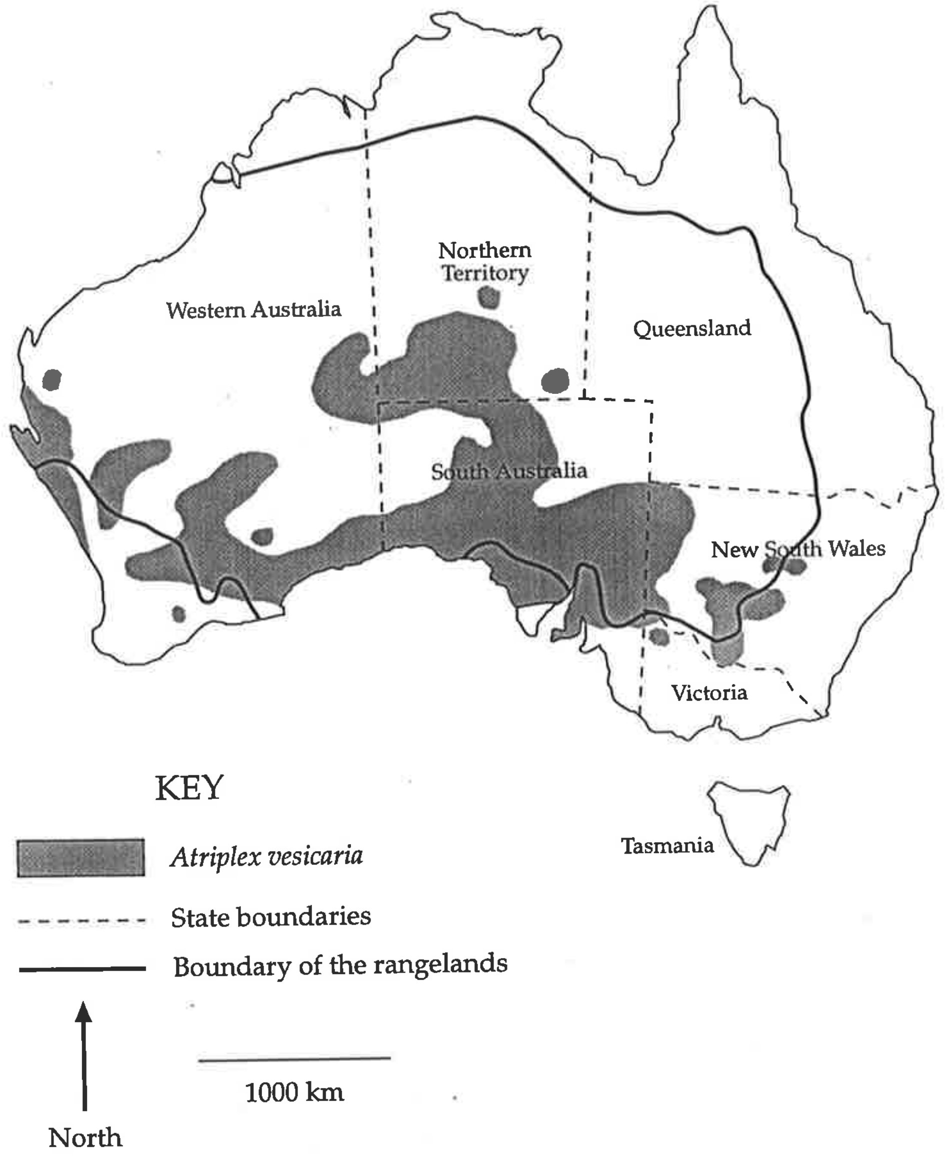

FIGURE 1.2. Approximate range of *Atriplex vesicaria* (composite from Wilson 1984, Wilson & Graetz 1979).

the forms (Parr-Smith & Calder 1979, Parr-Smith 1982). Of the variants, eight have been formally recognised as subspecies (Wilson 1984) even though some of the defining characteristics vary across edaphic and climatic contexts (Parr-Smith & Calder 1979, Osmond *et al.* 1980). Genetic variability in bladder saltbush is relatively high (Parr-Smith 1982, Pearson 1988) and hybridisation between the subspecies is likely (Anderson 1930). The eight subspecies are probably the major variants, and localised forms are likely to occur (Parr-Smith & Calder 1979).

Longevity, Growth and Survival

Long-term records from the T.G.B. Osborn Vegetation Reserve at Koonamore Station (South Australia) indicate that the half-life of *A. vesicaria* cohorts is about eleven years (Crisp 1978). The maximum life-span of individual shrubs appears to be about 25 to 30 years (Crisp 1978).

When there is sufficient soil moisture, bladder saltbush can grow very quickly (Noble 1977, Williams 1979). The response of shrubs to moisture varies depending on the ambient conditions. In cooler seasons, rainfall usually occurs in frequent small showers and the growth of bladder saltbush is relatively steady. In the hottest months, however, rains often occur as discrete large falls which initiate a pulse of growth (Noble 1977).

Bladder saltbush is considered to be drought deciduous (Osborn *et al.* 1932). In the absence of grazing, shrubs can lose all of their leaves during prolonged drought and then resprout when favourable conditions return (Osborn *et al.* 1932). Under grazing, however, shrubs which lose all of their leaves are likely to die (Knowles & Condon 1951, Leigh & Wilson 1970). This is because bladder saltbush initiates growth from young stems, and resprouting does not generally occur on mature branches (Leigh & Mulham 1971, but see Coleman 1982). Repeated grazing removes primordia and leaves and may deplete the reserves of total non-structural carbohydrate available for regrowth, resulting in the death of the plant (Leigh & Mulham 1971, Williams *et al.* 1978, Coleman 1982).

The Root System and Adaptation to Drought and Heat

The root system of bladder saltbush is considered to be relatively shallow, with most roots confined to the top 30 centimetres of the soil, but they can extend up to two metres horizontally (Osborn *et al.* 1932, Carrodus & Specht 1965, Jones & Hodgkinson 1970). During favourable conditions, short-lived feeding roots are produced close to the soil surface in response to light rain showers (Knowles & Condon 1951). *A. vesicaria* can reduce soil moisture to a significantly lower level than other chenopods (such as *Maireana sedifolia*) during drought conditions (Carrodus & Specht 1965).

In addition to its root system, bladder saltbush also exhibits other traits which help it to tolerate dry conditions. Wood (1925) demonstrated that bladder saltbush can absorb moisture via the vesicular hairs on the leaves. It has been suggested that this would allow saltbushes to use early-morning humidity, dew and small rain showers during dry periods (Osborn *et al.* 1932, Knowles & Condon 1951). This assumes that the plant has a mechanism to incorporate the water into metabolic processes. This has not been demonstrated as yet (Carrodus & Specht 1965). The absorption of water by the vesicular hairs on the leaves probably does help to slow transpiration (Carrodus & Specht 1965). When humidity falls below a threshold level, the dense mat of vesicular hairs on the leaf surface collapse to form a barrier to moisture loss (Osborn *et al.* 1932, Knowles & Condon 1951). In conjunction with a layer of sodium chloride excreted from inside the leaves, these collapsed vesicles result in high reflectance which may help to control the heat loads of leaves (Sinclair & Thomas 1970). These characteristics suggest that bladder saltbush is well adapted to the variable moisture conditions imposed by the climate and the soils it occupies (Noy-Meir 1973).

Reproduction and Recruitment

Flowering and seed set in bladder saltbush is opportunistic and can happen several times a year if favourable conditions occur (Wood 1936, Williams 1979). Like most *Atriplex* species, *A. vesicaria* relies on wind, rather than animals, for pollination and seed dispersal (Condon & Knowles 1952, Williams 1979). It is known that certain species of harvester ants can take large amounts of saltbush seed; however, this is not seen to be significant to the survival of saltbush populations (Briese 1982). Whether this is true in heavily grazed populations (which have low seed production) remains to be tested (Hunt 1995).

The fruiting body consists of a single seed surrounded by a thin pericarp (the true fruit) and is enclosed by a pair of papery bracteoles which may or may not have spongy appendages attached[2] (Bisalputra 1960). The seeds are lenticular in shape, about 1.5 to 2.5 millimetres in diameter, and are dimorphic (Beadle 1952). Hard seeds have a longer life span than soft seeds because they are less permeable to water (Beadle 1952). Many researchers suspect that the bracteoles surrounding the seed provide a dormancy mechanism in bladder saltbush. It has been suggested that seeds will not germinate until sufficient rainfall has washed the excess chloride from the bracteoles (Beadle 1952). This mechanism presumably prevents seeds from germinating in response to light rainfalls or dew.

Some researchers believe that recruitment is more likely during cooler seasons because prolonged high temperatures kill emerging radicles and desiccate young recruits (Beadle 1952, Williams 1979). However, recruitment has been recorded in all seasons (Crisp 1978, Eldridge & Westoby 1991). In summer, establishment probably only occurs when sufficient moisture is coupled with a period of cooler temperatures (Beadle 1952). Surviving cohorts of seedlings establish about once in five years (Graetz & Wilson 1984). The plants in chenopod shrublands usually display a clumped distribution (Osborn *et al.* 1932, Anderson 1967), which is a phenomenon common to these shrublands throughout the world (West 1982). Soil, litter and seed tend to accumulate around established plants to form mounds which, in turn, may provide favourable conditions for seed bed development (Osborn *et al.* 1932, Wood 1936).

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[2] Throughout this thesis, the term 'fruit' will be used to refer to the entire fruiting body (seed, pericarp and papery bracteoles).

Young bladder saltbush seedlings are often clustered around vigorous female plants, because the seeds do not disperse far from the mother plant (Williams *et al.* 1978, Williams 1979). However, many of the seedlings which establish under the mother plant subsequently die as a result of competition (Williams *et al.* 1978). Theoretically, plant establishment should thus be favoured between clumps, rather than within them. This is not the case, because the moisture and nutrient environment beneath mature shrubs is better for germination and early establishment. Furthermore, the areas between the clumps become sheep tracks, and seedlings which attempt to establish there are usually trampled (Williams *et al.* 1978). The activities of sheep thus determine some of the pattern seen in grazed populations. Small-scale pattern also occurs in the absence of grazing, because the plants modify many soil properties in their vicinity (Charley & McGarity 1964, Sharma 1973, West 1982). It must be noted that saltbush shrublands are also patterned at larger scales due to variations in soil type, topography and moisture conditions (Valentine & Nagorcka 1979, Eldridge 1986).

Ecological & Economic Value

Wilson & Graetz (1979) noted that *A. vesicaria* is "the most important" contributor to ecosystem stability in the chenopod shrublands. It is recognised as a soil-binding species which ameliorates soil erosion (Osborn *et al.* 1932, Leigh & Mulham 1971, Eldridge *et al.* 1990). It is this feature, in conjunction with its drought tolerance, that has made it an important contributor to stable pastoral productivity (Rhodes 1986).

Wood (1936) regarded bladder saltbush as the most important fodder shrub in arid Australia because it is nutritious and drought resistant. Beadle (1952) described it generally as "an important forage"; however, Eldridge *et al.* (1990) deemed it to be unimportant in average seasons. Scholz (1996) noted that conflicting opinions about the value of saltbush can be explained by differences in context. For example, pastoralists in less arid areas often have relatively reliable stands of highly productive pasture plants like *Medicago* and *Danthonia*. In these areas, bladder saltbush may not be a major component of the diet during average conditions (Clift *et al.* 1987). In more arid areas, however, saltbush tends to be grazed all of the time, regardless of conditions (Osborn 1925, Knowles & Condon 1951). This appears to be true in the chenopod shrublands of eastern Eyre Peninsula (South Australia) where this study was conducted (A.D. Nicolson & D.A. Nicolson, pers. comms, Hunt 1995).

It is widely accepted that bladder saltbush is relatively less palatable compared to grasses and forbs; however, the latter quickly dry out and disappear during dry periods and saltbush then becomes an important component of the diet (Leigh & Mulham 1964, 1966, 1967, Wilson & Graetz 1979). Bladder saltbush contains sufficient protein for wool growth and for the maintenance of general animal condition (Wood 1936, Leigh & Mulham 1971, Sharma *et al.* 1972). The high salt content of the species results in a high dependence on good quality water for those animals grazing it (Osmond *et al.* 1980). Unfortunately, the salt content of bladder saltbush is highest during summer and drought when sheep rely on it the most (Sharma *et al.* 1972).

Value as an Indicator Species

The ecological structure of rangeland communities is often greatly modified by grazing (Williams *et al.* 1978). The cover or density of the perennial component of the vegetation should be included in any monitoring program in the chenopod shrublands. This is because perennials represent the underlying stability of the system (Graetz & Ludwig 1978, Lange *et al.* 1994). This point has been recognised by the statutory pastoral management body in South Australia, which uses certain species of perennial chenopods as a basis for land condition assessment (Parliament of South Australia 1989, Lange *et al.* 1994). One of the important indicator species used in this process is bladder saltbush. Bladder saltbush is relatively palatable, more susceptible to grazing and trampling, and short-lived compared to other chenopod shrubs (Graetz & Wilson 1984). These features in combination make bladder saltbush an important early warning indicator of degradation in chenopod shrublands (Lange *et al.* 1994, Hunt 1995).

In the context of this thesis, palatability variation within the species may mean that some individuals are more susceptible to grazing than others, which could lead to monitoring at a finer scale than at present. This may mean that rangeland degradation could be detected even earlier.

EFFECTS OF GRAZING ON THE CHENOPOD SHRUBLANDS AND *ATRIPLEX VESICARIA*

Temporal and spatial variability in sheep behaviour influences community and population composition, range condition and ecosystem stability (Squires 1982). Long-term selective grazing may lead to populations and communities which are of relatively low palatability (Pearson *et al.* 1990). Sheep are known to be remarkably selective. For example, Lange & Willcocks (1980) showed that sheep in a large rangeland paddock were able to detect and consume lucerne cubes which made up less than 1/200,000th of the forage on offer. This degree of detection has also been shown by Ireland (1997) and Maywald (1993) using native plant species on eastern Eyre Peninsula.

Landscape Scale

It must be emphasised that the Australian flora did not evolve in the presence of large, ungulate herbivores (Osborn *et al.* 1932, Williams 1980, Squires 1989, Lange *et al.* 1994). Due to the lack of permanent surface water, much of the Australian rangelands would only have been grazed by transient populations of animals (Beadle 1959, Moore 1959). Furthermore, it is probable that the marsupials which grazed the country had different preferences to introduced livestock (Robertson *et al.* 1987). The general lack of anti-herbivory mechanisms in Australian rangeland plants supports this hypothesis (Mitchell 1991). Widespread damage occurred to the arid flora once livestock and the European rabbit were introduced (Adamson & Fox 1982), to the extent that it has been described as a "national loss" (Dixon 1892). It is generally accepted that a lack of knowledge, combined with periods of favourable climatic and pasture conditions, led the pastoral industry to overestimate the capabilities of the land (Ratcliffe 1959, Perry 1977, Purvis 1986, Green 1989, but see also Quinn 1997). The plants and soils were damaged further when rabbits invaded the pastoral areas (Ratcliffe 1959, Moore 1969, Perry 1977). Although it is generally believed that the worst pasture and soil degradation occurred 'in the past', overgrazing during periods of drought and economic depression still occurs (Purvis 1986, Pickup & Stafford Smith 1993).

In western New South Wales, early overgrazing of vegetation associations containing *Atriplex* led to the establishment of relatively stable disclimax grasslands (Leigh & Mulham 1964, Williams 1972). This modification is generally considered to be non-detrimental to the pastoral industry (Westoby *et al.* 1989); however, recent concerns with wool quality (e.g. tensile strength) may be changing this view (A.W. Nicolson, pers. comm.). In other areas (especially those with duplex soils) the shrubland has been directly replaced by relatively unpalatable shrubs, sparse herbaceous cover, or scalds (Beadle 1959, Leigh & Wilson 1970). This pattern occurs in much of South Australia, where the soils are highly erodable and the rainfall regime does not allow stable disclimax grasslands to form (Newman & Condon 1969, French & Potter 1975, Lange *et al.* 1984). It has been proposed that some of the land damaged in the early days of agricultural expansion may never recover (Jackson 1958).

Paddock & Population Scales

Sheep grazing on chenopod shrubland have a high dependence on water and must return to the waterpoint frequently (Wilson 1974). The consequent grazing and trampling pressure is thus greatest near the waterpoint (Squires 1981, Andrew 1988). The interactions between the animals, plants and soils surrounding the waterpoint is known as the piosphere (Lange 1969). The dynamics of the piosphere are determined by the capacity of stock to forage away from the waterpoint (Squires 1982). In the sheep lands, trampling and grazing pressures are highest within two kilometres of the water (Graetz & Ludwig 1978, Squires 1993).

According to the definitions of Dyksterhuis (1949), bladder saltbush is a "decreaser" species due to its susceptibility to grazing and trampling (Osborn *et al.* 1932, Barker & Lange 1970, Hacker 1987). Within a few years of stock being introduced to a new waterpoint, saltbush suffers high mortality (Andrew & Lange 1986b). This mortality, caused by grazing and trampling, is exacerbated by drought (Andrew & Lange 1986b). Bladder saltbush has few attributes which confer grazing tolerance or avoidance (Archer & Pyke 1991).

It has been suggested that beyond the 'sacrifice zone' near the waterpoint, some grazing increases the vegetative vigour of bladder saltbushes (Osborn *et al.* 1932, Wood 1937, Leigh & Mulham 1964, Graetz & Wilson 1984, Andrew & Lange 1986b). Although the shrubs may be vegetatively more vigorous, it is known that the saltbushes closer to water do not flower as much as those further away (Andrew & Lange 1986b, Hunt

1995). Furthermore, there are actually less shrubs close to the water due to increased mortality and restricted recruitment (Hunt 1995). Thus, the increase in vigour is often used as an example of how grazing can produce a more appetising resource for pastoral use, even though the overall picture indicates that many populations may be at risk of local extinction (Hunt 1995). This is because chronically grazed saltbushes channel energy into regrowth at the expense of reproduction and thus do not produce very many seeds (Hunt 1995). Furthermore, the seeds which are produced are relatively short-lived (Hunt 1995). In some cases, regeneration may only occur if seeds disperse from nearby reproductive populations (Hall *et al.* 1964). The rate of regeneration may also be affected by the degree to which the structure and fertility of the soil have suffered (Charley & Cowling 1968).

Herbivores Other than Sheep

Rabbits graze saltbush very rarely, presumably due to the high salt content, which would force them to drink (Wood 1932, Wood 1936, Knowles & Condon 1951, Hall *et al.* 1964). Rabbits usually obtain their water requirements from the food that they consume because free water is often absent from their home range (Short 1987). Rabbits have been known to ringbark and strip the foliage from saltbushes and other chenopod shrubs during dire feed shortages (Hall *et al.* 1964, Short 1985). However, Jessup (1951) noticed that rabbits in plague proportions did not actually destroy any areas of saltbush or bluebush in north-western South Australia during the 1940's.

It is generally accepted that the establishment of waterpoints where only ephemeral water sources existed before, has led to much greater use of the rangelands by kangaroos (Moore 1969, Leigh 1974). Kangaroos are known to graze chenopod shrubs when forage conditions deteriorate (Ellis *et al.* 1977, Stanley 1978, Barker 1987). Ellis *et al.* (1977) found that flat leaved chenopods (chiefly *Atriplex* spp.) made up only a small fraction (<10%) of the diet of red kangaroos and euros; however, seasonal and individual animal variability was often high. Barker (1987) suggested that perennial bluebush and saltbush may represent the "last dietary resort" for the red kangaroo. In a recent study in the Middleback region of South Australia, rabbits and kangaroos consumed very little saltbush over a period of several years (Hunt 1995).

PALATABILITY AND PREFERENCE

Definitions

It is necessary at this point to define two terms used extensively in the plant-herbivore literature and this thesis. The words palatability and preference have been used interchangeably in the past; however, scientists now accept that they are separate, but closely related terms.

Palatability is a *plant* characteristic which elicits a selective response in animals (Vallentine 1990, Stuth 1991). It is a relative entity which cannot be directly measured because many physical and chemical attributes of the plant and its environment combine to determine palatability (see Vallentine 1990).

Preference is an *animal* characteristic which involves the selection of some forages over others and is thus largely behavioural (Stuth 1991). It is determined by plant palatability and availability and is modified by the physiological status of the animal. Preference, unlike palatability, is measurable.

The Use of Preferences to Infer Palatability

It must be emphasised that palatability and preference are both relative entities, rather than absolute or fixed ones, and that they are quite specific to the context of the study. This point highlights the dynamic nature of the plants and the animals that graze them. As palatability cannot usually be measured, and preference can, ecologists use animal preferences to infer the relative palatability of plants. The assumption that consistent and repeated preferences are an indirect measure of relative palatability underlies dietary research and will be used in this thesis.

Palatability Variation Within Species

It is common knowledge that animals display preferences for some species over others when presented with a selection of different forages. Using the assumption outlined above, the cause of this is palatability variation between different species. Animals also selectively graze individual plants within a species and even show selectivity for different parts of the same plant. These fine-scale preferences are an indication of palatability variation within a species. Although Squires (1981) stated that management of a plant community should be at the level of the plant species, it must be recognised that herbivores can impact on plants at finer scales. Subspecies of big sagebrush (*Artemisia tridentata*) and black sagebrush (*A. nova*) are grazed to different extents by herbivores in the western United States (Sheehy & Winward 1981, Welch *et al.* 1981, Behan & Welch 1985, Welch & McArthur 1986). Sheehy & Winward (1981) noted that relative palatability ratings at the level of species rather than subspecies would be misleading and confusing for managers. There are also many examples of intraspecific variation in palatability for different species of *Atriplex*. Palatability variation between biotypes of the north American *A. canescens* is suspected but has not been tested (Richardson 1982). A recent study of *A. canescens* in Utah showed that sheep preferentially graze male shrubs over female ones in late spring (Maywald *et al.* 1997). This selectivity appears to be seasonal, as no difference was detected in late winter (Maywald *et al.* 1998). Stringi *et al.* (1994) demonstrated differences in palatability between genotypes of *A. halimus* in Italy. Recent observations from the temperate zone of South Australia indicate that sheep graze some individuals of *A. nummularia* whilst leaving others untouched (Jackson 1997). Different varieties of *A. nummularia* are known to be selectively grazed by livestock in Western Australia (Mitchell & Wilcox 1988). Rabbits selectively graze strains of several introduced and native *Atriplex* species in North America (Nord & Stallings 1975).

Only a few studies have identified the underlying causes of palatability variation within species. Some of these studies have found correlations between utilisation and secondary chemistry. For example, snowshoe hares and moose selectively browse the adult parts of Alaska paper birch because the juvenile growth contains much higher levels of a feeding deterrent (Reichardt *et al.* 1984). Mountain hares in Finland also selectively graze the juvenile growth over the mature growth in willows due to chemical deterrents (Tahvanainen *et al.* 1985).

Palatability Variation Within A. vesicaria

Preliminary evidence for palatability variation within bladder saltbush is largely anecdotal. Several researchers have suggested palatability variation occurs between ecotypes (Knowles & Condon 1951, Graetz & Wilson 1984), but none have tested it quantitatively. Graetz & Wilson (1984) implied that some ecotypes withstand grazing better than others because they vary in their susceptibility to defoliation. Knowles & Condon (1951) suggested that paddocks in New South Wales require periodic spelling because sheep relish the seedlings of bladder saltbush. However, quantitative studies in South Australia have shown that sheep tend to avoid grazing the seedlings, even when other forages are extinguished (Lange *et al.* 1992, Maywald 1993). Palatability variation between adult bladder saltbushes is supported by anecdotal reports at the inception of the T.G.B. Osborn Vegetation Reserve (Koonamore, South Australia). This reserve was formed by fencing off “the worst eaten out corner” of a pastoral paddock where “most of the perennial undershrubs in the original flora had disappeared" (Osborn 1925). Several comments indicate that some saltbushes were able to escape or tolerate the extreme grazing that killed most individuals of the once widespread population (Hall *et al.* 1964, pg 243):

> *"a few battered bushes, mostly of Atriplex vesicaria, were all that remained of the shrub cover"*
>
> *"practically all the original Atriplex bushes had been destroyed"* and;
>
> *"the odd Atriplex bush [was] left in the reserve in 1926"*

A quantitative study by Fatchen (1978) reports a similar pattern. In 1929 a transect was established in a virgin chenopod stand on Frome Downs Station, and surveyed prior to the introduction of stock to a new waterpoint. In 1929 there were 946 saltbushes on the transect. In 1974 there were only four saltbushes present. Although those four shrubs were not members of the original population (due to the lifespan of saltbush), they must have had some resistance which allowed them to establish and persist under grazing, when others could not. Similarly, diagrams published by Barker & Lange (1969, 1970) show scattered individuals of bladder saltbush close to waterpoints which were once dominated by saltbush. Those researchers thought that the presence of saltbushes close to long-established waterpoints was "strange". Lange (1969) noted that the chance of an individual plant escaping the attention of sheep in chenopod shrubland is negligible. Thus, it is likely that ungrazed individuals of relatively palatable species (like bladder saltbush) have been actively avoided. Pearson *et al.* (1990) found large variation in palatability within, and between, populations of bladder saltbush in South Australia. In their unreplicated trial, they found that populations with longer histories of grazing tended to consist of individuals of relatively lower palatability (Pearson *et al.* 1990).

Many researchers believe that the sexes of saltbush vary in their acceptability to herbivores. In separate studies, Williams *et al.* (1978) and Graetz (1978) found that the sex ratio of grazed saltbush populations was strongly biased in favour of the male phenotype. Graetz (1978) found a five-fold increase in the female to male sex ratio with increasing distance from water. At all distances from water, female shrubs were more likely to be grazed than male shrubs (Graetz & Wilson 1979). Williams *et al.* (1978) found that male plants were vegetatively more vigorous than females of the same lifestage and noted that this could be explained by selective grazing. Preferential grazing of females also tended to reduce their size in comparison to males (Graetz 1978). Beyond the sacrifice zone (where both sexes are trampled and grazed heavily), very few males are grazed at all which suggests that when sheep are at their most selective, they tend to graze females (Graetz 1978). Graetz (1978) suggested that sheep avoid the male shrub because the terminally placed male flowering spike acts as a mechanical obstruction to the preferred foliage below it. However, Williams (1972) believed that the sheep seek out and preferentially graze the succulent unripe fruits on female shrubs.

Although Graetz (1978) believed that selective grazing of the sexes would have no net ecological importance, other researchers noted that it reduced the reproductive vigour of females (Williams *et al.* 1978). Evidence to be presented in this thesis suggests that this may indeed have long-term effects for grazed bladder saltbush populations.

CONTEXT AND APPROACH

As previously noted, the geographical and edaphic range of bladder saltbush is very large and several subspecies occur. The research presented in this thesis was conducted in the semi-arid region of South Australia and was restricted to eastern Eyre Peninsula where *Atriplex vesicaria* subsp. *variabilis* is the most common. Furthermore, the research deals only with the interaction of Merino sheep and *A. vesicaria.* The species is grazed by cattle in the northern parts of its range; however, this area is small in comparison to the areas grazed by sheep. It is also known that other herbivores (e.g. rabbits and kangaroos) occasionally graze the species, but again this is considered to be less significant compared to the extent of sheep grazing.

One of the ubiquitous problems of field-based ecological projects is how to design statistically sound experiments. This is particularly pronounced at large spatial scales, where realism is high but replication is difficult (if not impossible). In order to compensate for this problem, I have taken a multi-faceted approach to the experimental work required for this thesis. I have conducted complementary experiments at several spatial and temporal scales in order to produce a set of conclusions with a high degree of reliability (Table 1.1).

TABLE 1.1. Summary of the experimental approaches used in this project.

	Paddock-Scale	Small-plot Grazing Trials	Cafeteria Trials
Scale	approx. 2500 ha	approx. 0.1 ha	approx. 0.01 ha
Realism	High	Moderate	Low
Replication	Difficult	Difficult	Easy
Flock Size	Large	Small	Small
Manipulation	Low	Moderate	High
Comments	Often the end result of historical grazing	Can test processes	Can test processes

The aim of the multi-faceted experimental approach was to achieve a balance of replication and realism using methods which are more powerful when used together than they are alone. This thesis begins at the middle of the continuum, with small-plot grazing trials (Figure 1.3). These trials were conducted to confirm that palatability variation occurs within *A. vesicaria*, and to develop hypotheses for further experimentation. The results of these trials led to paddock-scale research, where the plant-animal interaction was at its most realistic, but the opportunity for replication and manipulation was low. The complementary findings of the grazing trials and paddock-scale research were tested further using cafeteria experiments (Figure 1.3). At the cafeteria scale, the scope for replication was high but realism was very low. The removal of edaphic influences in this particular instance, however, provided very strong evidence to support the other aspects of the research. Taken together, the three lines of investigation provided a reliable picture of the interaction between Merino sheep and *Atriplex vesicaria* in the semi-arid rangelands of South Australia.

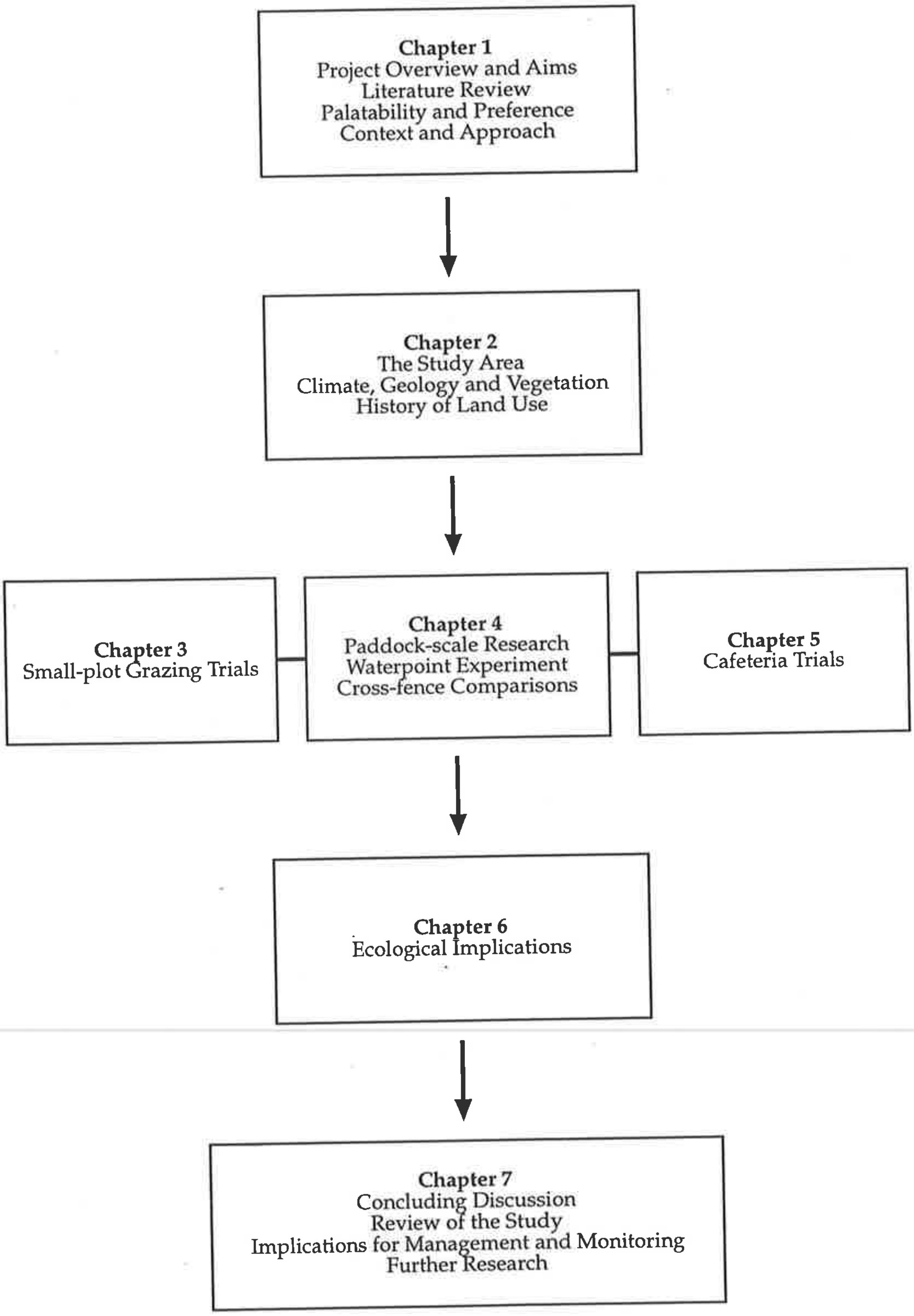

FIGURE 1.3. Structure of this thesis

CHAPTER 2
THE STUDY AREA

LOCATION

All research for this project was conducted on north-eastern Eyre Peninsula, South Australia (Figure 2.1). The grazing trials and cafeteria trials (Chapters 3 and 5) were conducted near the homestead at Middleback Station (32°57'S, 137°24'E), which is about 20 kilometres north-west of Whyalla. The paddock-scale research (Chapter 4) was conducted on Katunga, Roopena, Middleback and Myola Stations. These stations occupy the southern-most limits of the pastoral zone on Eyre Peninsula (Department of Environment and Natural Resources 1993). All climate data reported in this chapter are derived from records held by the Commonwealth Bureau of Meteorology (25 College Rd, Kent Town, South Australia) except where otherwise noted. The information in this chapter is intended as an overview of the entire study area, and detailed descriptions of the experimental sites appear in the appropriate chapters.

CLIMATE

Reid (1984) noted that the characteristic climatic features of the study area include:

- a highly erratic and unpredictable rainfall,
- a lack of seasonality in the rainfall distribution,
- long, hot summers and short, cool winters, and

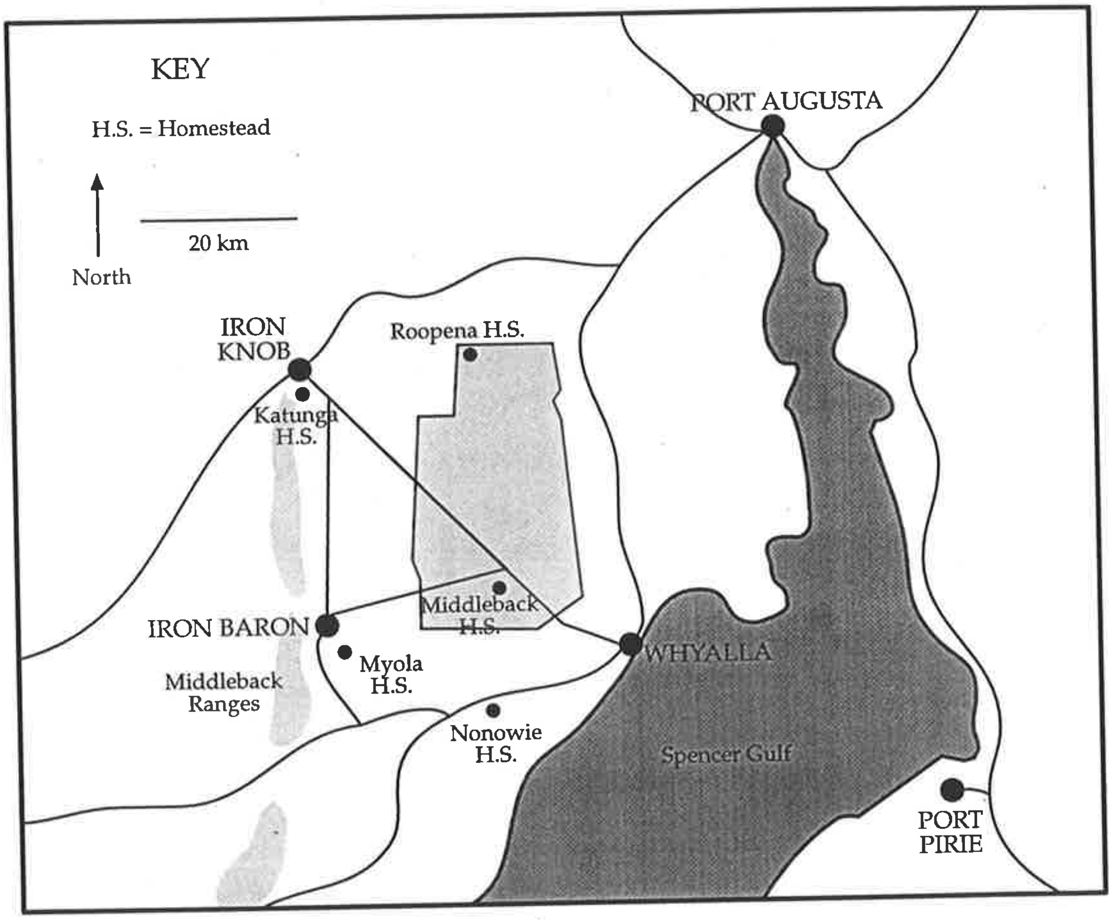

FIGURE 2.1. The location of the study area (including the Roopena pastoral lease) on north-eastern Eyre Peninsula, South Australia (after Wotton 1993).

- a large diurnal temperature range

Rainfall

Rainfall totals in the study area do not show marked seasonality; however, winter rain does tend to occur in small frequent showers, whilst summer rain often occurs in larger, less frequent falls (Lange 1971). About once every 20 years, cyclonic systems from northern Australia move south as rain depressions and produce large rainfalls in a short period of time. This usually happens in January or February and is considered to be important for the growth, reproduction and recruitment of some long-lived plant species (Lange 1971, Ireland 1997).

The means, medians and extreme rainfall years for three sites in the study area are shown in Table 2.1. The median is lower than the mean for all sites, and reflects a bias in the mean due to large (but infrequent) rainfall years. For this reason, the median may be a better indicator of the long-term rainfall conditions. The variability between the sites is a reflection of both the spatial and temporal patchiness of rainfall over the study area.

TABLE 2.1. Total annual rainfall information.

Station/Town	Time Period	Mean (mm)	Median (mm)	Min. mm (Year)	Max. mm (Year)
Middleback*	1925-1996	212	199	91 (1940)	511 (1973)
Roopena*	1892-1996	213	200	78 (1927)	537 (1974)
Iron Knob	1911-1996	220	202	83 (1957)	545 (1974)

*Station Records

Rainfall During the Study

This study was conducted between March 1994 and March 1997. As most of the research was done on Middleback Station, the Middleback rainfall records are used here as an indicator of the conditions throughout the study. Figure 2.2 shows the monthly totals which fell at Middleback during the study period. The two largest monthly totals occurred in July 1994 (91.6 mm) and January 1995 (91.8 mm). Several months of no rainfall occurred during the study period.

As expected, rainfall was variable across the three years of the study (Figure 2.3). The first year of the study (1994) was the driest. Only 148 mm fell in 1994, which is lower than the 72-year median value of 199 mm. Both 1995 and 1996 were wetter than the long-term median. These two years reached similar final totals (about 260 mm); however, the

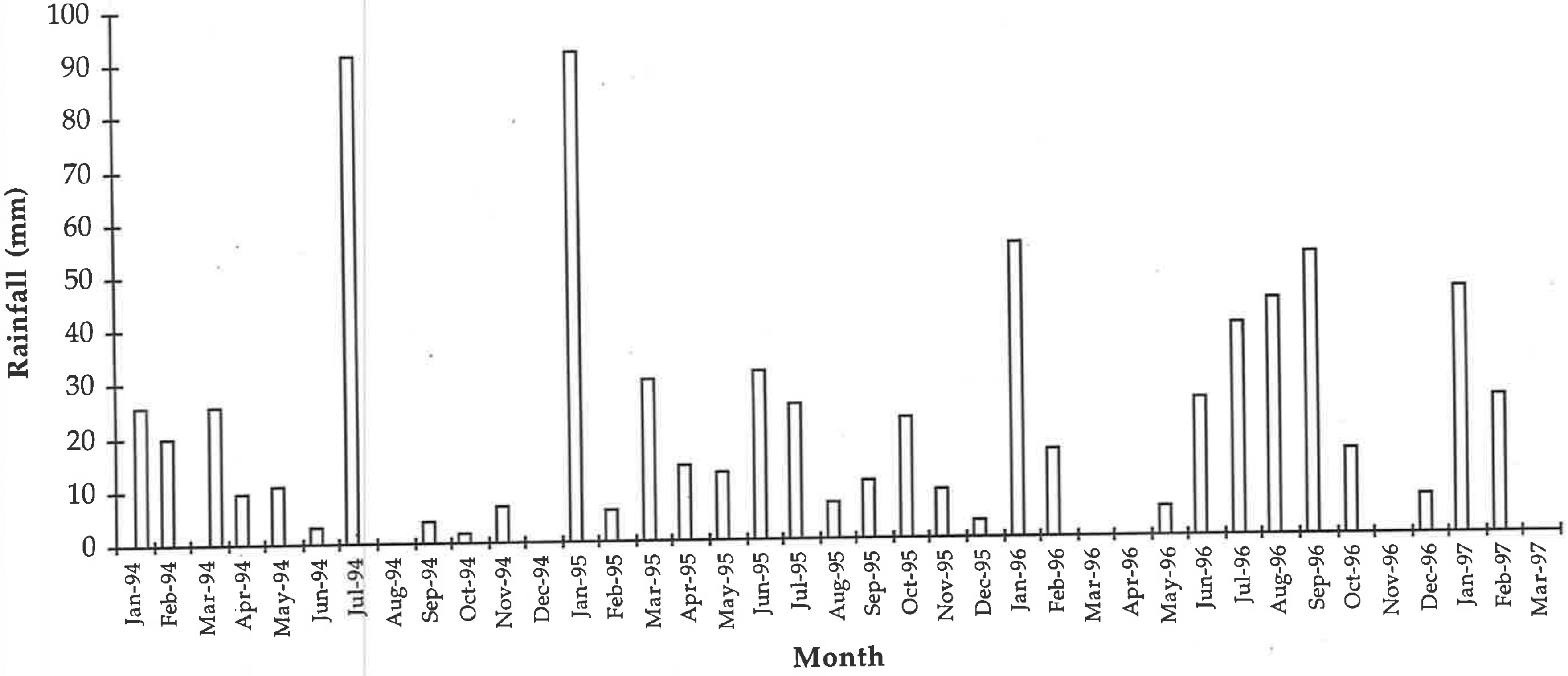

FIGURE 2.2. Monthly total rainfall at Middleback Station during the study.

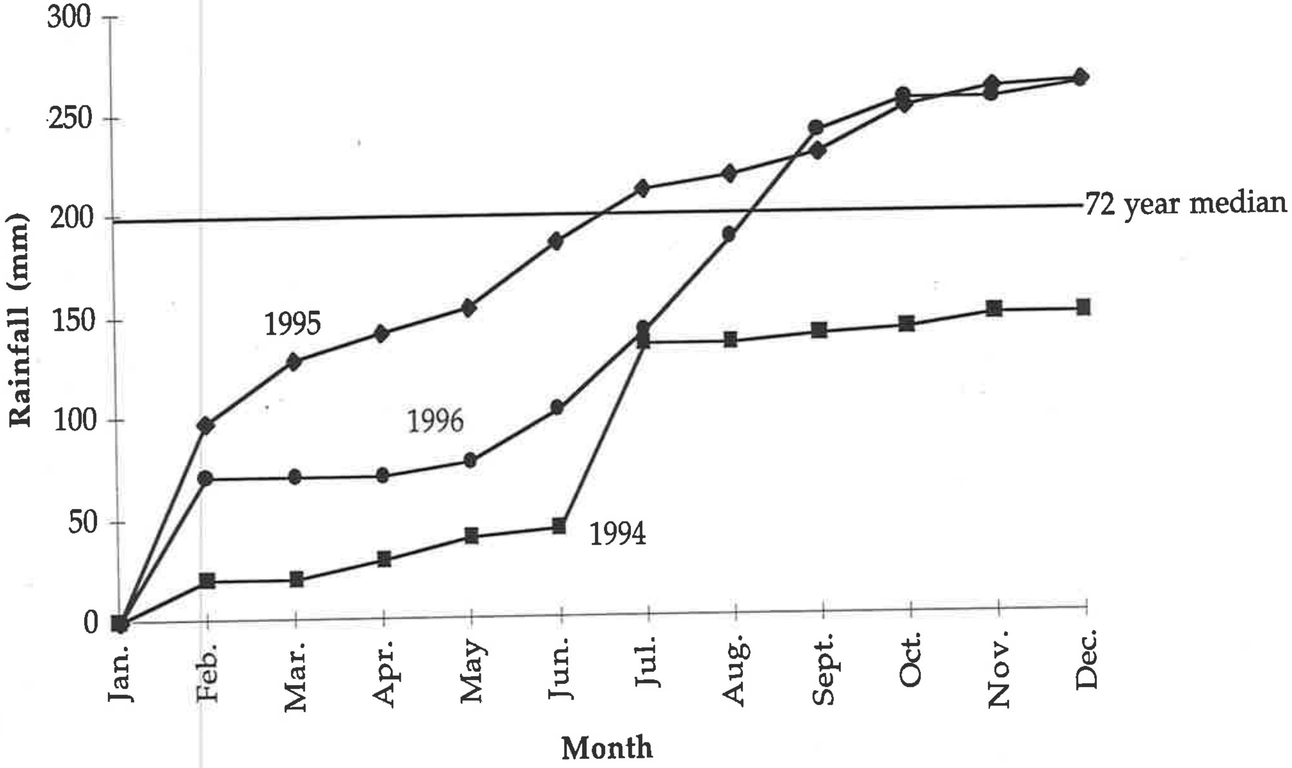

FIGURE 2.3. Cumulative rainfall at Middleback Station for the three years of the study.

distributions of rainfall on a monthly basis were quite different (Figure 2.3).

Temperature

The only temperature data recorded in the study area are those for the city of Whyalla, which is on the coast of Spencer Gulf (Figure 2.1). The mean daily maximum and minimum temperatures for each month are shown in Figure 2.4. The mean daily maximum temperature ranges from 28.9°C in January to 16.9°C in July. The mean daily minimum temperature ranges from 7.3°C in July to 18.7°C in February (Figure 2.4). The highest temperature ever recorded in Whyalla is 49.4°C, whilst the lowest is minus 2.0°C. It must be noted, however, that the temperature regime of Whyalla is moderated by the sea (Reid 1984, Gawler Ranges Soil Conservation Board 1996). Thus, the maximum temperatures throughout the study area tend to be higher than those for Whyalla, whilst the minima tend to be lower (Reid 1984).

Wind

Most pastoralists believe that wind influences the direction of movement of sheep in paddocks. Throughout the study area, it is accepted that the southern boundaries of paddocks tend to be the most heavily grazed because sheep graze into the predominant southerly winds. Although the influence of wind on sheep behaviour is largely anecdotal, contrasts in vegetation cover across fence-lines can be seen in aerial photographs and satellite images.

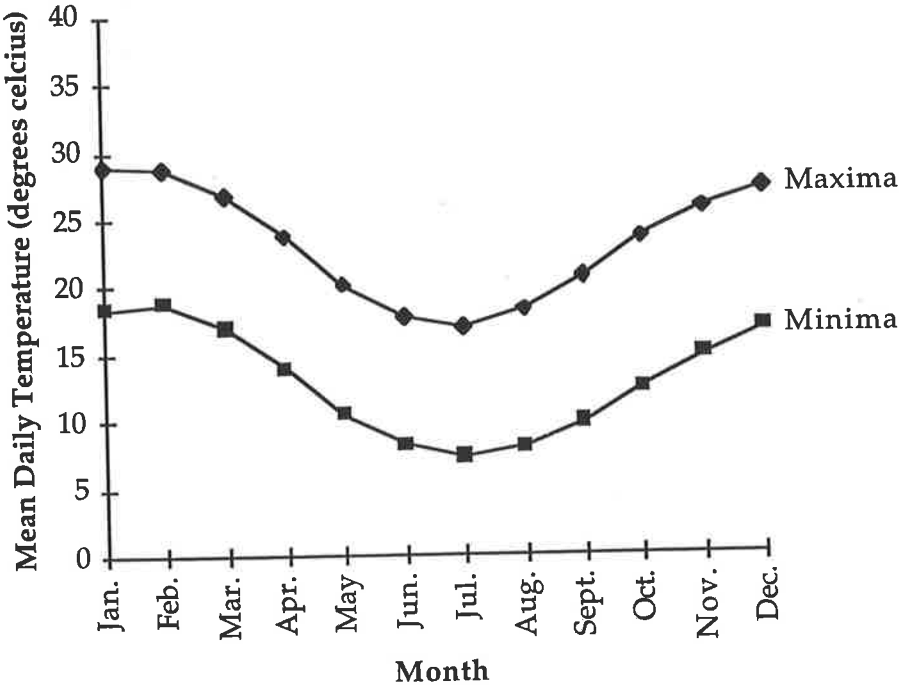

FIGURE 2.4. Mean daily maximum and minimum temperatures for each month at Whyalla, South Australia (1955 - 1996).

The only wind data available for the study area are for Whyalla between 1982 and 1991. The data confirm that southerly winds dominate the study area from September to April. North-westerlies dominate from May to August. The calmest wind conditions occur in May, whilst the strongest winds occur in October.

TOPOGRAPHY AND SOILS

Generally, the topography of the study area is low and gently undulating, and is characterised by a recurring system of interfluvial slopes, plains, washes and basins (Laut *et al.* 1977). The main exception to this is the Middleback Range which is a low set of hills on the western edge of the study area (Figure 2.1). Isolated hills also occur on Roopena Station.

The soils of the study area are mainly brown calcareous earths (Gc1.12) which are dark reddish-brown in colour (Wright 1985). The texture of these soils is predominantly sandy to clay-loam; however, horizons of cemented calcium carbonate can occur at depth (Wright 1985). Poorly drained crusty red duplex soils (Dr 1.43) are a feature of the basins and washes and are relatively saline (Wright 1985). These duplex soils are characterised by a surface crust which may carry a pavement of gravels, pebbles or stones (Wright 1985). The soils of the study area are often powdery and loose and prone to erosion when the vegetation or soil crust is destroyed (Wright 1985).

VEGETATION

Reid (1984) identified three main vegetation associations in the study area and these are summarised below.

Chenopod low open-shrubland

The two dominants of this association in lightly grazed areas are *A. vesicaria* and *Maireana sedifolia*. Bladder saltbush tends to grow in the low-lying basins and washes, whilst both species mix on the slopes and plains. Due to its susceptibility to grazing and trampling (see Chapter 1), bladder saltbush has declined in some areas and has been replaced by *M. pyramidata* (black bluebush). Other species commonly found in this association are *Rhagodia ulicina, Lycium australe* and *Atriplex stipitata.*

Western myall low open-woodland

The western myall (*Acacia papyrocarpa*) forms a sparse overstorey to chenopod shrubs over much of the study area. In low-lying areas, western myall becomes more densely distributed and can be found with other species such as *Alectryon oleifolius* and *Exocarpus aphyllus*. Other trees and shrubs which occur in the association include *Eremophila scoparia, Senna* spp., *Santalum acuminatum, Acacia oswaldii, Pittosporum phylliraeoides* and *Myoporum platycarpum. M. platycarpum* may sometimes dominate or codominate sparse woodland. Beneath the canopies of the western myall, a specialised berry-fruited chenopod flora occurs and includes *Enchylaena tomentosa, Rhagodia spinescens* and *Chenopodium gaudichaudianum.*

Black oak low woodland

Black oak (*Casuarina pauper*) propagates by suckering and typically forms large groves containing thousands of ramets. The chenopod understorey of black oak low woodland consists of bluebush, saltbush and/or black bluebush and berry-fruited chenopods.

HISTORY OF LAND USE

The main land use in the study area is wool production, which has occurred since the 1860's (Richardson 1925). The area now occupied by the city of Whyalla and eastern Middleback Station was first taken up for pastoralism in 1862 (Richardson 1925). The main factor limiting settlement of the area was the lack of reliable water. The sizes of holdings in the area varied considerably (mainly due to legislation) until the late 1800's. After this time, larger holdings were consolidated.

Mining leases for the Middleback Ranges were first granted in 1890 (Gawler Ranges Soil Conservation Board 1996). Mining of iron ore on a commercial scale started in 1898 and iron ore was first transported to Whyalla in 1901. Mining continues to the present day and steel production is the main industry of Whyalla.

CHAPTER 3
SMALL-PLOT GRAZING TRIALS

INTRODUCTION

At the inception of this study, there was some evidence to suggest that palatability variation occurs within *Atriplex vesicaria*. Some of the earliest observations were made at the T.G.B Osborn Reserve, which was established on a highly degraded area of Koonamore Station (South Australia) in 1925. Accounts of the condition of the saltbushes at the time the Reserve was formed (see Chapter 1) suggest that a few were able to survive the heavy grazing pressure that destroyed the rest of the population. Similar observations were made near Whyalla by Barker & Lange (1969, 1970), who found a few individuals near heavily grazed waterpoints. Although these examples demonstrate that some saltbushes can survive in very heavily grazed areas, no reasons have been given to explain why they can survive where most cannot.

During the past 25 years, small-plot grazing trials have been conducted in chenopod shrubland communities on Middleback Station (Lange *et al.* 1992). In these trials, it has often been observed that sheep refuse to graze individual saltbushes even when forage availability falls to very low levels. This situation is described in an entry in the Middleback Field Centre log:

"It is often noticeable that there are a few A. vesicaria which have been very lightly grazed by sheep amongst others defoliated (these are not A.

stipitata). One individual in our November grazedown trial where 95% of edible biomass was eaten in the enclosure was untouched throughout".

Mark Stafford Smith (7th April, 1993)

In addition to the examples already cited, many pastoralists in South Australia know from their own observations that bladder saltbushes vary in palatability (e.g. A.D., A.W. & D.A. Nicolson, R. Gloster, J. Mengersen, pers. comms).

Several researchers have speculated about causes of palatability variation in bladder saltbush. Even though Graetz & Wilson (1984) suggested that there was palatability variation between ecotypes, this remains untested. There is quantitative information, however, regarding palatability variation between the adults and seedlings of bladder saltbush. Experiments conducted at Middleback have shown that sheep avoid grazing saltbush seedlings, even when the availability of preferred forages declines (Lange *et al.* 1992, Maywald 1993). Knowles & Condon (1951), however, believed that paddocks in western New South Wales needed periodic resting to allow saltbush establishment because sheep preferentially grazed saltbush seedlings. Although the information is contradictory, it does suggest that there is a basis for palatability variation with age in bladder saltbush.

By far the most attention has focussed on the apparent palatability variation between the sexes. Several studies in New South Wales have reported male-biased sex ratios in grazed populations (Williams 1972, Williams *et al.* 1978, Graetz 1978). All studies found that males were more prevalent close to waterpoints. Williams (1972) noted that where females were surviving close to waterpoints, they were "stunted, poorly foliated and flowering weakly" compared to the males which were "large, well foliated and flowering profusely". There is uncertainty as to the cause of the selectivity. Williams (1972, 1979) suggested that sheep seek out and preferentially graze the succulent fruits on the females, whilst Graetz (1978) believed that the sheep actively avoid the male flower spikes.

Thus, there is accumulating evidence for palatability variation between the ecotypes, ages and sexes of bladder saltbush. Observations at Middleback have shown that sheep discriminate between adult shrubs of *Atriplex vesicaria* subsp. *variabilis* at scales of less than one metre. The experiments reported in this thesis were undertaken to examine this specific example of palatability variation.

Experimental Approach

As far as I can ascertain, no intensive dietary trials have been conducted to examine palatability variation between the adults of bladder saltbush. Small-plot grazing trials represent a thoroughly tested approach for studying the grazing behaviour of Merino sheep in the rangelands of the Middleback area (Noble 1975, Pearson *et al.* 1990, Lange *et al.* 1992, Maywald 1993). The small-plot method offered an appropriate balance of realism and manageability, and was thus used for the initial examination of palatability variation.

The aims of the small-plot grazing trials were:

- To verify that the sexes of bladder saltbush vary in their palatability in the Middleback area.
- To identify physical plant attributes which may influence the dietary behaviour of sheep.

METHODS

Study Site

Three separate grazing trials were conducted in Little One Mile Paddock, Middleback Station (Figure 3.1). The site, described by Lange *et al.* (1992), occupied a broad, flat swale dominated by an *Atriplex vesicaria - Maireana pyramidata* shrubland. Little One Mile is a small paddock which is rarely used for sheep grazing and is thus considered to be relatively pristine (A.W. Nicolson, pers. comm.). As the site had not been modified by continuous grazing by sheep, the saltbush population was expected to encompass a large range of palatability variation.

Trials were conducted in September 1994, February 1995 and January 1996. The first two were conducted in the same sheep-proof enclosure, which was 90 metres long, ten metres wide and oriented north-south. The enclosure was treated as nine contiguous ten x ten metre 'cells' and a holding yard was situated at the southern end of the enclosure (Figure

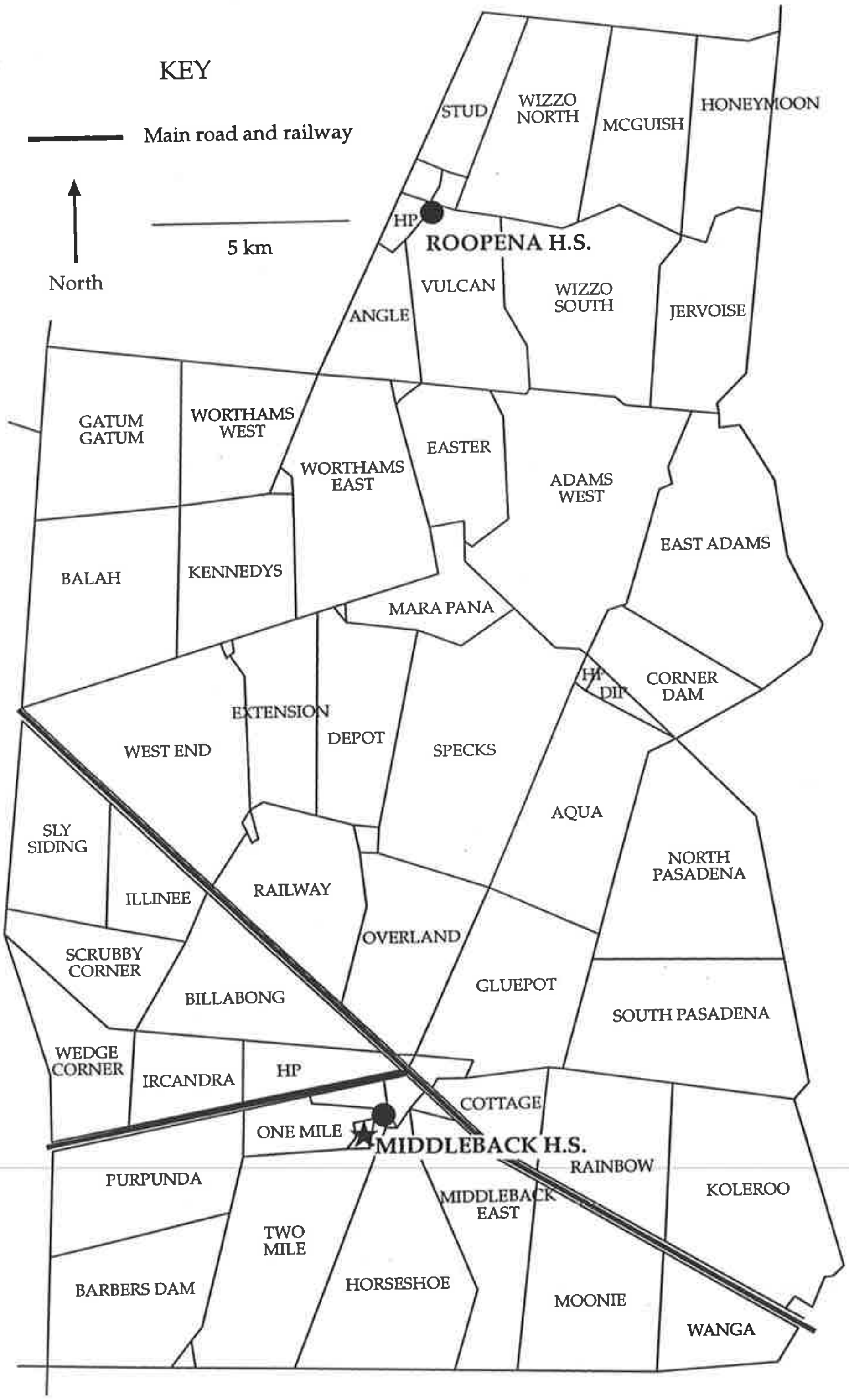

FIGURE 3.1. Paddock plan showing the location of Little One Mile Paddock (★) near Middleback homestead, Middleback Station.

3.2). A new enclosure was built for the January 1996 trial to provide a data set independent of the previous trials. Power analyses conducted on the results of the September and February trials indicated that fewer shrubs could be used. The enclosure used in January 1996 was 70 metres long, ten metres wide and was situated directly adjacent to the other plot.

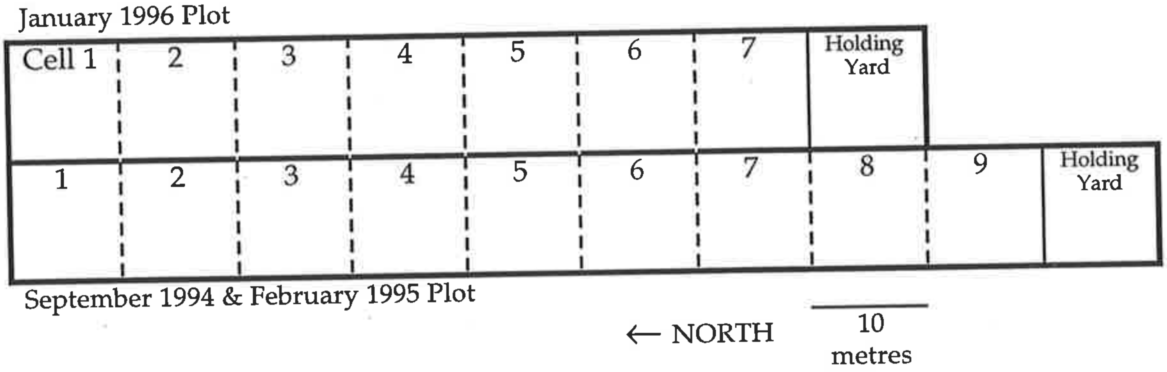

FIGURE 3.2. Diagrammatic representation of the small-plot grazing enclosures in Little One Mile Paddock, Middleback Station.

Experimental Shrubs

In September 1994, small aluminium tags were attached to the bases of about 24 sexually mature shrubs in each cell. Where possible, equal numbers of shrubs of both sexes were chosen. Although bladder saltbush populations are usually dominated by the male and female phenotypes (Williams 1979), the experimental population was dominated by female and bisexual plants in September 1994. As a result, the consumption of 106 females and 108 bisexuals was compared. In February 1995, however, the consumption of 93 females and 84 males was compared because most of the bisexual shrubs had changed sexual phenotype (Maywald 1996). A small number of shrubs died after the September trial and some had remained bisexual. For these reasons, less shrubs were monitored in the February trial. In January 1996, ten sexually mature shrubs of each sex were tagged in each cell, resulting in 70 female and 70 male shrubs.

Shrub Habit

The maximum width and height of every experimental shrub was measured before grazing commenced. The measurements were made using a metre ruler and were recorded to the nearest centimetre. The growth habit of each shrub was also classified as either erect or spreading. Erect shrubs were those with no branches touching the ground and spreading shrubs had at least one branch touching the ground. Height, width and habit were used to compare the architecture of the sexes prior to grazing. Shrub habit was also included as an experimental factor in the analyses to determine the influence of habit on consumption.

Additional Treatments in the September 1994 & February 1995 Trials

In addition to monitoring the consumption of shrubs on the basis of sex and habit, two extra treatments were included to determine the influence of foliage density and male flower spikes (Table 3.1). In addition to the literature previously cited, observations in paddocks at Middleback suggested that these factors may influence the grazing behaviour of herbivores. To investigate these aspects, the following treatments were applied to the experimental shrubs:

TABLE 3.1. Summary of experimental treatments for the September 1994 and February 1995 trials.

			Treatment				
			Wiring		Clipping		
Trial	Shrub Sex	Whole Controls	Treated Halves	Control Halves	Treated Halves	Control Halves	Total No. Shrubs
September 1994	Female	54 (108 halves)	52	52	-	-	106 (212 halves)
	Bisexual	35 (70 halves)	37	37	36	36	108 (216 halves)
February 1995	Female	40 (80 halves)	53	53	-	-	93 (186 halves)
	Male	30 (60 halves)	26	26	28	28	84 (168 halves)

(a) Wired shrub halves with control halves

This treatment was included to test the effect of foliage density on selectivity. The underlying assumption was that grazing from a densely packed plant should maximise the intake per bite and thus result in more efficient grazing. Randomly selected shrubs of both sexes were manipulated to create two choices in foliage density. For each of these shrubs, one half of the plant was left untreated and the other half was bunched together and tied with fine wire to produce a dense array of foliage. Whole shrubs could not be wired and compared directly to unwired control shrubs because palatability differences between different shrubs would have confounded the design. Thus, the untreated halves controlled for the increase in foliage density, whilst non-manipulated whole shrubs (described below) were used to control for the altered appearance of wired shrubs. Where possible, equal numbers of shrubs were chosen in each cell. The shrubs in even-numbered cells had the eastern halves wired, whilst shrubs in the odd-numbered cells had the western halves wired. This restricted randomisation was used to ensure that the trial remained manageable whilst controlling for any influence of shrub aspect.

(b) Clipped shrub halves with control halves

This treatment was included to test whether male flower spikes influence consumption and was thus applied to bisexual and male shrubs only. For each of the chosen shrubs, one half of the plant was left untreated whilst the other half had all of its male spikes removed by hand. As with the wiring treatment, the untreated halves were used to control for the removal of male spikes and whole shrubs (described below) were used to control for the altered appearance of the treated shrubs. The same restricted-randomisation pattern used to assign treatments to wired shrubs was also used for the clipped shrubs. The wiring and clipping treatments were assigned to different shrubs so that no shrubs received both treatments.

(c) Whole controls

Whole shrubs were used to control for the physical alteration of the wired and clipped shrubs described previously. As far as was possible, equal numbers of shrubs of each sex were chosen in each cell.

Additional Treatments in the January 1996 Trials

In light of the results of the first two trials, the wiring and clipping treatments were not included in the January 1996 experiment. Observations from the first two trials indicated, however, that sheep tended to reject male shrubs with the longest and/or densest flower spikes. To determine whether spike length was influential, a spike length category was assigned to every male shrub after visual inspection. The three categories were 'short', 'medium' and 'long'. For those shrubs with a mixture of spike lengths, the dominant category was recorded. A calibration of spike lengths was undertaken to quantify the means of the three size classes. The calibration shrubs were chosen randomly from the population directly adjacent to the experimental enclosures. One flowering branch was cut from each of ten shrubs of each spike size class to provide a total sample of 30 branches. These branches were bagged immediately and returned to the laboratory. The ten branches of a single size class were then emptied on to a clean piece of white paper and 25 spikes were chosen from the material as follows. With my eyes closed, I used a drawing compass to select a point on the paper and the spike closest to the compass point was cut from its branch using dissection scissors. This was repeated 25 times and the lengths of the selected spikes were then measured to the nearest millimetre. All material was then discarded and the area thoroughly cleaned before the next size class was prepared. The relationship between category and spike length is shown in Figure 3.3. All three categories were significantly separated (Prob>F= <0.001).

In addition to male spike length, the percentage of branches with spikes (males) or fruits (females) was estimated for each experimental shrub. Five classes were used: 1-20%, 21-40%, 41-60%, 61-80% and 81-100%. These classes were used to determine if spike and fruit density influenced consumption in the January 1996 trial.

Biomass Estimation

Immediately prior to each trial, the initial biomass of the experimental shrubs was estimated using the Adelaide Technique (Andrew *et al.* 1979). This non-destructive method relies on comparisons between the experimental shrubs and a visual standard. Estimates were made

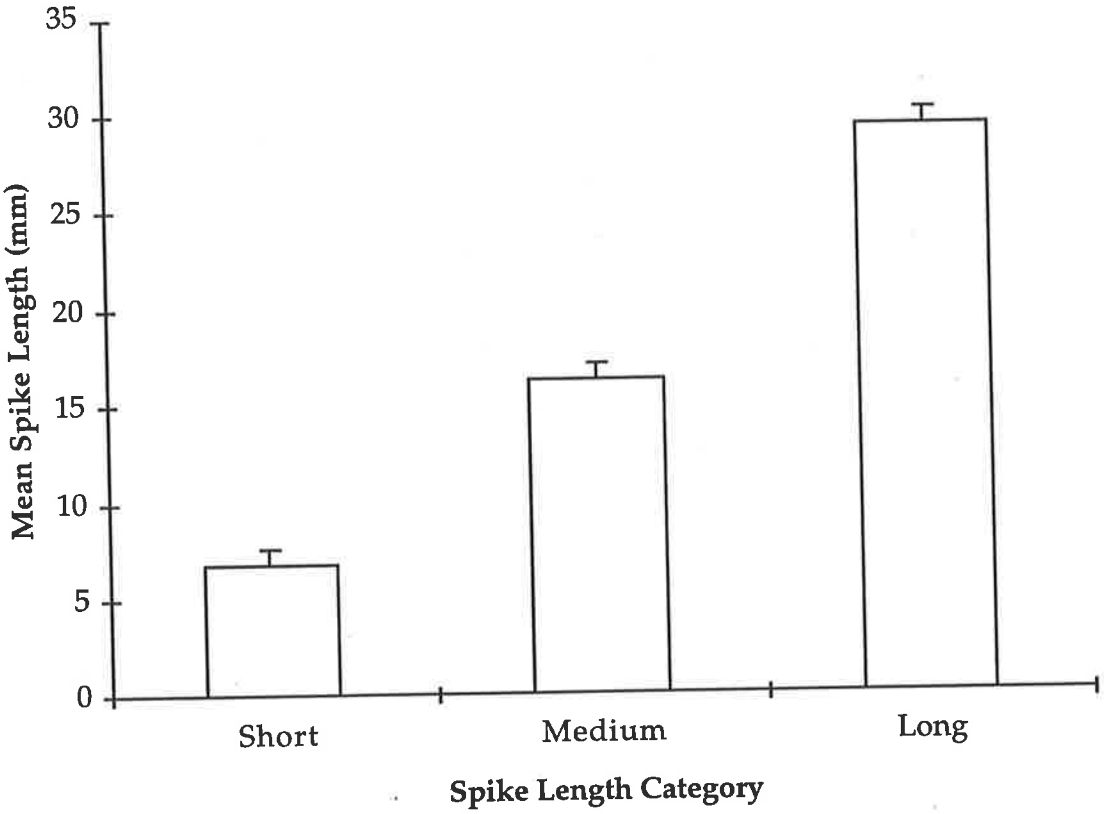

FIGURE 3.3. Calibration of the spike length categories January 1996. Error bars represent Standard Errors.

separately for the east and west halves of each experimental shrub because the treatments had been applied to different halves. A 'standard run' (as described by Andrew *et al.* 1979) was used to calibrate the visual standard and to produce a regression equation. The estimated number of standard-equivalents of the experimental shrubs were substituted into the equation to provide an estimate of initial biomass for each shrub half.

Biomass Consumption

Consumption was estimated using the microdot technique of Lange (1984). Five small paint dots were applied to the accessible foliage of each shrub half to provide a total of ten dots per shrub. The loss of microdots was monitored daily throughout each trial. The percentage of microdots lost was assumed to be directly proportional to the percentage of biomass lost (as demonstrated by Lange 1984). Microdots damaged by the sheep throughout the course of a trial were recorded and then discarded away from the site. This damage was subtracted from total biomass loss to provide an estimate of loss due to consumption. The new starting biomass was calculated for each day by subtracting biomass consumed and biomass damaged from the starting biomass of the previous day.

Experimental Sheep

Eighteen-month old Merino wethers were used in all trials because they were always available, whereas ewes were sometimes unavailable due to lambing. Eight sheep were used in the September 1994 and February 1995 trials. This provided a stocking rate of 89 sheep per hectare. The flocksize was reduced by one in the January 1996 trial to account for the smaller enclosure size. The experimental sheep were chosen from larger station flocks which had been mustered into the shearing yards, and a different flock was used in every trial. On the eve of each trial the sheep were put into the holding yard at the end of the experimental enclosure and left to settle. The sheep were let into the enclosure the following morning and left to graze for 24 hours. The sheep had unlimited access to water from a trough during the trials. At the end of each 24 hour period the sheep were quietly mustered into the holding yard and kept there whilst the microdots were recounted. Counting usually took about two hours and the sheep were let back into the enclosure after counting was completed. These procedures were repeated every day. All trials were terminated when the percentage of microdots fell below 20% of the initial number available. On average, this took four days.

Analyses

Shapiro-Wilk W tests were used to detect departures from normality in the height, width and initial biomass data. All data sets deviated significantly and transformations ($\log_{10}$) were subsequently applied. In all cases, transformation resulted in normally distributed data sets. After transformation, the heights, widths and initial biomass of the sexes were compared using Student's t-test.

Relative biomass consumption was calculated for each shrub by adding the consumption for the first two days and dividing it by the initial biomass. The data for the first two days were used because herbivores are most selective when the choice of forage is highest (Vallentine 1990). For the first two trials, relative biomass consumption was regressed with each experimental factor (sex, habit and treatment) in a generalised linear model. The number of interaction terms was restricted because the clipping treatment was applied to bisexuals and males only. For the third trial, analysis of variance (ANOVA) was used to examine the influence of spike length, spike density and fruit density on relative biomass consumption. After ANOVA, the Tukey-Kramer Honestly Significant Difference (HSD) test was used to identify the means that were significantly different. All analyses were performed using the JMP program (SAS Institute 1989).

RESULTS

September 1994

The initial biomass of the separate halves of the tagged shrubs were not significantly different (Prob>|t|=0.783), so the total biomass of each shrub was used to compare the sexes. The results indicated that the bisexual shrubs had slightly lower biomass compared to females (Prob>|t|=0.070, Table 3.2). The height to width ratio of the sexes was not significantly different (Prob>|t|=0.691, Table 3.2).

It is clear from Table 3.3 that sex was the most influential factor determining consumption of bladder saltbush in the September 1994 trial. Sheep consumed 36% of the female biomass available and only 21% of

TABLE 3.2. Summary of shrub features (means±standard errors) prior to each small-plot grazing trial.

Trial	Shrub Feature	Shrub Sex Male (bisexual in Sept. 1994)	 Female	Significance
September 1994	Initial biomass (g)	194.57±12.80	227.62±12.86	Prob>|t|=0.070
	Height:Width	0.82±0.03	0.84±0.03	Prob>|t|=0.691
February 1995	Initial biomass (g)	187.94±9.60	185.02±12.03	Prob>|t|=0.867
	Height:Width	0.73±0.02	0.76±0.02	Prob>|t|=0.442
January 1996	Initial biomass (g)	213.25±10.80	192.02±10.80	Prob>|t|=0.189
	Height:Width	0.76±0.02	0.84±0.02	Prob>|t|=0.031

the bisexual biomass. Shrub habit was of borderline significance but there was no significant interaction effect between sex and habit. The clipping and wiring treatments had no significant effect on consumption (Table 3.3).

TABLE 3.3. Summary of results for all three trials.

	Prob>F (degrees of freedom)		
	September 1994	February 1995	January 1996
Shrub Sex	<0.001 (1)	<0.001 (1)	<0.001 (1)
Shrub Habit	0.077 (1)	0.033 (1)	0.748 (1)
Sex x Habit	0.339 (1)	0.544 (1)	0.560 (1)
Treatment	0.807 (5)	0.626 (5)	-

February 1995

Shrub biomass prior to the February 1995 trial was not significantly different to that at the start of the September 1994 trial (Prob>|t|=0.136). This indicates that the biomass grazed from the shrubs in September was replaced by new growth during the rest period. Closer inspection of the data confirmed that 96% of the shrubs increased in biomass between the end of the September trial and the beginning of the February one. As in the previous trial, the biomass of the east and west halves was not significantly different (Prob>|t|=0.599) and the biomass of whole shrubs was thus used to compare the sexes. Male and female shrubs did not differ significantly in initial biomass (Prob>|t|=0.867, Table 3.2). The height to width ratio was also not significantly different between the sexes (Prob>|t|=0.442, Table 3.2).

The consumption results of the February 1995 trial mirror those of September 1994 (Table 3.3). Once again, shrub sex was the most influential factor determining consumption of bladder saltbush, with 54% of the female biomass being consumed compared to 30% of the male biomass. Shrub habit was of borderline significance, and there was no interaction between sex and habit. Once again, the clipping and wiring treatments had no significant effect on consumption.

January 1996

Once again, the initial biomass of female and male plants was not significantly different (Prob>|t|=0.189, Table 3.2). Unlike the previous two trials, however, the height to width ratios of the sexes differed significantly (Prob>|t|=0.031, Table 3.2). On average, females had greater height to width ratios than males.

The January 1996 trial was the third demonstration that sex was the most important determinant of consumption (Table 3.3). The relative consumption of the sexes was very similar to February 1995, with 57% of the initial female biomass consumed compared to 30% of the initial male biomass. Shrub habit was not a significant determinant of consumption in this trial.

More male shrubs had medium length (n=82) spikes than long (n=36) or short (n=22) ones. The mean relative consumption of the classes is shown in Figure 3.4. Although consumption of the length classes was not significantly different (Prob>F=0.4699), the trend indicates that consumption decreased with increasing spike length.

Relative consumption on the basis of spike and fruit density is shown in Figures 3.5 and 3.6. Male shrubs with lower densities of spikes were consumed more than those with higher densities (Prob>F= <0.001) and female shrubs with moderate densities of fruit were eaten less than those with lower or higher densities (Prob>F= <0.01).

DISCUSSION

It must be emphasised that these three trials were separate experiments and were not intended as true replicates of each other. The choice of three separate trials, rather than a single trial of three replicates, was necessary due to constraints imposed by time, expense and the availability of labour. The research effort had to be spread over three years to make the best use of the available resources.

The first aim in these trials was to verify that the sexes vary in their palatability in the Middleback area. The results show that sex was the most important of the factors measured. Females were consumed about 70% more than bisexuals in the first trial, 80% more than males in the second and 90% more than males in the third.

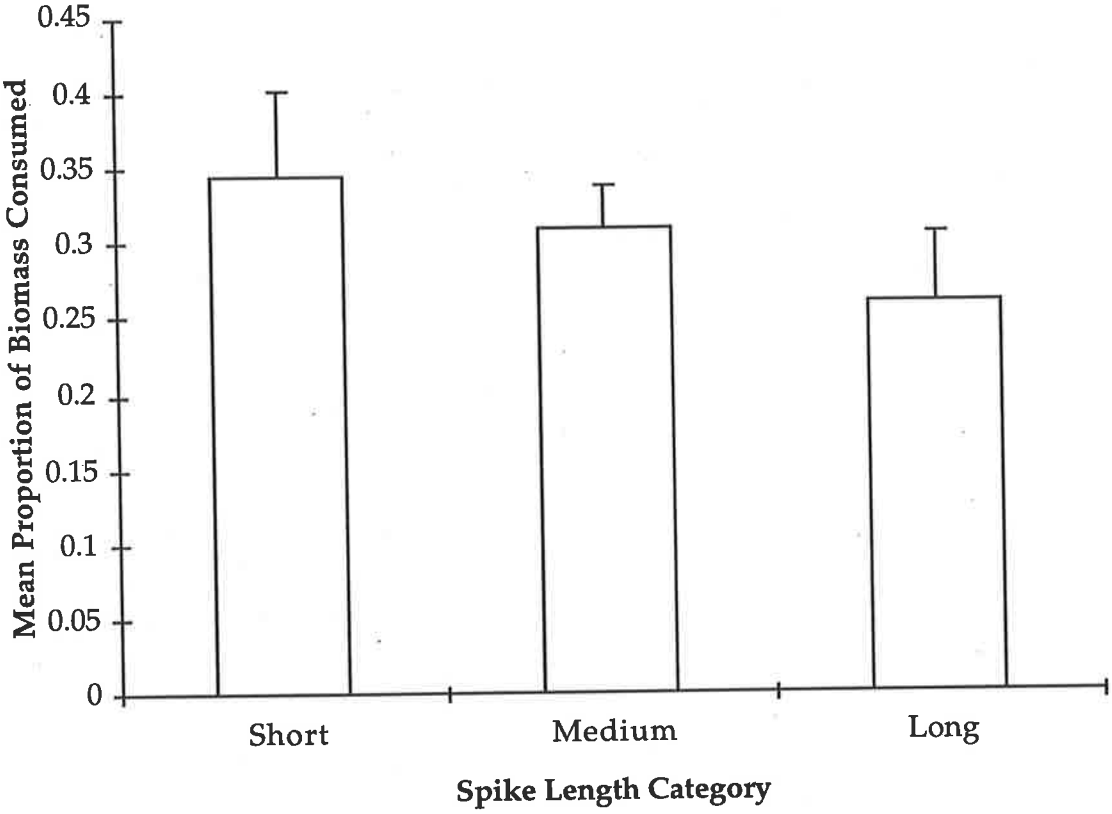

FIGURE 3.4. Consumption of male shrubs on the basis of relative spike length January 1996. Error bars represent Standard Errors.

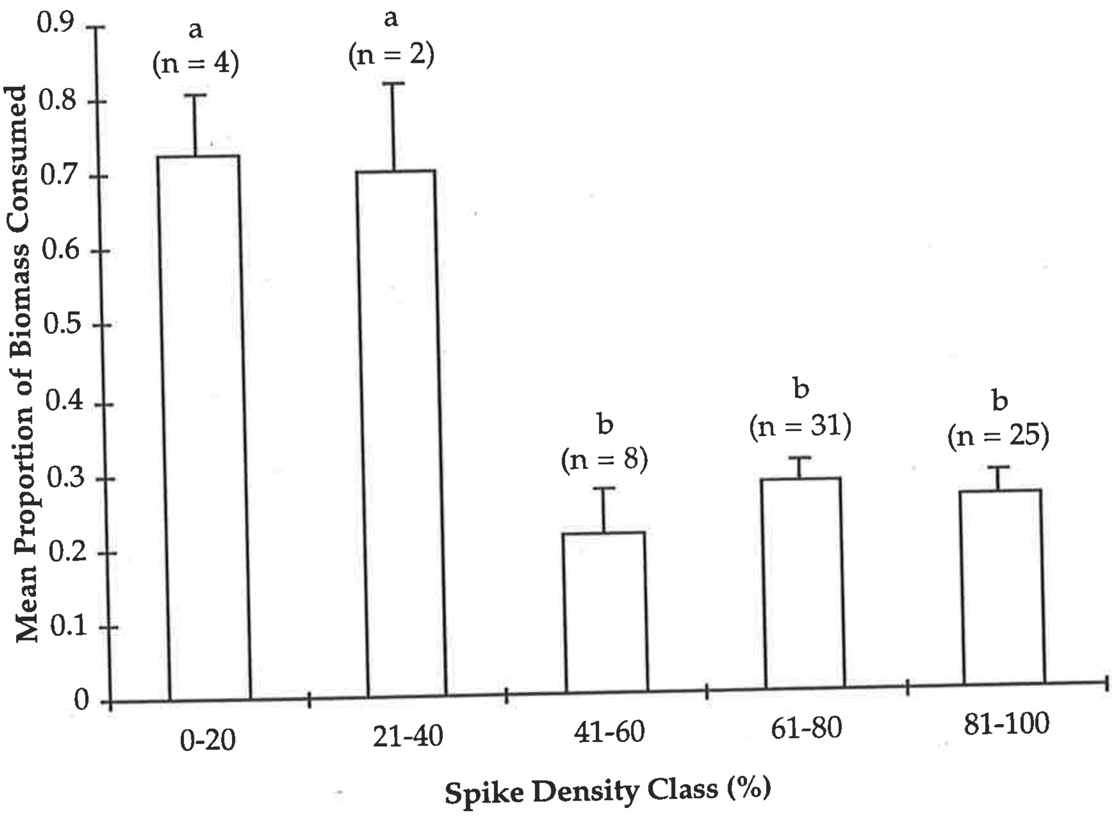

FIGURE 3.5. Consumption of male shrubs on the basis of spike density January 1996. Columns with the same letters signify means that are not significantly different. Error bars represent Standard Errors.

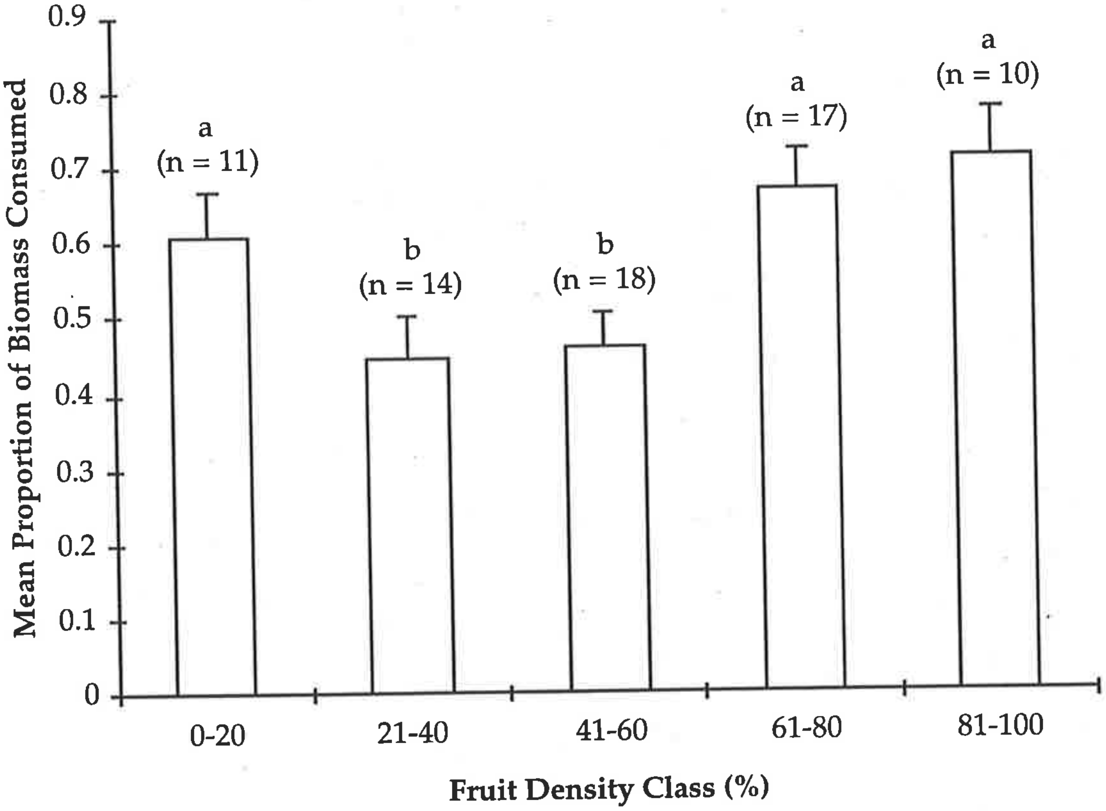

FIGURE 3.6. Consumption of female shrubs on the basis of fruit density January 1996. Columns with the same letters signify means that are not significantly different. Error bars represent Standard Errors.

The second aim in these trials was to identify physical plant attributes which influence grazing behaviour. Foliage density was not a significant determinant of consumption in these trials, even though it is known to influence herbivores in other contexts (Heady 1964, Vallentine 1990). The growth habit of shrubs appeared to be of some influence in the first two trials, but not in the third. Moderate fruit densities appeared to deter grazing in the third trial. No further trials were conducted to examine the influence of fruit density and this remains an avenue for further research. The third trial also indicated that male flower spikes were influential, even though the clipping treatment in the first two trials did not support this. There are at least two possible explanations for this result. Firstly, I suspect that the clipping treatment was not a very sound way to test the influence of spikes. If spikes deter sheep (as proposed by Graetz 1978), then the removal of them from one half of a shrub may not result in an increase in consumption of that half. This is similar to the situation where a plant which is considered to be relatively palatable is left ungrazed due to its proximity to a less palatable one (Heady 1964, Arnold 1987). Thus, the clipped half of a saltbush may not be grazed because of the close proximity of spikes on the non-clipped half. The second explanation is presented in light of results gained in later stages of the research. A few weeks before the beginning of the third trial, 55 millimetres of rain fell at Middleback and stimulated widespread reproduction in the chenopod shrubs. At the time of the third trial the saltbushes at the site were flowering and fruiting more heavily than in either of the previous trials. The males with the longest and most densely packed spikes tended to be consumed the least in the third trial. Given that the spikes were relatively smaller and sparser in the first two trials, I propose that the clipping treatment may not have greatly altered the clipped halves compared to the unclipped halves. This would explain why the removal of spikes had no significant effect in the first two trials whilst male spikes were influential in the third. In hindsight, the clipping treatment should have been included in the third trial to determine which of the explanations given above is the most likely. Nevertheless, the results of the cafeteria trials (reported in Chapter 5) support the findings of the third small-plot grazing trial and the second explanation presented here.

It might be argued that the small-plot trials did not provide a control for grazing by other herbivores, that the stocking rates did not reflect the normal district practice and that each trial was unreplicated. With reference to the first criticism, there were no rabbits in the vicinity of the site, and the other major herbivores (red and western grey kangaroos) tend to dissociate from sheep in the Middleback area (Andrew & Lange 1986c). No fresh rabbit or kangaroo dung was found in the enclosures during any of the three grazing trials.

With reference to the high stocking rate, it must be noted that the small-plot grazing trial method does not attempt to reflect the average stocking rate of the pastoral district. In fact, the method relies on the very high stocking pressure to investigate patterns and processes which may take months or years to develop in real station paddocks. The validity of using a high stocking pressure has not been rigorously tested; however, the preferences measured in small-plot trials are remarkably similar to those measured in other contexts (Jessup 1951, Leigh & Mulham 1966, Robards *et al.* 1967, Andrew & Lange 1986b).

These three trials demonstrated that the preferences for the different sexes of bladder saltbush are quite consistent through time. This is remarkable given that the three trials were conducted in three different years, in contrasting seasonal conditions, in two different plots, using three different flocks of sheep. In fact, a single experiment with three replicates may not have revealed the full extent or consistency of the behaviour. The results support the findings from piosphere studies in western New South Wales and the anecdotal observations made throughout southern Australia. This suggests that the cues influencing the sheep are quite strong and appear to elicit the same grazing behaviour from sheep separated through space, time and edaphic context. Other lines of enquiry, which augment the findings of these small-plot grazing trials are presented in subsequent chapters.

CHAPTER 4
PADDOCK-SCALE RESEARCH

INTRODUCTION

The small-plot grazing trials demonstrated that sheep at Middleback selectively graze the sex phenotypes of bladder saltbush. The results suggest that the underlying cues must be relatively consistent and strong because the same outcome was achieved in three separate trials which were conducted under different conditions. To assess whether the results gained in the small-plot grazing trials were typical of the area in general, evidence at the paddock-scale was required.

The two main questions addressed in this chapter are:

- Do sheep selectively graze the sexes of saltbush in an ungrazed population in an operational station paddock?
- Do paddock populations of saltbush with long histories of grazing have male-biased sex ratios?

To investigate the first question, a new waterpoint was installed in an ungrazed population of bladder saltbush. This work was similar to the approach used in the small-plot grazing trials, but was extended to the paddock-scale. Instead of small groups of sheep confined to a small area, the results of the paddock experiment reflect the cumulative behaviour of a large flock of sheep which were left to graze without disturbance.

The second question was investigated using carefully selected cross-fence comparisons throughout the wider study area. The cross-fence method is used to compare heavily grazed populations on one side of a fence to ungrazed (control) populations on the other. As the control sites are not grazed by sheep, they reflect the characteristics of the plants and soils as determined by climate and soil type, and thus provide useful sites for determining the structure of plant populations in the absence of grazing (Graetz & Ludwig 1978). To minimise confounding influences (such as variation in topography, soils and vegetation composition), cross-fence comparisons were used in preference to surveys of grazing gradients from waterpoints (Graetz & Tongway 1986, Tiver 1994). The cross-fence comparisons were used to measure both historical and current effects of grazing on bladder saltbush populations.

For clarity, the methods and results of the waterpoint experiment are reported prior to those for the cross-fence comparisons. The results of each approach are briefly discussed as they are presented and the wider implications of the results are then discussed fully at the end of the chapter.

WATERPOINT EXPERIMENT

METHODS

Study Site

The waterpoint experiment was conducted in the north-east corner of Hatchards Paddock, Katunga Station (Figure 4.1). This site was chosen

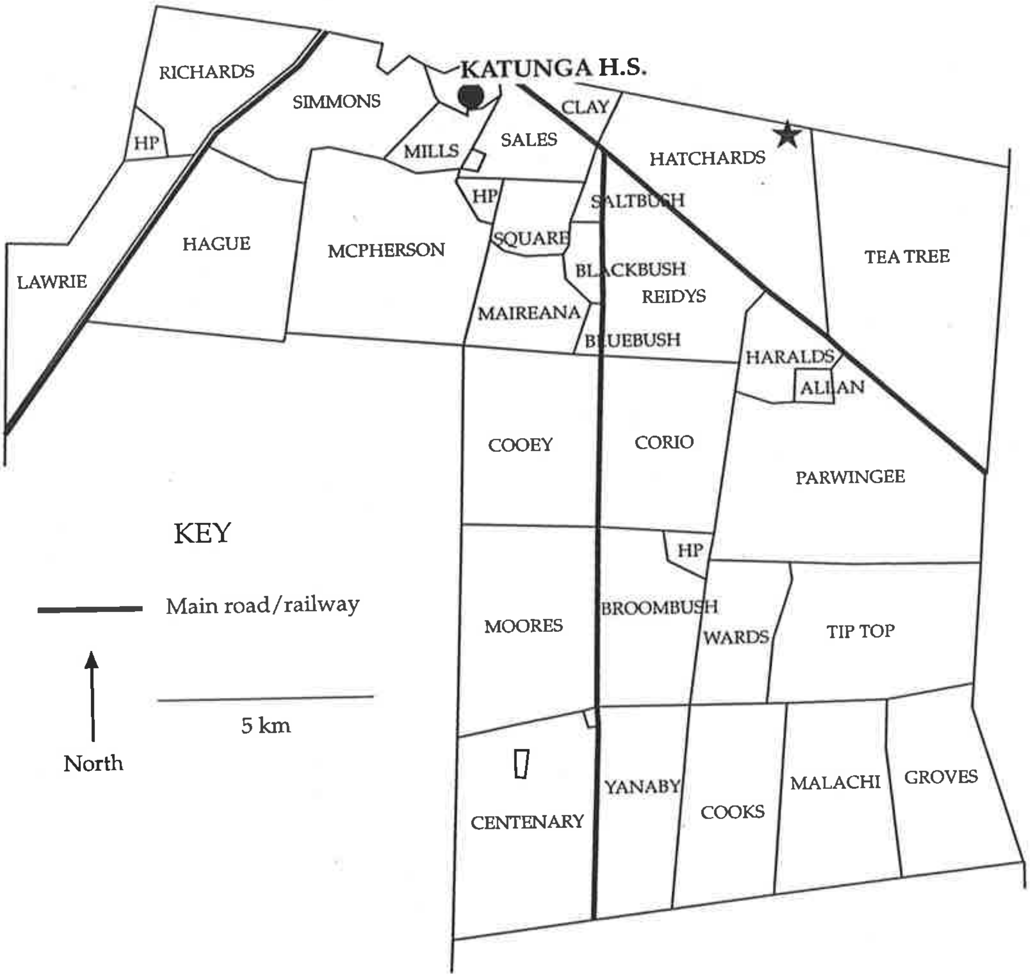

FIGURE 4.1. Paddock plan showing the location of the waterpoint experiment (★) in the north-eastern corner of Hatchards Paddock, Katunga Station.

because the lessees believed it to be an area of the paddock rarely visited by sheep (A.D. & D.A. Nicolson, pers. comms). The main reason for this appears to be the lack of water in the north-eastern corner of the paddock. The intact lichen crust, low amount of sheep dung, lack of bitten stems on the shrubs and absence of established sheep tracks indicated light and sporadic sheep pressure before the experiment. Close examination of dead saltbushes at the site also supported this belief. In contrast to grazed sites where the brittle stems of saltbush are highly susceptible to breakage by passing sheep (Osborn *et al.* 1932), the dead saltbushes at the Hatchards site were intact, with delicate terminal stems still present. Similar features also characterised the initial conditions of a previous study of this type in the Middleback area (Andrew & Lange 1986a) and can be seen in the ungrazed stands of saltbush on the T.G.B. Osborn Reserve at Koonamore (R. Sinclair, pers. comm.).

Trough and Tank

In October 1995, a concrete trough was placed at the site. The trough was oriented north-south and a tank was located at the northern end (Figure 4.2). The tank was connected to a permanent pipeline located 50 metres north of the trough. The trough was not filled with water until April 1996. At this time, the other two waterpoints (to the west) were turned off and the new trough became the sole waterpoint in the paddock.

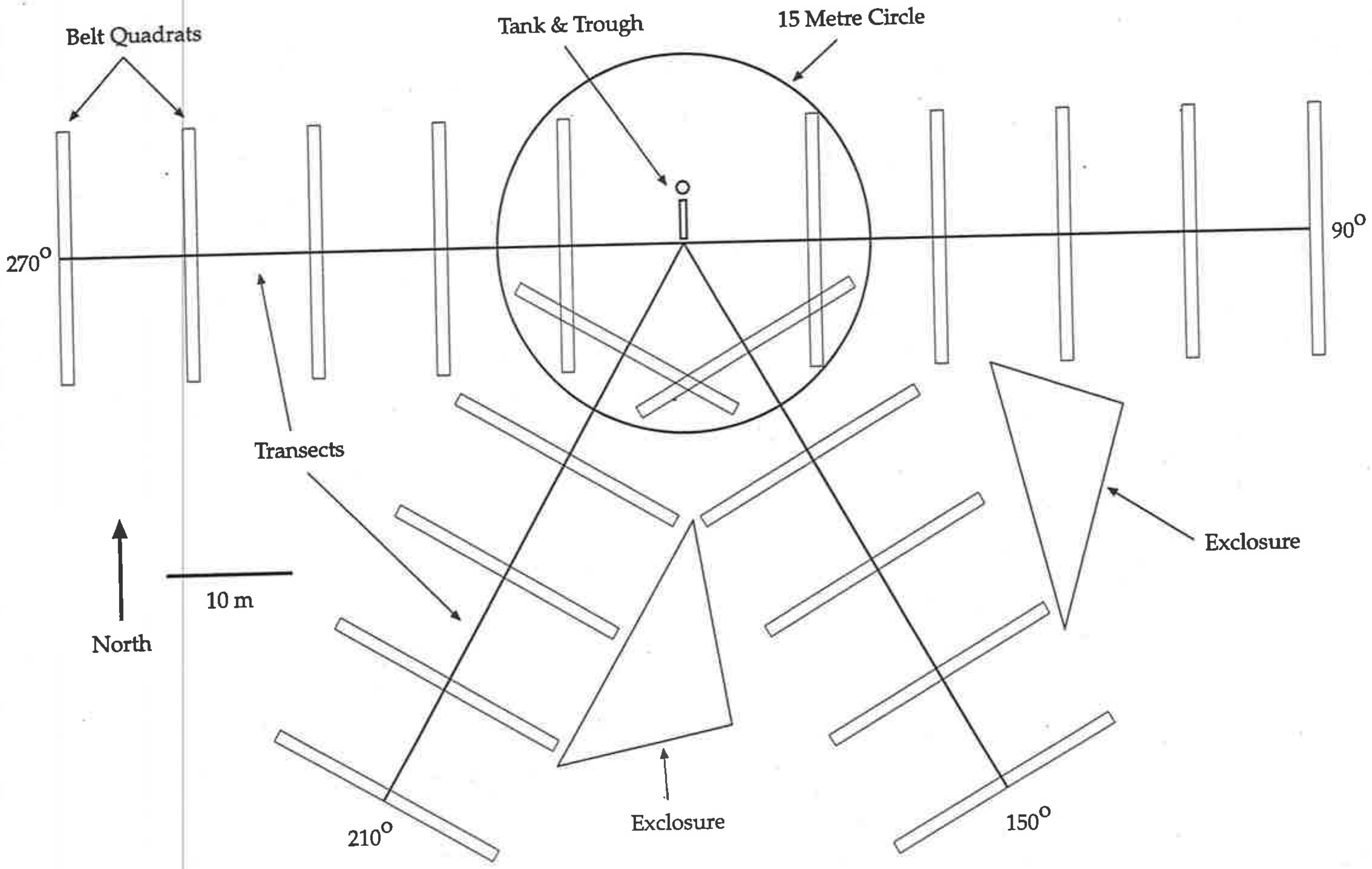

FIGURE 4.2. Experimental layout at the Hatchards site.

Experimental Shrubs, Belt Quadrats and Exclosures

The 75 adult saltbushes closest to the trough were chosen to monitor biomass consumption because it was likely that these would be the first to receive sustained grazing pressure. All 75 shrubs were within 15 metres of the trough and each was labelled with a short, numbered aluminium tag. The maximum height, maximum width and biomass of each shrub were measured before the sheep were introduced. The heights and widths were measured using a metre ruler and were recorded to the nearest centimetre. Biomass was estimated using the Adelaide Technique (Andrew *et al.* 1979). The percentage of branches with flower spikes (males) or fruits (females) was also recorded. In March 1996, ten microdots were applied to each shrub (Lange 1984). The microdots were monitored five times, at two-day intervals, once the sheep were introduced.

Five belt quadrats were arranged at ten metre intervals on each of four transects radiating away from the trough (Figure 4.2). No transects were located north of the tank because a track passed within 50 metres in that direction. The belt quadrats were 20 metres long and one metre wide, providing a sample of 250 shrubs within a 50 metre radius of the trough. Before sheep were introduced to the site, the sex and grazing status of every saltbush on the belt quadrats was recorded. Shrubs were classified as grazed if they had bitten stems, stunted heights and succulent regrowth. Shrubs were classified as ungrazed if they lacked these features. In addition to the saltbush data, the belt quadrats were used to monitor the numbers of fresh kangaroo and sheep dung pellets at the site over time.

To assess the extent of grazing by other herbivores, two sheep-proof exclosures were built within 50 metres of the trough (Figure 4.2). Thirty adult shrubs were labelled with a short, numbered aluminium tag in each exclosure. Using the methods already described, the maximum height, maximum width and biomass of the tagged shrubs were measured before sheep began using the new trough. The percentage of branches with spikes or fruits was also recorded. In March 1996, ten microdots were also applied to each of these shrubs and these were monitored concurrently with the 75 shrubs in the open.

The maximum height, maximum width, biomass, flowering, fruiting and belt quadrat data were collected in late March 1996, immediately before the sheep were introduced. These data were collected again two weeks after grazing commenced and once more after five months. Microdot loss was monitored every two days for a total of ten days once the sheep began using the new trough. A flock of about 150 ewes was introduced on the 9th of April, 1996. The number of sheep in the paddock varied between 150 and 220 from April to September 1996 (Katunga Station records). The flock was never manipulated experimentally whilst the trough was in use.

Analyses

Shapiro-Wilk W tests were used to detect departures from normality in the data sets. Where data sets deviated significantly, transformations were attempted. In all cases the transformations did not improve the distributions, which indicated that the departures from normality were great. The non-parametric Kruskal Wallis test was thus used to compare the physical attributes of the shrubs. The Wilcoxon two-samples test was used to assess changes in shrub density on the belt quadrats over time. All analyses were performed using the JMP program (SAS Institute 1989). Unfortunately, there was only a small number of female shrubs near the trough (n = 6). Consequently, a statistical comparison of the consumption of the sex phenotypes near the trough was not undertaken. Instead, Ivlev's Electivity Index (Lechowicz 1982) was used to demonstrate the order of preference for the sex phenotypes:

$$\mathrm{ELECTIVITY}_{(i)} = \frac{c_{(i)}/C - b_{(i)}/B}{c_{(i)}/C + b_{(i)}/B}$$

Where:
$c_{(i)}$ is the biomass consumed from sex phenotype i.
C is the biomass consumed from both sex phenotypes.
$b_{(i)}$ is the initial biomass of sex phenotype i.
B is the total initial biomass of both sex phenotypes.

I chose to use this particular index for this study because it has a symmetrical range (Lechowicz 1982). The potential values of the index range from -1 to +1. A negative value indicates that a phenotype is avoided whilst a positive value indicates preferential consumption. A value of zero is indicative of non-selective grazing. In this study, Ivlev's Electivity Index was only used qualitatively to produce a rank order of preferences for the sexes (as recommended by Lechowicz 1982 and Norbury & Sanson 1992).

RESULTS

Prior to Grazing

In March 1996, the adult saltbush population at Hatchards was naturally male-biased (5.8 : 1 : 4.3; Male : Female : Vegetative). There were no bisexual saltbushes at the site. The high percentage of male and vegetative shrubs (and shortage of female and bisexual shrubs) indicates that the population was in a droughted condition immediately prior to the experiment (Maywald, 1996). This is supported by the rainfall data for the site, which is presented in Chapter 6 (Figure 6.1). The density of saltbushes on the belt quadrats was 0.73 shrubs/m^2 (1.4 m^2/shrub). Only one shrub on the belt quadrats was classified as grazed. The ratio of fresh sheep pellets to kangaroo pellets on the belt quadrats was 0.09 : 1 (Figure 4.3).

Kruskal Wallis tests (Table 4.1) showed that there were no significant differences in mean biomass, height to width ratio or the percentage of male stems with flower spikes between the 75 shrubs in the open and the shrubs in the exclosures. Due to the prolonged dry conditions at the site (see Figure 6.1), the shrubs were quite dessicated. This resulted in a

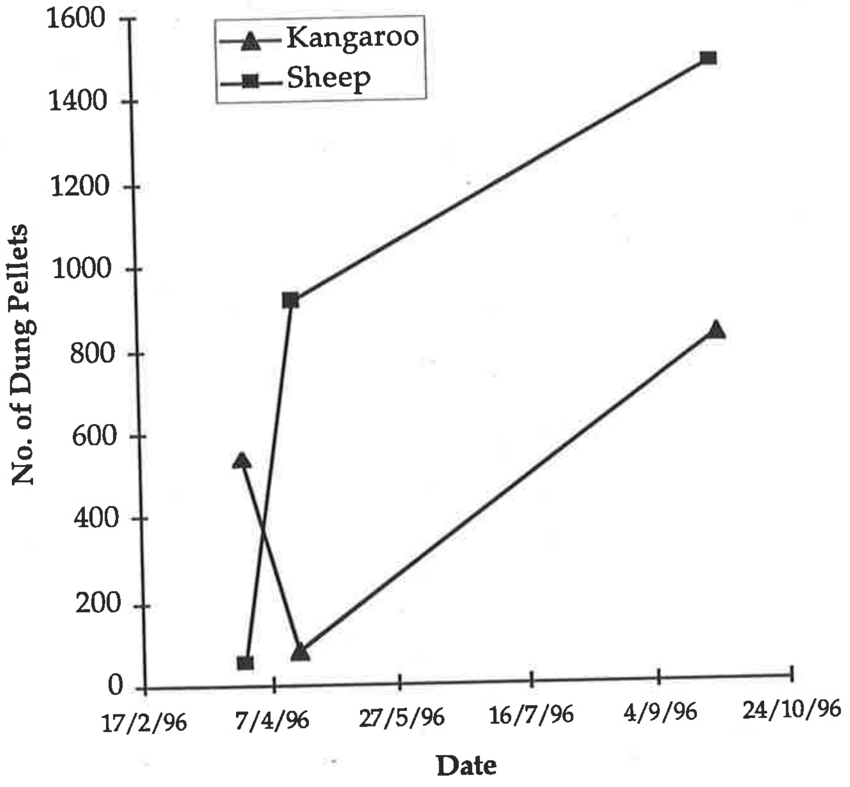

FIGURE 4.3. Change in the number of fresh kangaroo and sheep dung pellets on the belt quadrats at Hatchards.

relatively low mean biomass for the population (Table 4.1). Fruiting was very low in March 1996 (all females had <10% fruiting branches).

TABLE 4.1. Comparison of shrub features (means±standard errors) prior to the introduction of sheep at Hatchards (March 1996).

	Position of Shrub Population		
Shrub Feature	Inside the Exclosures	Outside the Exclosures	Significance
Biomass (g)	34.34±2.94	33.96±2.64	Prob>ChiSq=0.911
Height:Width	1.07±0.05	0.98±0.05	Prob>ChiSq=0.226
% flowering branches (male shrubs)	49.66±5.42	61.10±4.56	Prob>ChiSq=0.148

Grazing Data

Within the first three days of the experiment the soil crust had been completely pulverised within ten metres of the trough, sheep tracks had formed in all directions and some of the shrubs had been completely defoliated. After nine days it was obvious that there had been a large increase in sheep dung at the site and that most of the grazed shrubs were adjacent to the sheep tracks. These sheep tracks had intensified to the point where they were clearly visible 50 metres beyond the trough. The speed with which these changes took place is consistent with the findings of Andrew & Lange (1986a).

Ivlev's Electivity Index showed that female shrubs (IE = 0.08) were preferred over males (IE = -0.01). Only nine microdots out of 518 (1.7%) were lost from shrubs inside the exclosures. Close inspection revealed that none of these control shrubs had bitten stems and that the loss of microdots was closely proportional to the sex ratio. These results suggest that losses inside the exclosures were due to natural excision. Within two weeks, the number of fresh sheep dung pellets had risen dramatically compared to kangaroo pellets (Figure 4.3), resulting in a sheep-biased ratio of 11.7 : 1.

After five months, the number of shrubs classified as grazed had risen from one to 145. Figure 4.4 shows that the ratio of grazed to ungrazed shrubs on the belt quadrats rose substantially for females and vegetatives, but only slightly for males. This is further evidence that female saltbushes were preferred to males. There was no significant change in shrub density in the belt quadrats (Prob>|Z|=0.2453), indicating that saltbush mortality was relatively low. This supports the findings of Andrew & Lange (1986b) who measured a low rate of saltbush mortality in the first two years of a similar waterpoint experiment. After five months, the numbers of fresh sheep and kangaroo dung pellets were higher again, but sheep pellets were still more numerous (1.8 : 1; Figure 4.3).

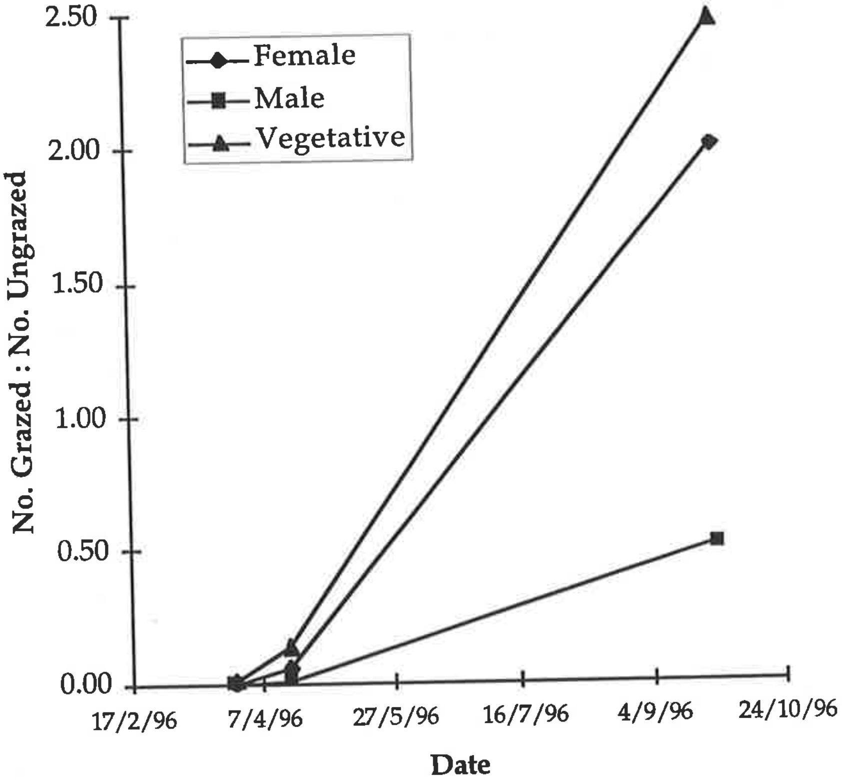

FIGURE 4.4. Change in the ratio of grazed shrubs to ungrazed shrubs on the belt quadrats at Hatchards.

TABLE 4.2. Comparison of shrub features (means±standard errors) after five months of grazing at Hatchards (September 1996).

Shrub Feature	Position of Shrub Population		Significance
	Inside the Exclosures	Outside the Exclosures	
Biomass (g)	126.94±8.50	38.00±7.53	Prob>ChiSq= <0.001
Height (cm)	45.68±2.01	21.13±1.78	Prob>ChiSq= <0.001
Width (cm)	51.31±3.08	25.88±2.73	Prob>ChiSq= <0.001
% flowering branches	58.07±5.07	26.25±8.15	Prob>ChiSq= <0.01
% population with male flowers	40	16	
% fruiting branches	29.66±3.40	7.29±5.14	Prob>ChiSq= <0.01
% population with fruits	42	19	

Several shrub features were adversely affected by grazing at the new trough. Within five months, the mean biomass, height and width of the shrubs outside the exclosures had been significantly reduced compared to those inside (Table 4.2). More male shrubs were flowering inside the exclosures compared to outside, and the male shrubs inside had significantly more flowering branches (Table 4.2). This pattern was similar for females (Table 4.2). The effects of grazing on reproduction and shrub 'fitness' at Hatchards will be discussed further in Chapter 6.

CROSS-FENCE COMPARISONS

METHODS

The small-plot grazing trials and the waterpoint experiment at Hatchards confirmed that sheep preferentially graze female bladder saltbushes. If this selectivity is typical and has been occurring for some time, sites with long grazing histories in the study area would be expected to be relatively more male-biased than ungrazed sites. The same sites should also show that current grazing pressure is greater on female shrubs compared to male shrubs. The cross-fence method was thus used to answer the following questions:

- Is the ratio of male to female shrubs higher on grazed sites compared to ungrazed (or sporadically grazed) sites?

- Is current grazing pressure greater on females compared to males?

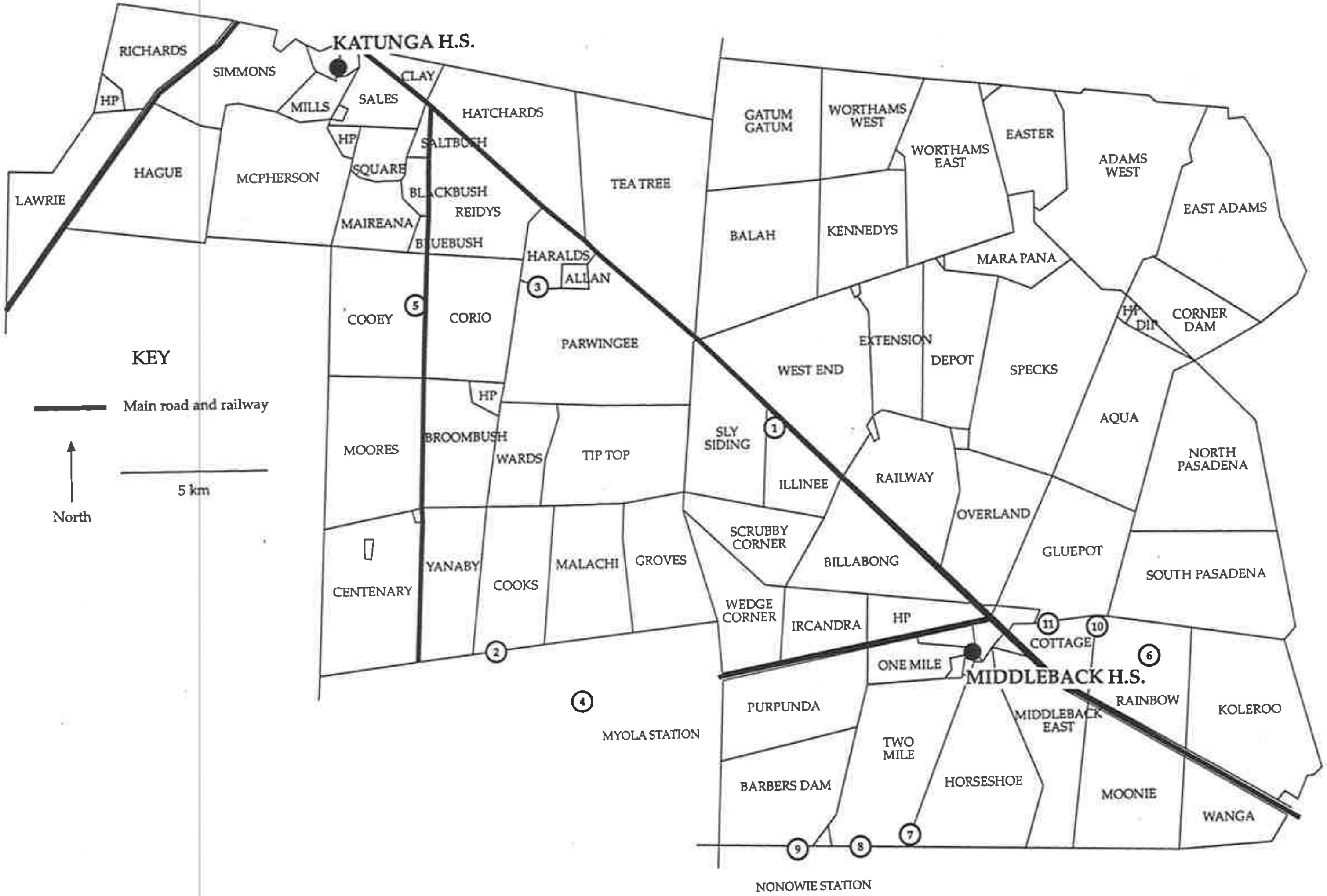

FIGURE 4.5. Paddock plan showing the location of the eleven cross-fence comparison sites. Numbers correspond with those in Table 4.3.

Study Sites

After consultation with several local lessees, and an extensive reconnaissance survey, eleven cross-fence sites were located which were suitable for study. To be suitable, a site had to have saltbush on both sides of the fence, a visually obvious difference in grazing pressure and a known history.

The cross-fence comparisons were conducted on Middleback, Nonowie, Katunga and Myola Stations (Figure 4.5). The location and a general description of each site appears in Table 4.3. Power analyses on data from similar work indicated that 36 shrubs were required to provide a representative sample. Consequently, the sex and current grazing status (grazed or ungrazed) of the 36 shrubs closest to the fence was recorded on each side. Usually, the density of shrubs on the ungrazed side was higher than the grazed side, and this resulted in a quadrat of reduced depth away from the fence (Figure 4.6).

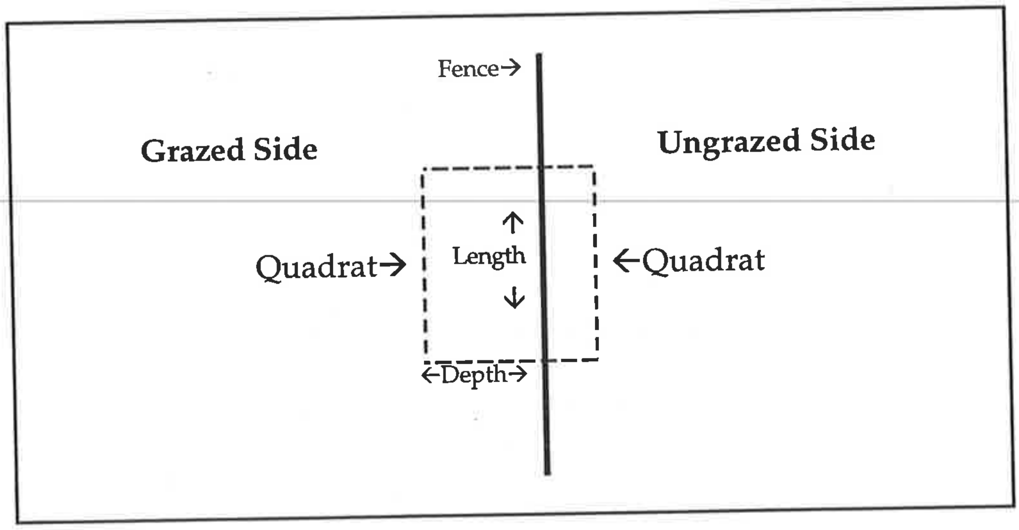

FIGURE 4.6. General layout of a cross-fence comparison site.

TABLE 4.3. (page 1 of 3). Details of the cross-fence comparison sites.

Site No.	Station	Mapsheet & Location	Grazed Side (length x depth)	Ungrazed Side (length x depth)	General Description & Associated Species
1	Middleback	Roopena 6332-11 QD164602	Illinee Pdk (15m x 5m)	Holding Pdk (15m x 3m)	Slight run-off site with sparse *Casuarina pauper* overstorey. Sandy soil. *Maireana pyramidata, M. sedifolia, Dissocarpus biflorus, Ptilotus obovatus.*
2	Katunga/ Myola	Iron Baron 6332-111 QD064519	Rainbow Pdk (15m x 5m)	Cooks Pdk (15m x 2m)	Open, treeless run-off site. *M. sedifolia, M. pyramidata, M. georgei, Atriplex stipitata.*
3	Katunga	Iron Baron 6332-111 QD085647	Haralds Pdk (20m x 5m)	Parwingee Pdk (20m x 3m)	Open, treeless run-off site. Many sheep tracks in Haralds. *M. sedifolia, M. georgei, M. pyramidata, Rhagodia spinescens, Eremophila scoparia, Sclerolaena* spp.
4	Myola	Roopena 6332-11 QD107504	Faraway Pdk (27m x 10m)	Rail Reserve (27m x 3m)	Run-off rise. *M. sedifolia, M. georgei, Sclerolaena* spp. Vegetation thicker on Reserve side.
5	Katunga	Iron Baron 6332-111 QD043645	Cooey Pdk (30m x 5m)	Road Reserve (30m x 3m)	Run-on depression. Heavy grazing inside paddock. *M. sedifolia, M. georgei, M. pyramidata, A. stipitata.*

TABLE 4.3. continued. Details of the cross-fence comparison sites.

Site No.	Station	Mapsheet & Location	Grazed Side (length x depth)	Ungrazed Side (length x depth)	General Description
6	Middleback	Roopena 6332-11 QD295515	Yingani Dam (60m x 5m)	Rainbow Pdk (60m x 2m)	Run-on site. Yingani Dam small and ephemeral. Heavy grazing inside dam yard, light grazing in Rainbow Pdk. Survey conducted along eastern fence of dam yard. *Maireana brevifolia, M. sedifolia, R. spinescens, Marrubium vulgare, Enchylaena tomentosa*. Saltbush and bluebush thicker in Rainbow Pdk.
7	Middleback	Randell 6331-1 QD176450	Holding Yard (16m x 75m)	Horseshoe Pdk (16m x 10m)	Holding Yard quite bare, with dry *Carrichtera annua* and *Sclerolaena* sp., one *Maireana astrotricha* and several saltbushes. Dense saltbush in Horseshoe with *M. pyramidata, M. sedifolia, Sclerolaena* sp. Grazing light in Horseshoe. Grazing historical in Holding Yard.
8	Middleback/ Nonowie	Randell 6331-1 QD195450	Two Mile Pdk (50m x 5m)	Winter Pdk (50m x 3m)	Run-on site. No overstorey on Two Mile side. *Alectryon oleifolius* on Winter side. Bush density lower on Two Mile side. *A. stipitata, M. sedifolia, M. pyramidata, M. georgei, Sclerolaena* spp., *Rhagodia ulicina*. Lots of sheep dung in Two Mile, none in Winter. Intact lichen and *C. annua* in Winter.

TABLE 4.3. continued. Details of the cross-fence comparison sites.

Site No.	Station	Mapsheet & Location	Grazed Side (length x depth)	Ungrazed Side (length x depth)	General Description
9	Middleback/ Nonowie	Randell 6331-1 QD209449	Barbers Dam Pdk (70m x 10m)	Kirrani Pdk (70m x 5m)	Low-lying run-on site. *M. pyramidata*, *M. sedifolia*, *M. astrotricha*, *Carthamus lanatus*, *Sclerolaena* spp., *R. spinescens*, *P. obovatus*, *Solanum* sp., *Marrubium vulgare*. Saltbush thicker on Kirrani side. Lots of sheep dung on Barbers Dam side.
10	Middleback	Roopena 6332-11 QD277527	Cottage Pdk (50m x 30m)	Rainbow Pdk (50m x 10m)	Run-off rise. *M. sedifolia*, various grasses, very little saltbush south of the Cottage trough, thick saltbush in Rainbow.
11	Middleback	Roopena 6332-11 QD257527	Gluepot Pdk (25m x 3m)	Cottage Pdk (25m x 3m)	Treeless, run-on depression. *M. pyramidata*, *M. georgei*, *Sclerolaena* spp., *E. scoparia*.

ANALYSES AND RESULTS

To determine whether current grazing pressure was greater for females than males on the grazed sites, the proportion of grazed shrubs was calculated and then compared for each phenotype:

$$\text{Proportion Grazed}_{(i)} = \frac{\text{No. shrubs grazed}_{(i)}}{\text{Total no. shrubs}_{(i)}}$$

Where (i) is sex phenotype (male or female)

Table 4.4 demonstrates that grazed sites had male-biased sex ratios and that proportionately more females showed evidence of current grazing pressure than males. Wilcoxon two-samples tests performed on the pooled data confirmed that these results were statistically significant (sex ratio Prob>|Z|= <0.05, current grazing Prob>|Z|= <0.05). Closer inspection revealed that the total number of females and males was similar when the ungrazed sites were pooled (180 males, 165 females). On the grazed sites, there were less males and females (101 males, 30 females) and more vegetative shrubs (220 compared to 42 on the ungrazed sites). These data show that although the numbers of both sexes declined, the reduction in females was much greater. Only 32% (32/101) of the males on the grazed sites showed evidence of current grazing compared to 77% (23/30) of the females. Thus, it would appear that grazing adversely affects the survival and reproductive abilities of both sexes; however, females are affected to a greater extent.

TABLE 4.4. Results of the cross-fence comparisons.

Site (Grazed side first)	M:F on grazed side.	M:F on ungrazed side.	Is the M:F higher on the grazed site?	Proportion females grazed	Proportion males grazed	Is current grazing pressure higher for females than males?
Illinee-Holding	7.5:1	2:1	Yes	0.5	0.2	Yes
Rainbow-Cooks	1:1	0.6:1	Yes	1.0	0.5	Yes
Haralds-Parwingee	6:1	0.5:1	Yes	1.0	0.2	Yes
Faraway-Rail	4:1	1.8:1	Yes	1.0	0.5	Yes
Cooey-Road	*	0.6:1	*	*	*	*
Yingani-Rainbow	9:1	2.5:1	Yes	1.0	0.9	Yes
Holding-Horseshoe	5.5:1	0.8:1	Yes	#	#	#
Two Mile-Winter	1.7:1	1.1:1	Yes	0.8	0.1	Yes
Barbers Dam-Kirrani	2.1:1	1.1:1	Yes	0.6	0.2	Yes
Cottage-Rainbow	3.5:1	0.8:1	Yes	1.0	0.3	Yes
Gluepot-Cottage	10:1	2.1:1	Yes	1.0	0.7	Yes

*There was only one shrub reproducing on the very heavily grazed Cooey site.
#The Holding paddock was not currently grazed. Site was only used to show effects of historical grazing.

DISCUSSION

The waterpoint experiment at Hatchards was used to determine whether a large flock of sheep would discriminate between the sexes of saltbush at a previously sporadically and lightly grazed site. Within two weeks of grazing, palatability variation between the sexes of bladder saltbush had been revealed. Ivlev's Electivity Index, and the ratio of grazed to ungrazed shrubs on the belt quadrats, confirmed that female saltbushes were grazed preferentially. Controls for grazing by other herbivores left no doubt that the biomass loss was attributable to sheep.

The waterpoint experiment relied on the assumption that the site had not received sustained herbivore pressure and that the current saltbush population had not been modified by grazing. All observations at the site prior to the installation of the waterpoint supported this assumption. Unlike the small-plot grazing trials, which used small flocks of sheep in a restricted area, the flock at Hatchards was left to graze at the new waterpoint without disturbance. The results thus reflect the cumulative effects of natural sheep behaviour. I believe that the combination of an unmodified plant population and an undisturbed station flock resulted in a rigorous context for testing palatability variation at the paddock-scale.

Preferential grazing of female saltbushes was also detected at the cross-fence sites. Current grazing pressure was significantly higher on females than males, and the sex ratios were significantly male-biased on all grazed sites. This outcome occurred regardless of topography, soils, plant community and grazing history. The cross-fence comparisons reported here thus infer a link between current grazing behaviour and male-biased sex ratios. As these results support the findings of the piosphere studies in New South Wales, this study suggests that sheep may differentially graze the sexes of bladder saltbush throughout its range.

It must be noted, however, that male-biased sex ratios are not always a result of selective grazing. The saltbush population at Hatchards was naturally male-biased, as were several of the ungrazed cross-fence sites. Williams (1972) suggested that saltbush populations which had male to female ratios greater than 2:1 are at risk of extinction. Three of the ungrazed cross-fence sites in this study, and the population at Hatchards, had ratios of this magnitude. It is unlikely that any of these populations were at risk of extinction because they all had reproductive females, small shrubs, seedlings and accumulated seed beneath the bushes. In several of the grazed populations, however, the sex ratios were very imbalanced and reproductive output appeared to be suppressed. It is possible that these populations are at risk of extinction unless the grazing pressure is relaxed. This issue is discussed further in Chapter 6.

The cross-fence comparisons suggest that the cues which stimulate selective grazing must be strong because the results were consistent even though the sex, age and maternal line of the sheep varied between sites. This is also supported by the fact that ewes were used in the waterpoint experiment whilst wethers were used in the small-plot grazing trials. The next chapter reports a series of intensive cafeteria trials which investigated the cues in bladder saltbush which elicit selective grazing responses from sheep.

CHAPTER 5
CAFETERIA TRIALS

INTRODUCTION

The small-plot grazing trials and the waterpoint experiment at Hatchards demonstrated that sheep preferentially graze the female phenotype of bladder saltbush. The behaviour was detected in different seasons and amongst sheep differing in age, sex and maternal line. Furthermore, the cross-fence comparisons showed that selective grazing over a longer period has altered the sex ratios of bladder saltbush populations in the study area. Taken together, these findings indicate that the cues which trigger the behaviour must be relatively strong and consistent. The cafeteria trials reported here were designed to investigate the cues in bladder saltbush which stimulate selective grazing.

Graetz (1978) believed that the male flower spikes of bladder saltbush deter sheep and the results of the small-plot grazing trials reported in Chapter 3 support this hypothesis. Observations made in the first two trials indicated that sheep tended to avoid male shrubs with long and/or dense spikes. These observations were confirmed quantitatively in the final trial. As a result of the speculation in the literature, and the evidence from earlier stages of this research, it was logical to investigate the role of the male spike in more detail. This was achieved using cafeteria trials.

Cafeteria trials allow animals to make choices from two or more forages presented to them in a strictly controlled environment. This method has been used to investigate the dietary behaviour of many herbivores including impala (Frost 1981), deer (Schwartz *et al.* 1980, Gillingham & Bunnell 1989a, Gillingham & Bunnell 1989b), hares (Reichardt *et al.* 1984, Tahvanainen *et al.* 1985), horses (Houpt *et al.* 1990), camels (White & Robards 1997) and sheep (Kenney & Black 1984, Burritt & Provenza 1989a, Burritt & Provenza 1989b). By removing plants from the confounding influences of their environment, the plant cues which stimulate selective grazing can be investigated. Unlike many other methods used for studying dietary behaviour, the cafeteria method can be strictly replicated and controlled. Furthermore, the presentation of the plant material can be manipulated in ways not possible using small-plot or paddock trials (i.e. Schwartz *et al.* 1980). In combination with other methods (see Chapter 1), cafeteria trials are thus useful for investigating the interaction between herbivores and their food plants. The cafeteria procedures reported here were fully developed during this project and several preliminary trials were conducted to establish and refine the methods.

Once the method was established, three separate trials were conducted. Each trial built on the results of the previous ones and the entire set thus represents a sequential development of hypotheses. The aims of the cafeteria trials were:

- To confirm that sheep selectively graze the sexes of bladder saltbush in a cafeteria environment.

- To investigate whether the removal of male spikes increases the consumption of male shoots.

- To verify that the male spike is a visual cue to an underlying deterrent in male plants.

METHODS

Cafeteria Layout

The cafeteria was set up in a shearing yard at Middleback Station. Six rows of ten untreated jarrah stakes were arranged in a grid pattern (Figure 5.1). The stakes were 30 centimetres long and were driven ten centimetres into the ground. Plant samples were attached to these stakes during the trials. Replicates had to be conducted on different days because the shearing yards only allowed space for one grid. Furthermore, several hours were required between replicates to prepare the plant samples.

Experimental Sheep

Ten mixed-sex hoggets were selected from larger station flocks for each trial. On the eve of each replicate the experimental sheep were mustered into a holding yard devoid of feed. Sheep had access to water at all times. Between replicates, the sheep were released into a fully vegetated paddock to resatiate. A different flock was used for each of the three trials.

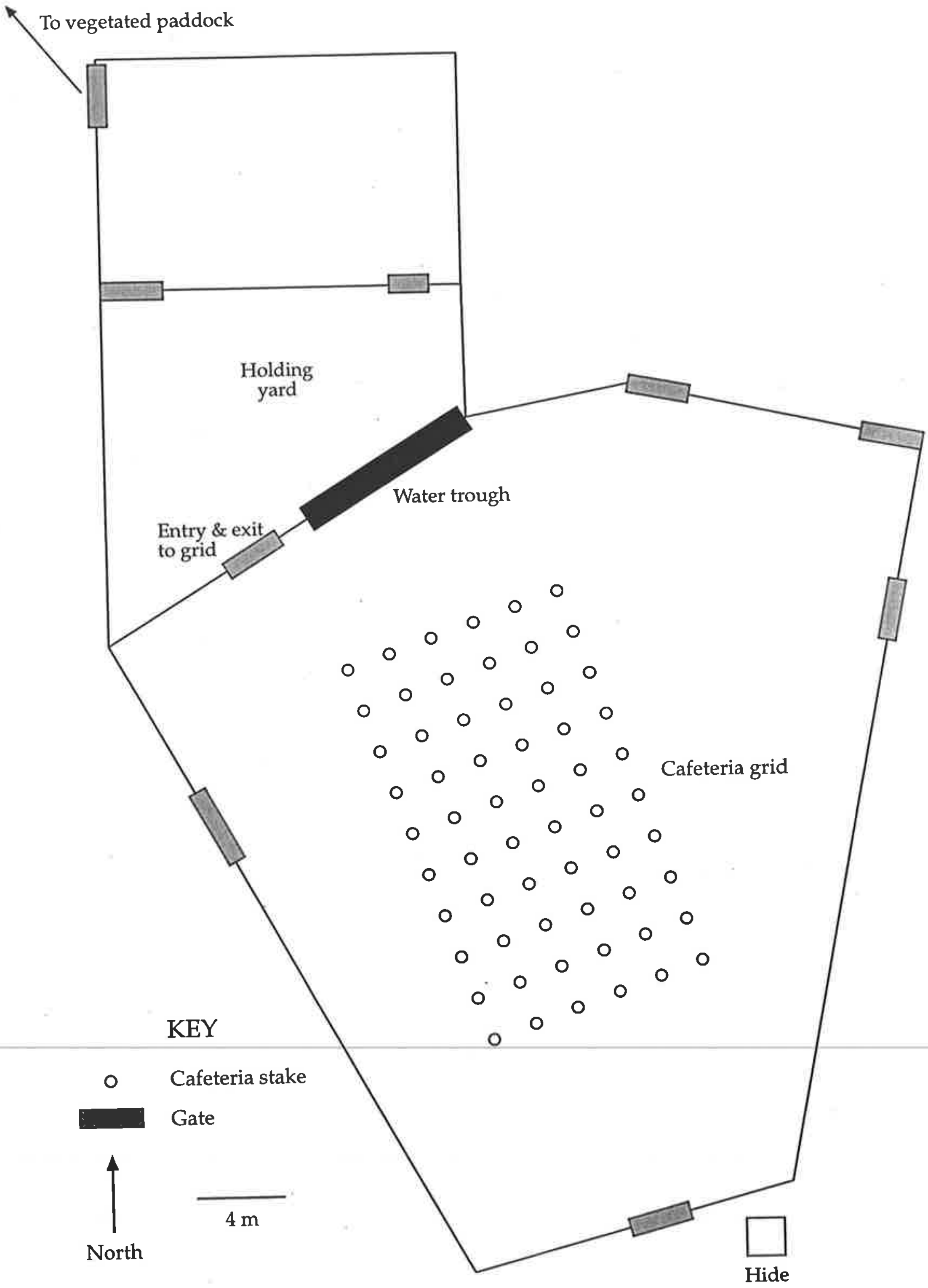

FIGURE 5.1. Layout used for the cafeteria trials.

Preparation of the Samples

All plant material used in the trials was harvested from shrubs in Little One Mile Paddock, Middleback Station (Figure 3.1). As noted previously, this paddock has rarely been used by sheep and the plant community is thus considered to be relatively pristine (A.W. Nicolson, pers. comm.). As a result, the saltbush population was expected to encompass a large range of palatability variation.

On the eve of each replicate, six large plastic tubs were filled with rainwater to a depth of five centimetres. Bunches of plant material were cut from shrubs in Little One Mile Paddock and were stored in the tubs with their stems immersed in the water. Material was cut from heavily fruiting female and heavily flowering male shrubs to maximise the visual expression of shrub sex. Three tubs of material were collected for each sex and the two sexes were kept separate. Loose-fitting lids were placed on the tubs and they were transported back to the on-site laboratory. Material from different tubs (of the same sex) was used to construct 'composite' samples. The composite method was used to maximise the uniformity of samples within treatments and to minimise any palatability effects due to individual source shrubs. The samples were constructed on a digital balance to ensure that the initial biomass of the samples were consistent. The final fresh weights of all samples were between 40 and 50 grams. Samples were tied at the base with unbleached string and their weights were recorded. The samples of a single treatment were prepared together and returned to the same tub. Different treatments were stored in different tubs. Loose-fitting lids were put on the tubs, which were kept in the laboratory overnight.

Experimental Treatments

(a) October 1995 - male versus female trial

The design and treatments used in each trial are summarised in Table 5.1. Two treatments were compared in the first trial. Thirty female and thirty male samples were prepared for each replicate. The male material varied widely in the density, length and maturity of spikes because the source shrubs were at various stages of flower production. Female material used in this trial had only mature, dry fruits. The two treatments were used to confirm that sheep would preferentially graze female bladder saltbush in a cafeteria environment. Four replicates were conducted.

(b) April 1996 - spike removal trial

Four treatments were compared in the second trial (Table 5.1). As in the first trial, there was a female and a male treatment (with 15 samples in each). The third treatment consisted of male samples which had all of the male spikes removed using fine dissection scissors. This treatment was included to test whether the removal of spikes would stimulate consumption. To control for any effects due to the physical cutting by the scissors, a fourth treatment was included. A strictly perfect clipping control was not possible because all male branches had spikes and clipping could not be done without removing some of these (and thus

TABLE 5.1. Summary of the designs of the cafeteria trials.

Trial	No. treatments	No. samples in each treatment	No. replicates	Description of treatments
October 1995	2	30	4	Male Female
April 1996	4	15	3	Male Female Clipped male Clipped female
September 1996	3	20	4	Female Hidden male with spikes Hidden male without spikes

confounding the control). The fourth treatment thus consisted of female samples which had the tips of nearly all shoots removed with the scissors. About one centimetre was cut from the tip of each female shoot to simulate the removal of spikes on the males. Cuts were made diagonally to prevent a hedged-look. All samples of all treatments had a final weight between 40 and 50 grams. The male material used in this trial had well-developed spikes which were releasing pollen, whilst all female material had ripe fruits.

(c) September 1996 - hidden male trial

Three treatments were compared in the final trial, with 20 samples in each (Table 5.1). The first treatment consisted of pure female samples which were not manipulated any further. The other two treatments consisted of female-dominated samples which had male material hidden inside them. The first of these had intact male material hidden inside whilst the other included male material with all spikes removed. For both of the hidden male treatments, the male material contributed 20 to 25% of the biomass of each sample and was enclosed by female material. Care was taken to ensure that the male material was completely hidden. The hidden male treatments were used to test whether the sheep could still detect the presence of male material in the absence of an obvious visual cue. The two different types of male material (clipped and non-clipped) were used to determine whether there was any difference in the detectability of material with or without spikes. The male material used in this trial had a mixture of old and new spikes and the female material had only unripe fruits.

Replicate Procedure

A random-number table was used to assign all samples to the 60 stakes before each replicate (Zar 1984). The tubs containing the samples were transported to the cafeteria yard about one hour before sunrise. Trials were conducted at dawn for two reasons. Firstly, the samples were less likely to wilt because maximum air humidity occurs around sunrise (Osborn *et al.* 1932). Secondly, sheep in chenopod shrublands normally commence grazing around this time (Squires 1974, Squires 1981). The samples were attached to the stakes using nylon cable-ties and five microdots were applied to each sample using a quick-drying marker pen. After all dots were applied, the sheep were let into the yard. Once grazing began, the sheep were observed from a hide south of the yard for the duration of all replicates. Notes were made on their behaviour and grazing patterns at intervals not exceeding ten minutes. When sheep were actively grazing or moving, notes were made continuously. Each replicate was stopped as soon as all stakes had been visited at least twice. A visit was considered to have occurred if a sheep passed within half a metre of a stake. Visits to stakes were recorded on a diagram of the grid. Naturally, some stakes were visited more often than others; however, a trial did not end until the last stake had been visited twice. This method of determining the endpoint was used to ensure that all samples had the potential to be grazed or rejected by the sheep. At the end of each replicate, the sheep were quietly mustered out of the cafeteria and into the large vegetated paddock near the shearing yards. The microdots remaining on the samples were then recounted. Any microdots which had been broken off and not eaten were recorded as damaged. All material was then cleared from the grid and discarded away from the site. The percentage of microdots eaten from each sample was assumed to be directly proportional to the percentage of initial biomass eaten (after Lange 1984).

Analyses

Analysis of variance (ANOVA) was used to compare the biomass consumption of the treatments. Where the 'day' term was not significant, no interaction term was included in the ANOVA. Where appropriate, pairwise comparisons were made using the Tukey-Kramer HSD test. All analyses were performed using the JMP program (SAS Institute 1989).

RESULTS

October 1995 - Male versus Female Trial

The ANOVA showed that both 'day' and 'treatment' were significant, but importantly, there was no significant interaction between them (Table 5.2). Figure 5.2 shows that the female treatment was consumed significantly more than the male treatment, which supports all the findings to date. This result also confirmed that the cues for selective grazing are features of the plant rather than the environment, and allowed further use the cafeteria method to test other hypotheses.

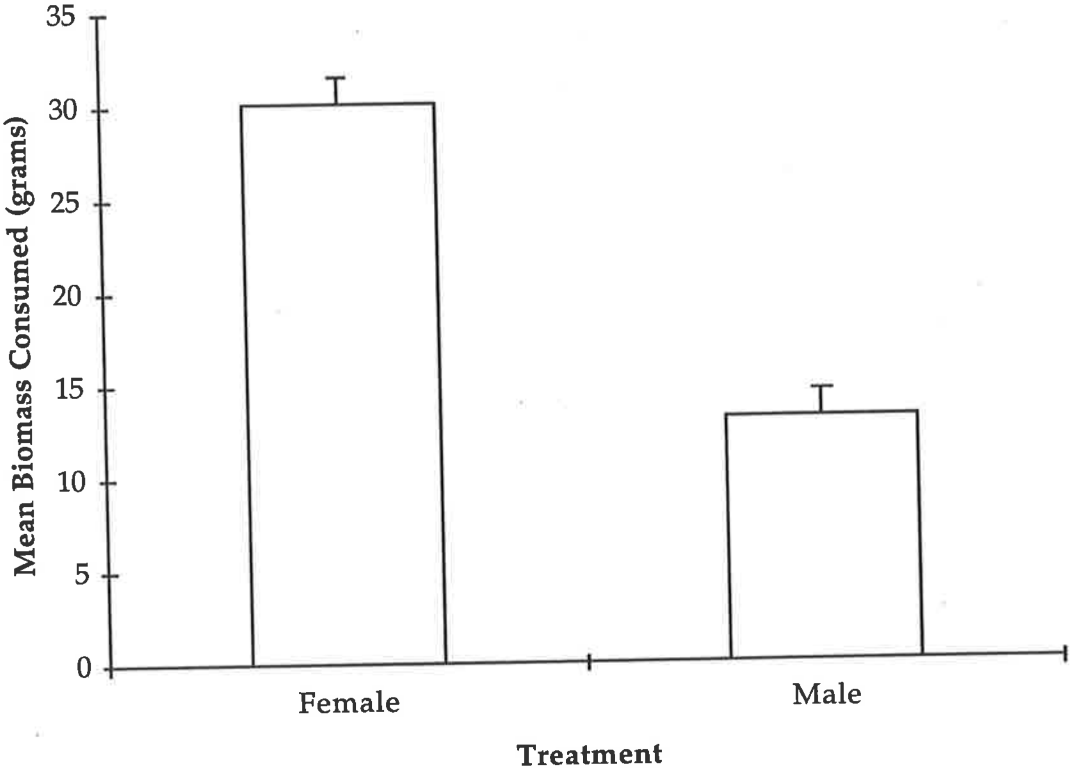

FIGURE 5.2. Preferential consumption of the female treatment in the October 1995 cafeteria trial. Error bars represent Standard Errors.

TABLE 5.2. Summary of results for all three cafeteria trials.

	Prob>F (degrees of freedom)		
	October 1995	April 1996	September 1996
Treatment	<0.001 (1)	<0.001 (3)	<0.001 (2)
Day	<0.001 (3)	0.5758 (2)	0.1229 (3)
Treatment x Day	0.5662 (3)	-	-

April 1996 - Spike Removal Trial

'Treatment' was the only significant term in the model (Table 5.2) and the results for all replicates were thus pooled for display in Figure 5.3. As expected, the removal of male flower spikes stimulated consumption of male material. The consumption of the non-clipped and clipped female treatments was not significantly different, indicating that clipping *per se* did not influence consumption.

September 1996 - Hidden Male Trial

Once again, 'treatment' was the only significant term in the ANOVA (Table 5.2). Figure 5.4 shows that the pure female treatment was consumed significantly more than either of the two hidden male treatments. This demonstrates that sheep were able to detect male material without an obvious visual cue. Although it appears that the

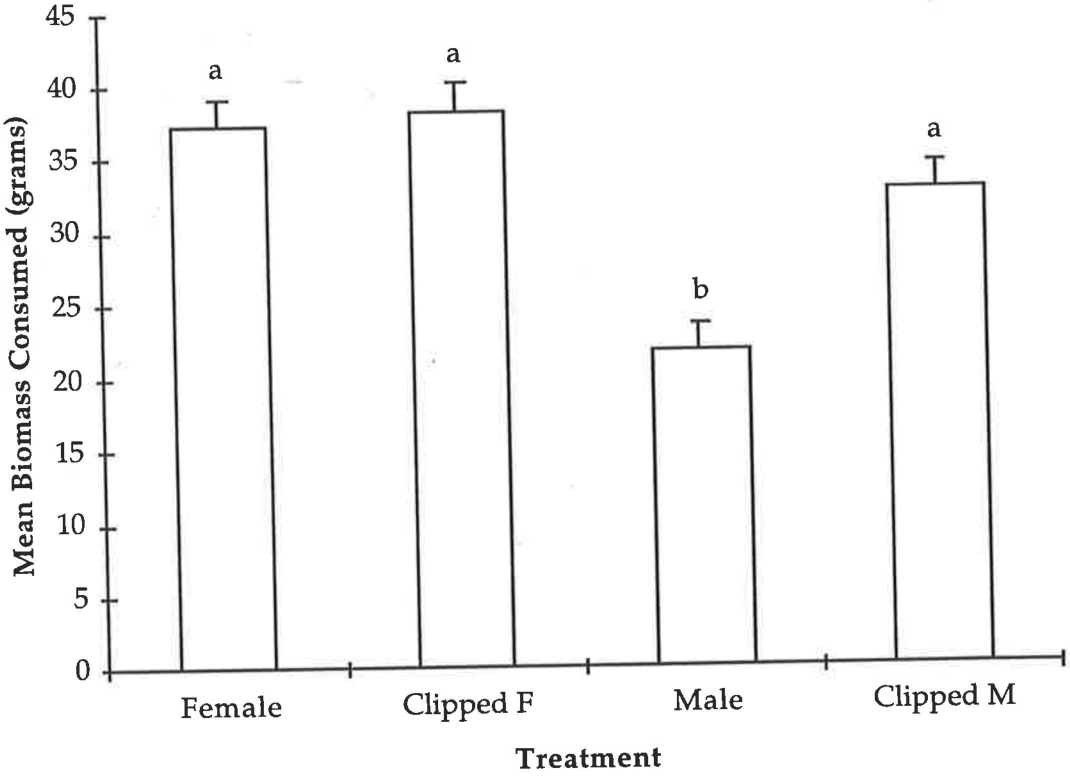

FIGURE 5.3. The effect of spike removal in the April 1996 cafeteria trial. Columns with the same letters signify means that are not significantly different. Error bars represent Standard Errors.

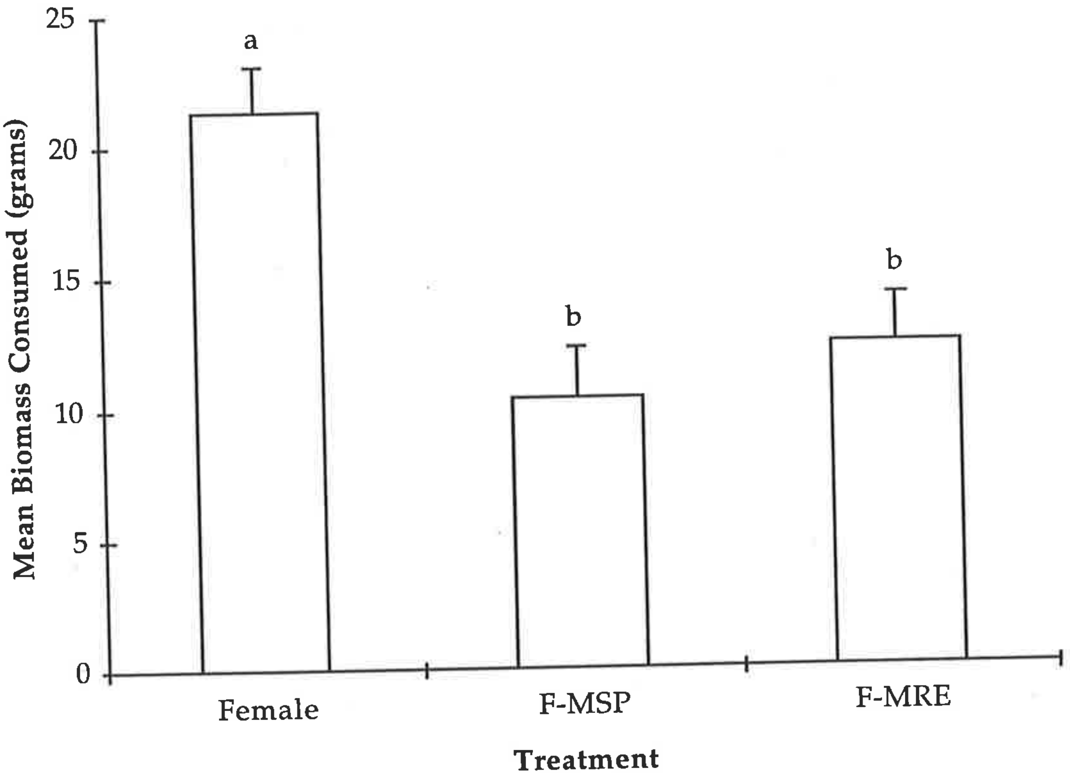

FIGURE 5.4. Consumption of treatments in the September 1996 cafeteria trial. F-MSP represents female samples with male material hidden inside with spikes intact. F-MRE represents female samples with male material hidden inside with spikes removed. Columns with the same letters signify means that are not significantly different. Error bars represent Standard Errors.

clipped male treatment may have been consumed slightly more than the non-clipped treatment, this was not statistically significant.

DISCUSSION

The extensive use of the cafeteria method relied on the assumption that the cues underlying palatability variation were a feature of the plants rather than their environment. This assumption was validated in the first trial. As in the small-plot grazing trials and the waterpoint experiment at Hatchards, the female phenotype was preferred.

The removal of male flower spikes increased the acceptability of male material. As clipping had no significant effect on the consumption of female samples, it can be argued that clipping *per se* was not the cause of increased consumption of clipped male samples. The use of clipped females as a control assumed that the sexes would not differ in their response to the physical treatment of clipping. At this time, there is no reason to doubt this assumption. The results of the second trial thus confirm that the male spike is a cue to sheep. In the final trial sheep were able to detect and avoid female samples containing both clipped and non-clipped male material, indicating that there is a deterrent throughout the male phenotype rather than in the spike alone. These observations suggest that sheep use the male flower spike principally as a visual cue but can also respond to an olfactory cue when spikes are not visually obvious. This suggestion is supported by behavioural observations recorded during the three trials. These observations indicated that sheep were often able to reject flowering male samples without having to smell or taste them. At other times, sheep would take prolonged sniffs at the male samples and could reject them without having to taste them. Occasionally sheep had to taste male samples. Taken together, these observations, and the results of the final two trials suggest that the olfactory cue may vary in strength over time. Unfortunately, characterisation of the olfactory cue was beyond the scope of this study and this remains an avenue for further research.

The results of these cafeteria trials have confirmed that the nature of the palatability variation in bladder saltbush is a deterrent in the male phenotype. If the cue for selective grazing was an attractant in the female, the three treatments in the final trial should have been consumed equally. Although beyond the scope of this project, the results of these trials demonstrate that more research is required to characterise the male deterrent and determine how it influences the grazing behaviour of sheep.

CHAPTER 6
ECOLOGICAL IMPLICATIONS OF SEX-BASED SELECTIVITY

INTRODUCTION

Selective grazing is known to modify patterns and processes in plant populations and ecosystems (Ellis *et al.* 1976, Trlica & Rittenhouse 1993) and has been implicated in the modification of pattern in bladder saltbush populations (Williams *et al.* 1978). The behaviour of the herbivore, intensity and frequency of grazing and the life cycle stage of the plants ultimately determine the severity of these changes (Jameson 1963, Bastrenta 1991, Trlica & Rittenhouse 1993).

Observations made during my research on bladder saltbush suggest that grazing adversely affects plant size and reproduction. These observations are consistent with the findings of Williams (1972), Williams *et al.* (1978), Andrew & Lange (1986b) and Hunt (1995). Similar results have been reported for perennial daisies in the rangelands of South Africa (Milton 1994) and for jojoba in the Sonoran desert (Roundy & Ruyle 1989). Height, biomass, number of fruits produced, number of seeds produced and seed weight are all indicators of the influence of grazing on plant fitness (Paige & Whitham 1987). The results of the waterpoint experiment conducted at Hatchards (Chapter 4) provided quantitative evidence that grazing significantly reduced the heights, widths and biomass of bladder saltbushes. Furthermore, grazing reduced the percentage of shrubs in flower and fruit and the percentage of branches with flowers and fruits (Chapter 4). These results suggest that grazing may affect the ability of individual saltbushes to contribute to the next generation. The preferential grazing of the female phenotype is potentially serious because seed production is likely to be impaired. To have serious long-term effects on population dynamics, however, grazing would have to keep female shrubs in a reduced state almost permanently.

The aims of the experiments reported in this chapter were:

- To demonstrate that grazing has reduced the number of reproductive shrubs in a wide range of grazed populations.
- To quantify the effect of grazing on fruit number[3], total fruit weight and seed number.
- To confirm that grazing has adversely affected the heights, widths and biomass of grazed saltbushes in a moderately grazed paddock population.
- To demonstrate that sheep return to graze the same individuals repeatedly and keep them in a reduced state.

METHODS

Cross-fence Comparison Sites

The cross-fence comparison sites (described in Chapter 4) were used to demonstrate that grazing limits the number of reproductive shrubs in grazed populations. The data from the cross-fence surveys were used to

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[3] The term 'fruit' refers to the entire fruiting body (seed, pericarp and bracteoles).

determine the ratio of vegetative to reproductive shrubs for the grazed and ungrazed population at each of the eleven sites.

Hatchards Paddock Site (Katunga Station)

In conjunction with a moderately grazed site in Two Mile Paddock (described later), the Hatchards site was used to quantify the effect of grazing on the reproductive output of female shrubs.

The physical and experimental features of the site have been fully described in Chapter 4; however, a brief summary of the experiment is presented here. In April 1996, a flock of sheep was introduced to a new waterpoint which had been placed in a relatively pristine population of bladder saltbush. The maximum height, maximum width, biomass and the percentage of branches with flowers/fruits were measured for each protected and unprotected saltbush before the introduction of the sheep. These features were remeasured two weeks after grazing commenced and again after five months. The protected shrubs were situated inside two exclosures which were built within 50 metres of the trough (Figure 4.2). The 75 shrubs closest to the trough were left unprotected and were used to quantify the effects of grazing. Prior to grazing, there were no significant differences in height, width, biomass, the percentage of male stems with flower spikes or the percentage of female branches with fruits between the protected and unprotected populations (Chapter 4).

Five months after grazing commenced, several reproductive aspects were compared for protected and unprotected female shrubs at the Hatchards site. This happened to coincide with a period of favourable rainfall conditions (Figure 6.1) which stimulated widespread reproduction in saltbushes throughout the wider study area. Reproductive output was assessed by matching pairs of female shrubs from the protected and unprotected populations on the basis of biomass. Nine pairs of shrubs, ranging from 36 to 110 grams fresh weight, were selected. All branches were cut from the shrubs and put into labelled plastic bags. Harvesting was done before the fruits were fully ripe to minimise fruit losses. The fruits were removed from the branches by hand, put into paper bags and dried at 78°C for 48 hours. The number and total dry weight of fruits was then determined for each shrub. The number of seeds was also determined after the seeds were removed from the fruits.

Two Mile Paddock Site (Middleback Station)

In addition to quantifying the effect of grazing on fruit production, this site was used to confirm previous results showing that grazing adversely affects the height, width and biomass of bladder saltbushes. This site was also used to demonstrate that sheep return to the same plants that have been grazed previously and keep them in a chronically reduced state.

In August 1994, a sheep-proof exclosure measuring 44.5 by 52.5 metres was built 600 metres south-east of Barbers Dam in Two Mile Paddock (Figure 6.2). An unfenced area of identical dimensions was situated on the western side of the exclosure. The site was dominated by bladder saltbushes and a count revealed that about half of them showed no signs

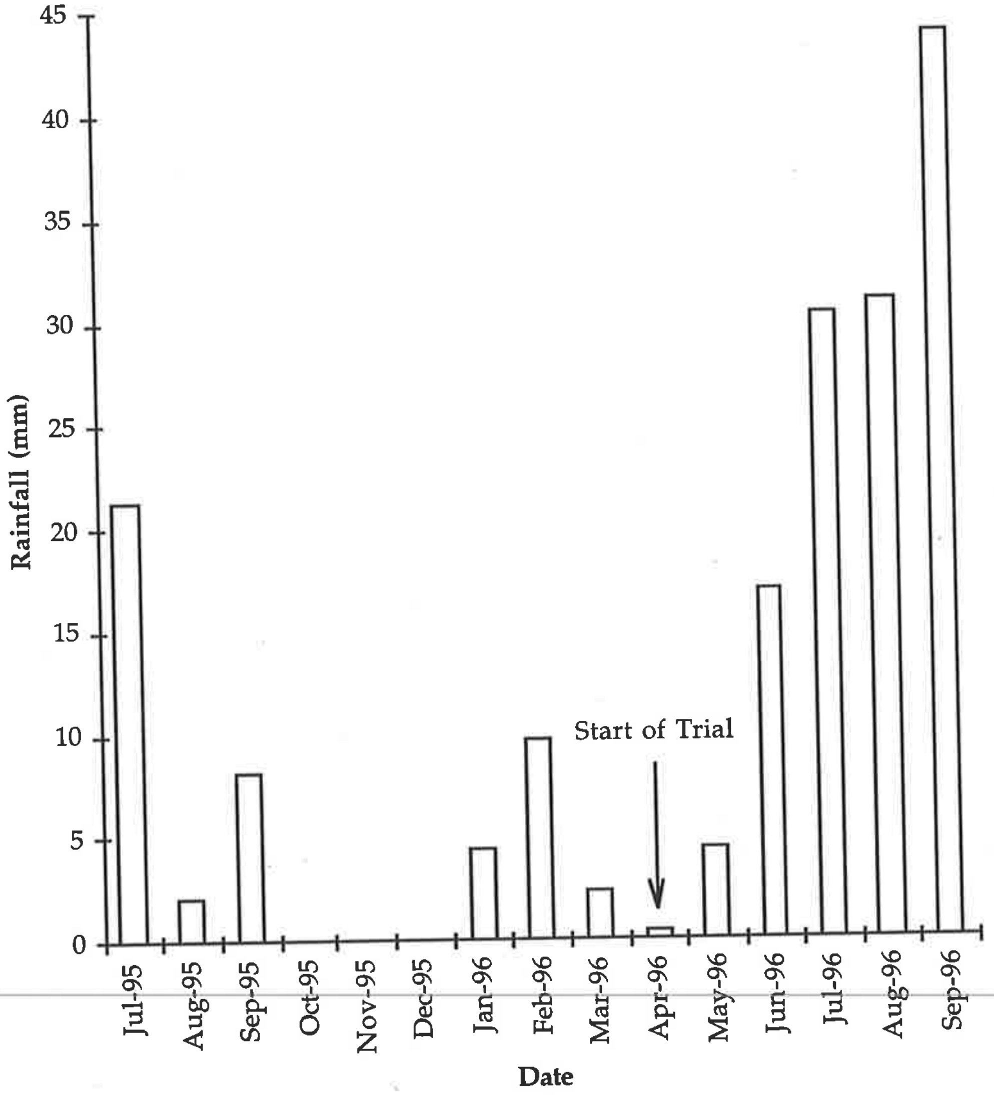


FIGURE 6.1. Rainfall at Iron Knob prior to and during the Hatchards experiment. (Data from the Commonwealth Bureau of Meteorology, Adelaide, South Australia).

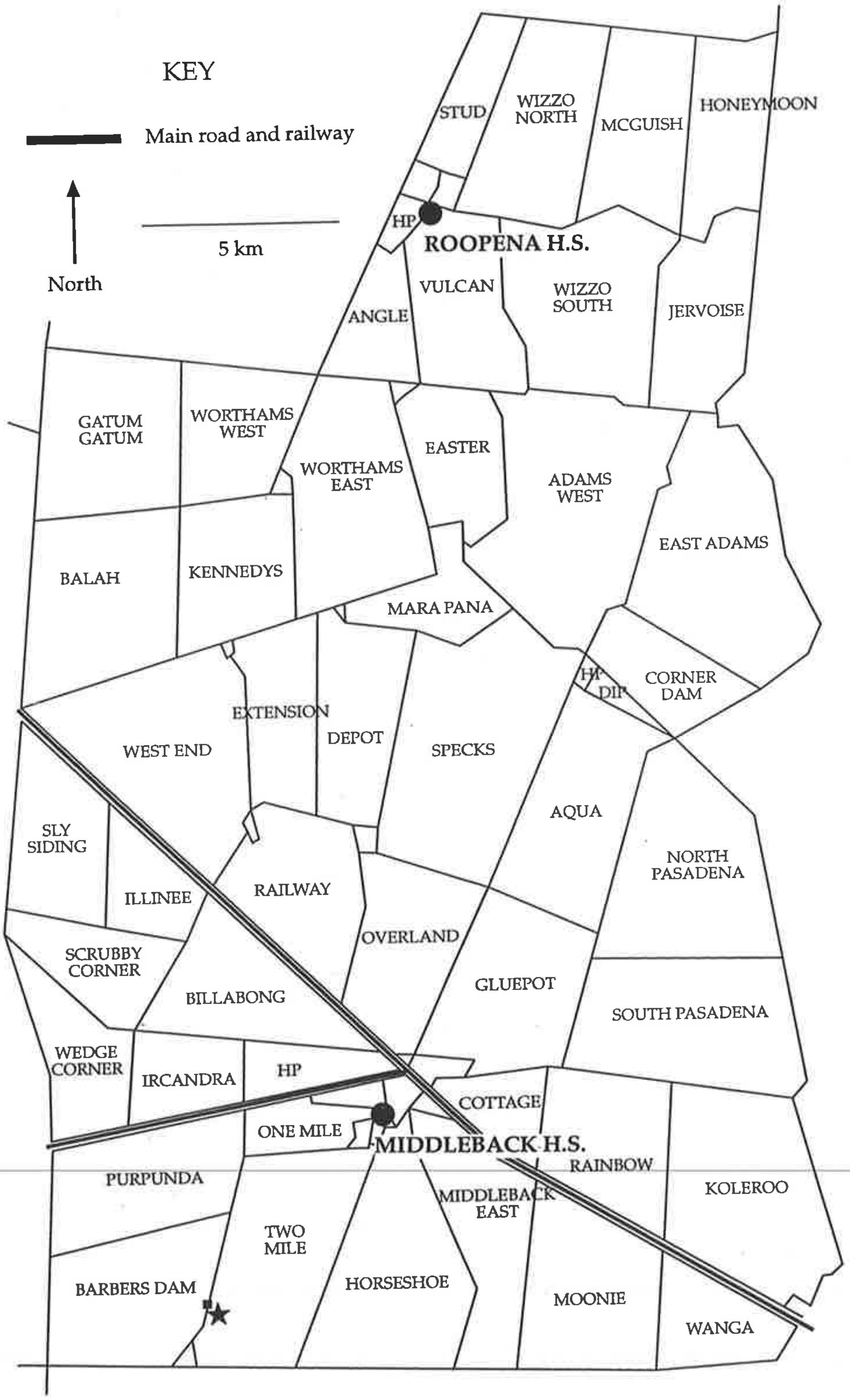


FIGURE 6.2. Paddock plan showing the location of the exclosure (★) in Two Mile Paddock, Middleback Station. Barber's Dam is shown by the black square.

of grazing, whilst the other half appeared to be very stunted. This observation suggested that grazing pressure was only moderate, even though the site was close to a dam which has been in use for about 100 years.

After the exclosure was constructed, it was temporarily divided into 63 squares using string lines. Within this temporary grid, an average of two grazed and two ungrazed shrubs were tagged in each square. Ungrazed shrubs were defined as having upright growth habits, slender branches and unbitten stems. These shrubs usually had a low ratio of wood to leaf biomass. Grazed shrubs had stunted growth habits, bitten stems and a high ratio of wood to leaf biomass. The use of a grid ensured an even distribution of grazed and ungrazed experimental shrubs throughout the exclosure. In total, 115 shrubs of each grazing status were tagged. The unprotected area adjacent to the exclosure was divided into four imaginary squares of equal size. Within each square, eighteen shrubs of each grazing status were tagged yielding a total of 72 grazed and 72 ungrazed shrubs. The sample sizes were higher inside the exclosure because an extra 43 shrubs of each grazing status were originally set aside for harvesting experiments. These harvesting experiments were never conducted and the data from these shrubs were subsequently incorporated in the study. The sex, maximum height, maximum width and biomass of all shrubs were surveyed on several occasions over 2.5 years. Maximum heights and widths were measured with a metre ruler and recorded to the nearest centimetre and biomass was determined using the Adelaide

Technique (Andrew *et al.* 1979). Data from the first (August 1994) and the final (March 1997) surveys are presented here to demonstrate that grazing adversely affected plant height, width and biomass at a moderately grazed site.

Female saltbushes outside of the exclosure were also used to compare the fruit production of grazed and ungrazed shrubs at this site. The data from the final survey were used to identify pairs of grazed and ungrazed shrubs with similar biomass. Eight pairs, with fresh weights ranging from 25 to 115 grams fresh weight, were identified this way. The collection and preparation methods used at Two Mile were identical to those described for Hatchards. In light of the seed data from Hatchards, only the number and total dry weight of fruits were determined for the Two Mile samples.

In addition to the morphological and reproductive aspects, the shrubs at Two Mile were used to monitor grazing pressure at the site over time. Grazing was monitored using paint indicators similar to those used by Price *et al.* (1989) for *Atriplex canescens*. Using the grazing status recorded in August 1994, twenty grazed and twenty ungrazed shrubs were marked with indicators in both the fenced and unfenced sections of the site. These shrubs were chosen using a random-number table (Zar 1984). Indicators consisted of small orange paint slashes applied two centimetres from the tips of five stems on each shrub. Indicators were applied to one stem on each of the north, east, south and west aspects, with the fifth one applied to a central stem. On small shrubs, less than five indicators were applied. Indicators were applied to a different set of shrubs on three occasions. A summary of the total number and placement of the indicators is shown in Table 6.1. The indicators were relocated after three or eight months and recorded as grazed or ungrazed. Shoots which had stripped stems and blunt tips were considered to be grazed.

Analyses

Shapiro-Wilk W tests were used to detect departures from normality. Where data sets deviated significantly, appropriate transformations were attempted. In all cases the transformations did not improve the normality of the data sets, indicating that the departures were large. The data were thus analysed non-parametrically. The Wilcoxon two-samples test was used to compare reproductive output with grazing status at both the Hatchards and Two Mile sites. Correlation was used to determine whether there were significant relationships between plant biomass and reproductive output. The mean maximum height, maximum width and biomass of the grazed and ungrazed shrubs at Two Mile were compared on two occasions. The data from the first survey (August 1994) were analysed using the Wilcoxon two-samples test. To determine whether subsequent protection from grazing allowed any recovery, the results of the final survey were grouped according to grazing status and position (protected or not protected). These data were analysed using the Kruskal Wallis test, as were the grazing indicator data. Where the Kruskal Wallis test gave a significant result, the Tukey-Kramer HSD test was used to identify the means which were significantly different. All analyses were performed using the JMP program (SAS Institute 1989).

TABLE 6.1. Summary of grazing indicators applied to shrubs at the Two Mile Paddock site.

Date Applied	Date Measured	Number of Indicators				
		Grazed Status* Inside Exclosure	Ungrazed Status* Inside Exclosure	Grazed Status* Outside Exclosure	Ungrazed Status* Outside Exclosure	Total
August 1995	April 1996	100	100	100	100	400
April 1996	December 1996	95	92	89	87	363
December 1996	March 1997	95	93	84	78	350

* Refers to the grazing status recorded in August 1994 at the time the exclosure was erected.

RESULTS

Cross-fence Comparison Sites

Table 6.2 shows the ratio of vegetative to reproductive shrubs for the grazed and ungrazed populations at each of the cross-fence sites. The ratio of vegetative to reproductive shrubs in the grazed populations was two to 350 times higher than in the ungrazed populations, confirming that grazing had reduced the number of shrubs which could reproduce.

Hatchards Paddock Site

In September 1996, grazed shrubs had significantly fewer fruits than shrubs protected from grazing ($Prob>|Z| = <0.01$, Figure 6.3a), which resulted in a significantly lower total dry weight of fruits ($Prob>|Z| = <0.05$, Figure 6.3b). The correlation between total number of fruits and total number of seeds was highly significant ($Prob>F= <0.0001$, $r^2=0.95$), which was expected because bladder saltbush fruits only contain a single seed. There were no significant relationships between plant biomass and the number of fruits produced ($Prob>F=0.2095$, $r^2=0.097$), or plant biomass and total fruit dry weight ($Prob>F=0.0739$, $r^2=0.186$).

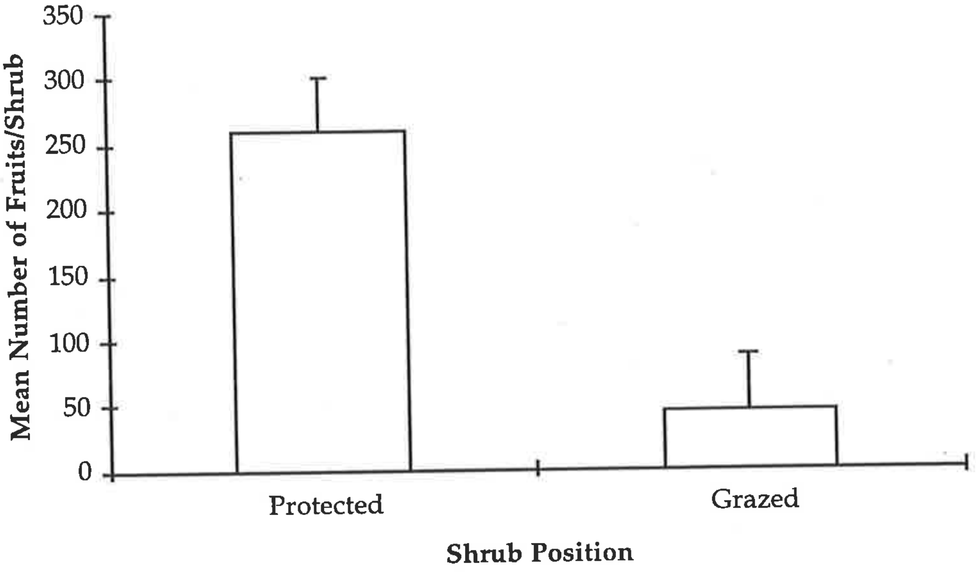
Two Mile Paddock Site

The fruit data from Two Mile strongly supported the results from Hatchards. In March 1997, grazed shrubs produced significantly fewer fruits than ungrazed shrubs ($Prob>|Z| = <0.01$, Figure 6.4a). Once again this resulted in a significantly lower total dry weight of fruits for grazed shrubs ($Prob>|Z| = <0.01$, Figure 6.4b). As at Hatchards, there was no

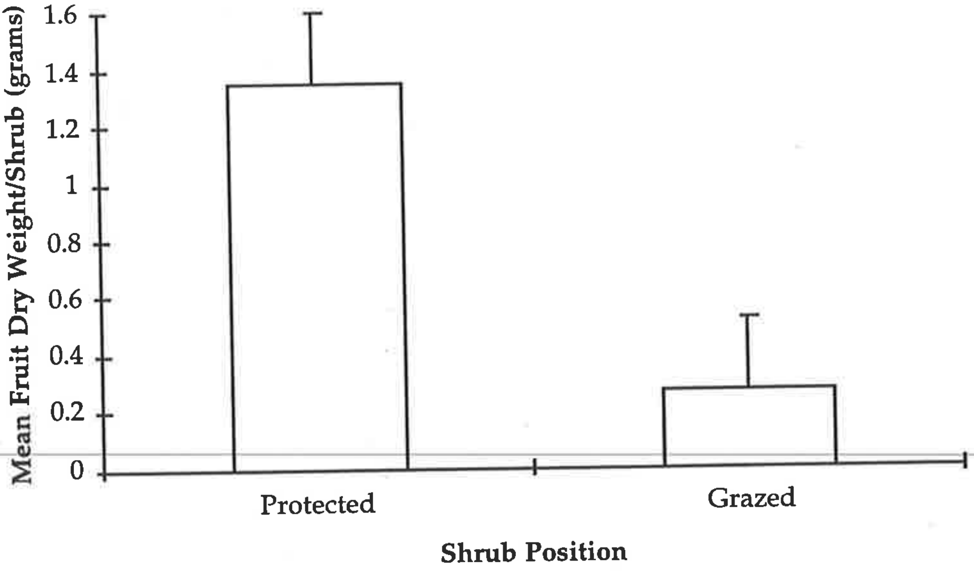
TABLE 6.2. Summary of the ratio of vegetative (V) to reproductive (R)* shrubs at each cross-fence site.

Cross-fence Site	V:R Grazed Site	V:R Ungrazed Site	Is V:R higher on the grazed site?
Illinee-Holding	1.1:1	0.2:1	Yes
Rainbow-Cooks	8.0:1	0.3:1	Yes
Haralds-Parwingee	4.1:1	0.1:1	Yes
Faraway-Rail	1.4:1	0.1:1	Yes
Cooey-Road	35:1	0.1:1	Yes
Yingani-Rainbow	2.6:1	0.2:1	Yes
Holding-Horseshoe	0.2:1	0.1:1	Yes
Two Mile-Winter	0.5:1	0.1:1	Yes
Barbers Dam-Kirrani	0.5:1	0.1:1	Yes
Cottage-Rainbow	1.0:1	0.1:1	Yes
Gluepot-Cottage	2.3:1	0.3:1	Yes

* Reproductive component is total number of females, males and bisexuals.

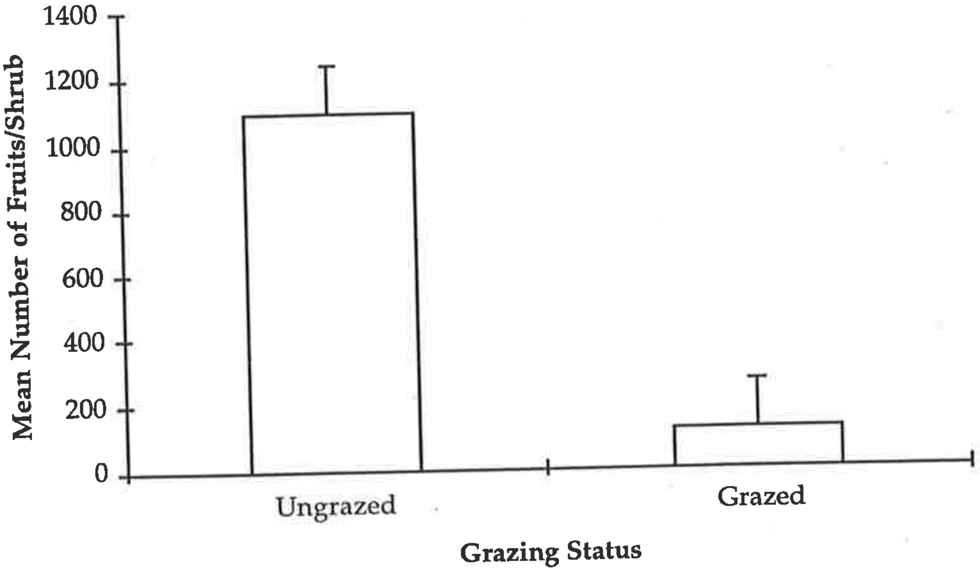


(a) Fruit number

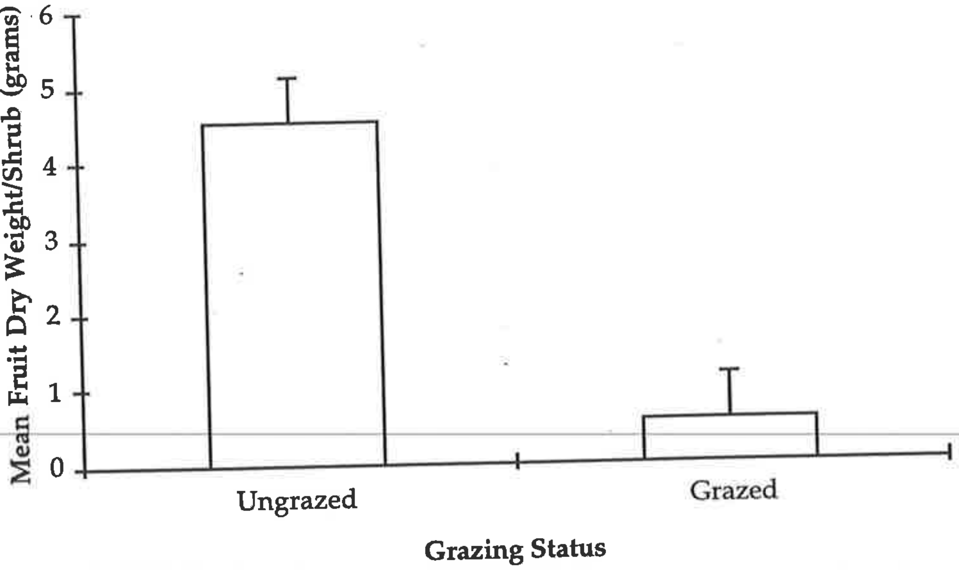


(b) Total fruit weight

FIGURE 6.3. Influence of grazing on fruit number and total fruit weight at the Hatchards site after five months of grazing. Error bars represent Standard Errors.



(a) Fruit number



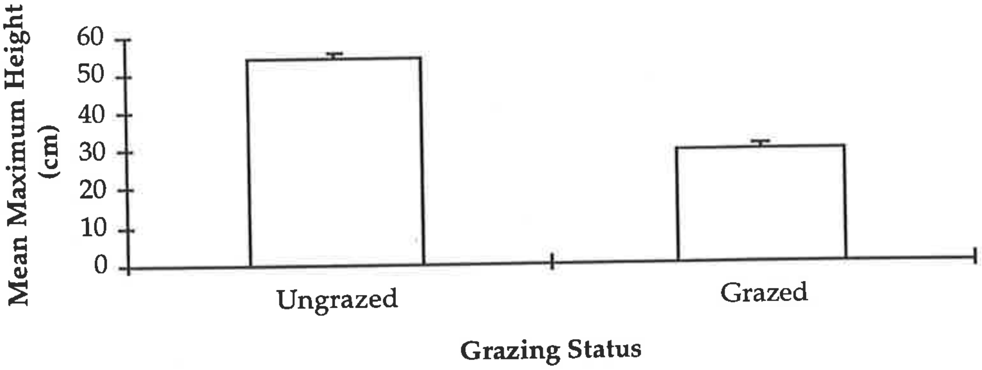
(b) Total fruit weight

FIGURE 6.4. Influence of long-term grazing on fruit number and total fruit weight at Two Mile. Error bars represent Standard Errors.

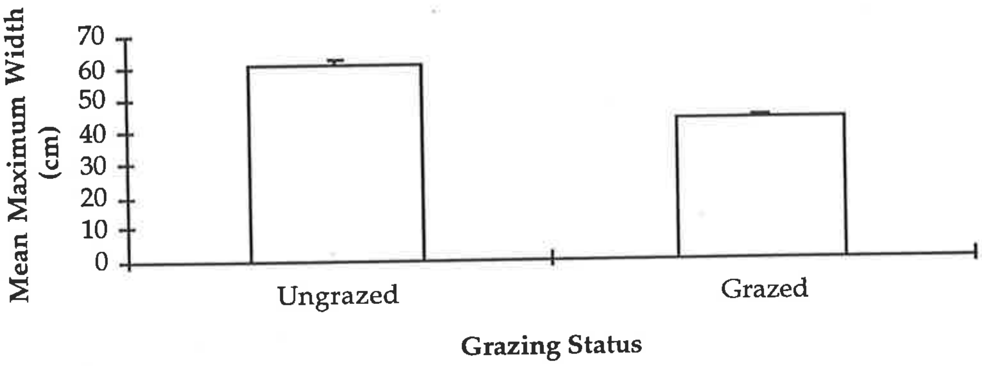
significant relationship between shrub biomass and the number of fruits produced (Prob>F=0.1197, r^2=0.164), or shrub biomass and the total dry weight of the fruits (Prob>F=0.1099, r^2=0.1723).

The first survey of plant height, width and biomass at the Two Mile site showed that ungrazed shrubs were significantly taller, wider and had significantly more biomass compared to grazed shrubs (Figures 6.5a-c). The differences between grazed and ungrazed plants outside the exclosure were maintained over the 2.5 years of the study (Figures 6.6a-c). Shrubs which were initially classified as grazed and then protected from grazing for 2.5 years were unable to overcome their deficient heights, widths and biomass (Figures 6.6a-c).

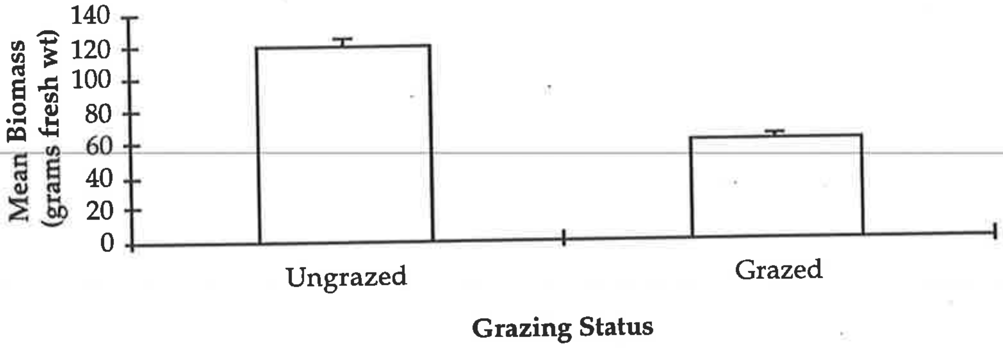
The results of the grazing indicator experiments are presented in Figures 6.7a-c. Between August 1995 and April 1996 significantly more shoots were grazed from grazed status shrubs outside the exclosure than any other group (Figure 6.7a). Inside the exclosure, seven shoots out of 200 showed evidence of grazing. Five of these were on grazed status shrubs and two were on ungrazed status shrubs. This low level of grazing can be attributed to kangaroos and supports the idea that kangaroos did not graze saltbushes very much during the trials. This finding is consistent with low levels of kangaroo grazing recorded in a similar study by Hunt (1995). The results from the second set of indicators (April 1996 - December 1996) showed that no grazing occurred inside the exclosure at all (Figure 6.7b). Only grazed status shrubs outside the exclosure lost indicators to grazing. Grazing pressure appears to have been low at the site during this period



(a) Height

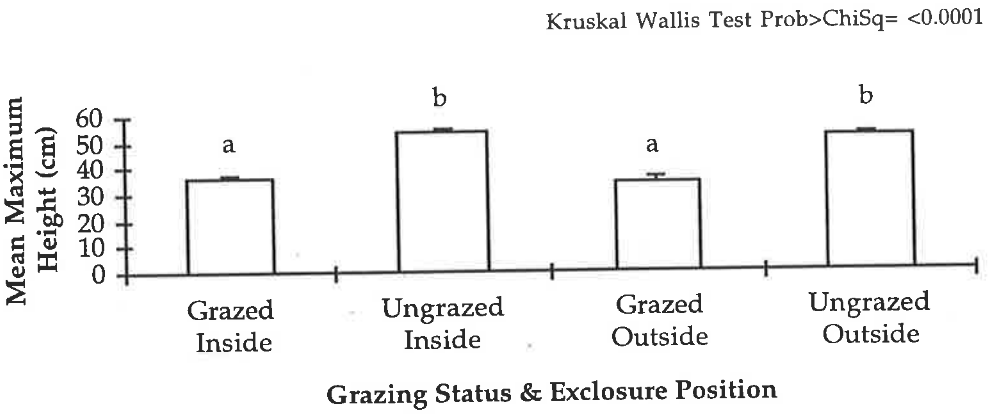


(b) Width

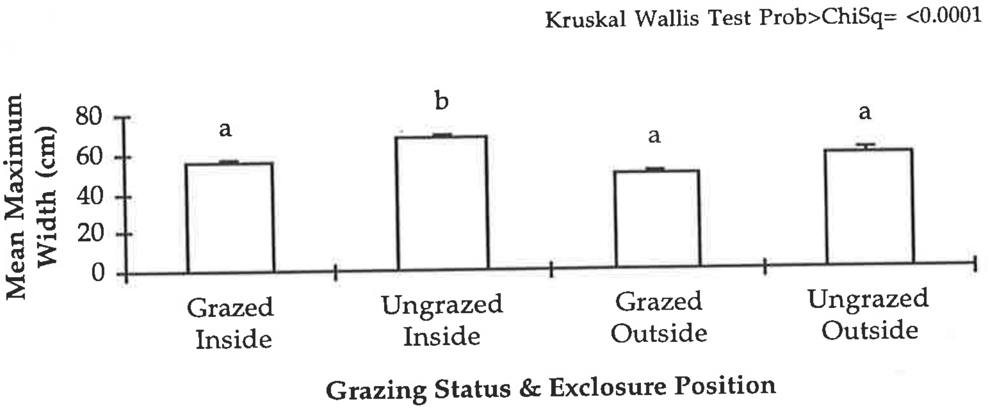


(c) Biomass

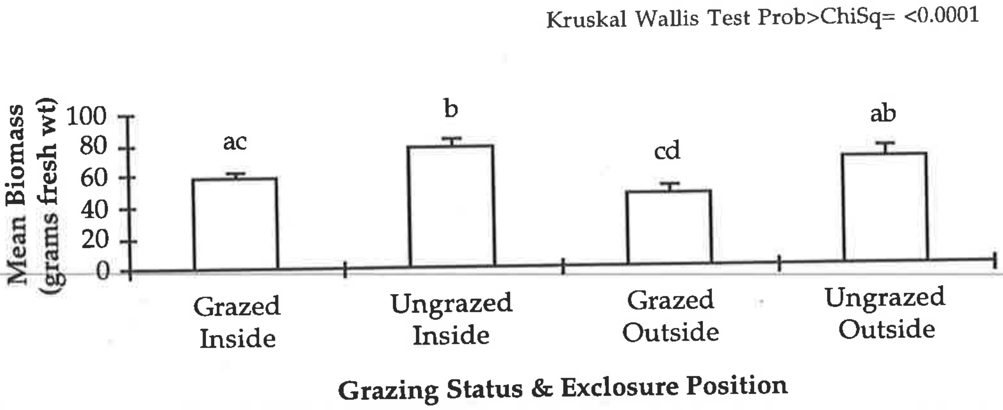
FIGURE 6.5. Influence of grazing on plant height, width and biomass at the Two Mile site (prior to protection from grazing). Error bars represent Standard Errors.



(a) Height

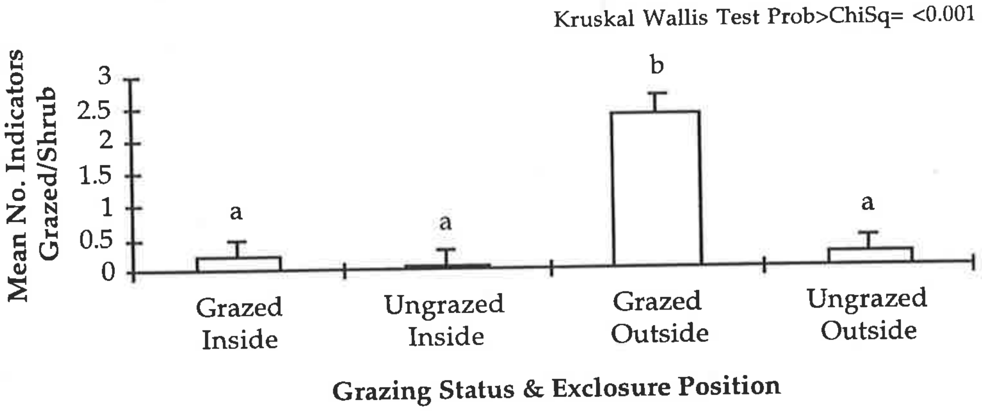


(b) Width

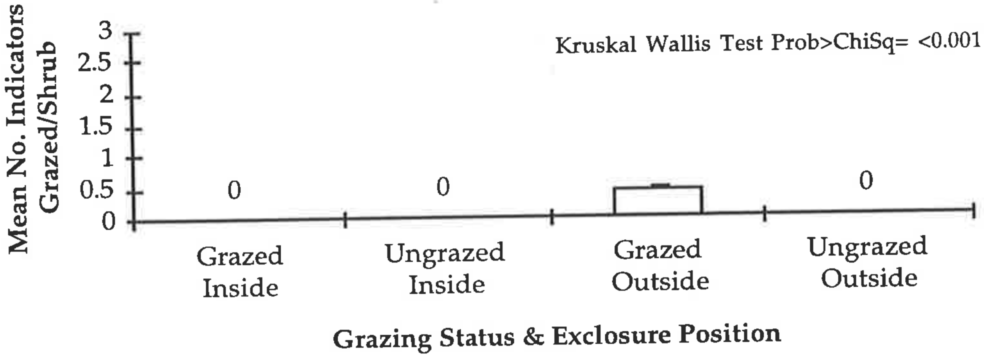


(c) Biomass

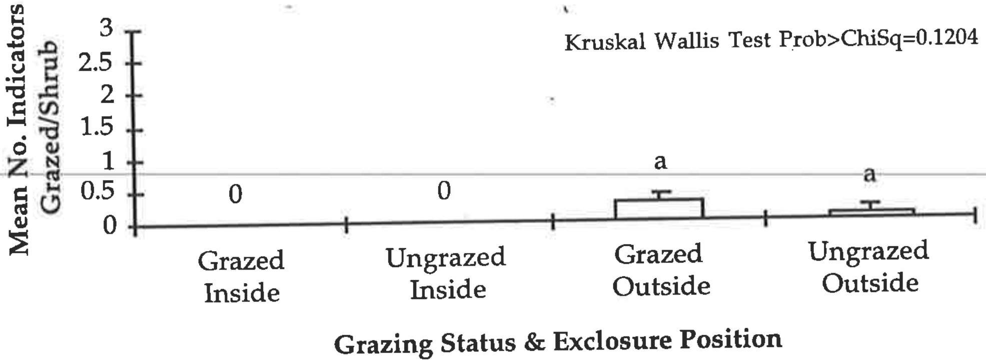
FIGURE 6.6. Influence of grazing on plant height, width and biomass at the Two Mile site (after 2.5 years protection). Columns with the same letters signify means that are not significantly different. Error bars represent Standard Errors.



(a) August 1995 to April 1996



(b) April 1996 to December 1996



(c) December 1996 to March 1997.

FIGURE 6.7. Loss of indicators at the Two Mile site due to grazing. Columns with the same letters signify means that are not significantly different. Error bars represent Standard Errors.

(Figure 6.7b). The final set of indicators (December 1996 - March 1997) also showed that no shoots were grazed from shrubs inside the exclosure (Figure 6.7c). Once again, the grazed status shrubs outside the exclosure lost the most indicators to grazing. Grazing pressure at the site was also relatively low during this period (Figure 6.7c). Over the course of the three sets of indicators, only 6/265 (< 2.5%) were grazed from ungrazed status shrubs outside the exclosure. This demonstrates that sheep rarely graze shrubs which have not been grazed before.

DISCUSSION

It must be emphasised at the outset that any detailed study of the ecological implications of selective grazing would have to be a very large one. The results of this research were intended to quantify only a few of the influences of grazing on bladder saltbush, and dealt only with above-ground plant components. Even with these limitations, the information presented in this chapter has added to the understanding of the interaction between sheep and bladder saltbush.

Initially, casual observations suggested that grazing reduces the heights, widths, biomass and reproductive output of grazed saltbushes. The first quantitative results in this study which support these observations were collected at the Hatchards site (Chapter 4). Without exception, the results were supported at the Two Mile site and concur with the findings of other studies on bladder saltbush (Graetz 1978, Andrew & Lange 1986b, Hunt 1995). It is of note that the findings at Two Mile reflected the cumulative effects of grazing over many years whilst those from Hatchards were the result of only five months of grazing. It appears that the changes induced by grazing appear soon after sheep are introduced and are maintained indefinitely.

Perhaps the most serious impact of selective grazing in this case is the reduction of reproductive output. Grazing has been shown to delay flowering and fruiting and decrease the number of flowers and seeds produced in many species (Williams 1972, Harper 1977, Willard & McKell 1978, Roundy & Ruyle 1989, Andrew & Lange 1986b, Milton 1994). Seed production is usually one of the first processes to be affected by defoliation because plants channel energy into regrowth at the expense of reproduction (Crawley 1983, Obeso 1993). Some evidence for this response can be seen in long-grazed stands of bladder saltbush. Without exception, the ratio of vegetative to reproductive adult saltbushes was higher in grazed populations compared to ungrazed ones on the cross-fence sites. Hunt (1995) showed that grazing limits flowering in bladder saltbush and that the amount of seed in the soil in grazed populations is negligible. The results of my study have confirmed that grazed shrubs produce less seeds (Hatchards and Two Mile). The suppression of reproduction at the Hatchards site is particularly noteworthy given that favourable rainfall conditions had stimulated reproduction throughout the wider study area.

Hunt (1995) suggested that recruitment in heavily grazed bladder saltbush populations was directly limited by the lack of seeds in the soil. However, seed input is not the only threat to the seed bank and subsequent recruitment. Defoliation has been shown to influence seed size and viability in several plant species (Archer & Tieszen 1986, Marshall *et al.* 1986, Obeso 1993). Further studies are required to determine whether grazing also poses these threats to the seed bank in bladder saltbush. The effect of seed predation by ants in grazed populations also requires investigation.

To be of serious long-term influence to populations, grazing must keep shrubs in a chronically reduced state. The grazing indicator data from Two Mile showed that sheep returned to the same shrubs repeatedly and only rarely grazed from shrubs which had not been grazed before. Herbivores are known to return to previously grazed shrubs because succulent new growth and tender leaves are more accessible on grazed shrubs than ungrazed shrubs (Leigh & Mulham 1964, Price *et al.* 1989, Vallentine 1990). Animals tend to avoid previously ungrazed shrubs because of accumulated rank growth (Vallentine 1990). Presumably the palatability factors which caused selective grazing in the first place also ensure that certain shrubs are revisited.

Grazed shrubs which were protected from grazing for 2.5 years at Two Mile were unable to recover significantly their heights, widths and biomass. This implies that there is little hope of them recovering their reproductive output in this time frame. Observations made at the site and quantitative research by Hunt (1995) directly support this view. As seed longevity in the field appears to be relatively short (probably less than five years), extinction of the saltbush seed bank is likely to occur in heavily grazed populations (Clift *et al.* 1989, Hunt 1995). In combination, slow shrub recovery and depleted seed banks suggest that long periods of spelling or protection will be required for grazed saltbush populations to recover. Unfortunately, the time-scale required appears to be many years (Hall *et al.* 1964) and may not be economically acceptable to managers. The annual relaxation of grazing pressure when herbaceous species are present[4] is unlikely to be long enough for grazed saltbushes to recover and reproduce. In any case, there is evidence to suggest that in the semi-arid areas of South Australia, where herbaceous cover is generally low, this relaxation only occurs in years of above-average rainfall (Hunt 1995, A.D. Nicolson, pers. comm., D. Maywald, pers. obs.).

All of the results presented in this chapter support the belief that grazing does reduce the fitness of saltbush populations. Given that female shrubs are more likely to be grazed, the reduction in reproductive output has potentially serious consequences for recruitment and population dynamics. This is likely to be critical in heavily grazed populations where females are unlikely to escape grazing. The long-term effect (if any) of lower fruit production in moderately grazed populations (like Two Mile) is unknown.

It is obvious from the results presented in this chapter that more research on the effects of grazing on the ecology of saltbush populations is

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[4] The inbuilt rotational grazing system proposed by Graetz & Wilson (1984).

required. Avenues for further research are presented in the next chapter, along with a summary of the entire study and some suggestions for the management of bladder saltbush populations.

CHAPTER 7
CONCLUDING DISCUSSION

INTRODUCTION

Atriplex vesicaria Heward ex Benth. has been described as "the most important" contributor to ecosystem stability in the chenopod shrublands of southern Australia (Wilson & Graetz 1979). As it is also relatively drought tolerant, palatable and nutritious, it is an important species for stable pastoral productivity. Although *A. vesicaria* has been studied extensively for both ecological and pastoral purposes, there are several aspects of its basic biology which remain poorly understood. Until now, one of these aspects has been palatability variation between adults of the species. This study represents the first thorough investigation of this phenomenon.

This project aimed to:

- Verify that the sex phenotypes of bladder saltbush vary in their palatability.
- Characterise some of the spatial and temporal contexts of the palatability variation.
- Identify the cues in bladder saltbush which influence the behaviour of sheep.

- Highlight some of the ecological implications of intraspecific variation in palatability, and how these may influence pastoral land management and monitoring.

These aims were investigated using several experimental techniques which encompassed a range of temporal and spatial scales. In this chapter I briefly review these techniques and summarise the main conclusions. I also speculate on why male bladder saltbushes deter sheep and put forward some suggestions for the monitoring and management of grazed saltbush populations. Avenues for further research are presented at the end of the chapter.

REVIEW OF THE STUDY

This study made use of a multi-faceted experimental approach. This was necessary to overcome some of the shortfalls of experimental design in field situations. For example, at the paddock-scale realism is high but the scope for replication is very low, whilst at the other extreme, cafeteria trials are easy to replicate but are not very realistic. In order to achieve a balanced understanding of palatability variation in bladder saltbush, a suite of complementary techniques was implemented.

Small-plot Grazing Trials (Chapter 3)

Prior to this study no intensive dietary experiments had been conducted to investigate palatability variation between the adults of *A. vesicaria*. Furthermore, palatability variation between the sex phenotypes had never been rigorously confirmed in South Australia. I conducted three intensive dietary trials to determine whether bladder saltbushes varied in their palatability. The results of the three trials confirmed that plant sex was the main determinant of consumption. Female saltbushes were preferentially grazed over male and bisexual ones. Importantly, the results were repeated in trials which were conducted in different years, seasonal conditions and experimental plots, using different flocks of sheep. Given the variability in the dietary behaviour of individual animals (Arnold 1960, Arnold 1964, Langlands 1969, Ellis *et al.* 1976), this outcome gave the first indications that the cues influencing the sheep must be quite strong. The demonstration that female saltbushes are preferentially grazed concurred with the findings of the piosphere studies in New South Wales.

Paddock-scale Research (Chapters 4 & 6)

Data from the more realistic paddock-scale were required to consolidate the findings of the small-plot grazing trials. A large-scale dietary study was conducted by introducing a station flock to a new waterpoint situated in a sporadically and lightly grazed population of bladder saltbush. The results confirmed that female saltbushes were preferentially grazed over male ones. Data from this experiment also demonstrated that sheep reduce the heights, widths, biomass and reproductive output of grazed saltbushes and that these reductions can occur within the first few months of grazing.

The findings of the small-plot grazing trials and the waterpoint experiment suggested that palatability variation between the sex phenotypes may be a feature of the wider study area. A series of cross-fence comparisons were surveyed to determine whether this hypothesis could be supported. The sites were widely scattered throughout the study area and varied in topography, vegetation composition and grazing history. The sites were used to ascertain whether current grazing pressure was higher on females than males and to determine whether grazed sites had male-biased sex ratios. Without exception, more females than males showed evidence of recent grazing and the sex ratios of the grazed sites were male-biased. These results infer a link between current selective grazing (as witnessed in the grazing trials) and male-biased sex ratios at the paddock-scale.

Throughout the study, several detrimental effects of selective grazing were identified. Grazing was shown to adversely affect plant size and reproduction, a result which supports previous studies on bladder saltbush (Williams 1972, Graetz 1978, Williams *et al.* 1978, Andrew & Lange 1986b, Hunt 1995). I have shown that the heights, widths, biomass, percentage of branches with flowers/fruits and number of shrubs able to reproduce all decline under grazing. These effects were detected in the short-term experiment at Hatchards and at sites with long histories of grazing. In the first instance these effects are detrimental to individual plants; however, they appear to have flow-on effects to the grazed population as a whole. Selective grazing of female bladder saltbushes appears to be particularly serious for the population given that females produce the seed. This is consistent with Hunt (1995) who suggested that continuous grazing (even at conservative stocking rates) leaves many saltbush populations at risk of local extinction.

Cafeteria Trials (Chapter 5)

The results of the small-plot grazing trials and the paddock-scale research implied that the cues which trigger selective grazing must be relatively strong and consistent. Throughout this project, observations and quantitative evidence suggested that the male flower spike is a deterrent to sheep. The male flower spike has been suspected as a deterrent for many years (Graetz 1978). Three replicated cafeteria trials were conducted to confirm the hypothesis that sheep avoid grazing male plants because of the male flower spike. The method relied on the assumption that sheep would discriminate between the sexes in the highly artificial cafeteria environment. This assumption was verified in the first trial, which also confirmed that the female was the preferred phenotype. The removal of male flower spikes increased the acceptability of male material, which indicated that the male flower spike is a cue to sheep. However, the final trial showed that sheep were also able to detect and avoid both flowering and clipped male material hidden within female material. This suggested that there is also an olfactory cue associated with male shrubs that may vary in concentration over time. Overall, the results of the cafeteria trials suggested that sheep use the male flower spike as a visual cue and can avoid male plants by sight. In the absence of a visual cue, sheep use olfaction to detect male shrubs. In order of importance, the senses used by the sheep in this particular example of selective grazing appear to be sight, olfaction and then taste.

SPECULATION ON WHY MALE SALTBUSHES DETER SHEEP

It is generally believed that the Australian flora did not evolve in the presence of large ungulate herbivores and that prior to European settlement, much of the arid interior would only have been grazed by transient populations of marsupials (Osborn *et al.* 1932, Beadle 1959, Moore 1959, Williams 1980, Lange *et al.* 1994). The lack of physical deterrents (such as spines, thorns and stinging hairs) and adaptations (like protected meristems and basal resprouting) suggest that herbivory by vertebrate animals has not been an important selective pressure for *A. vesicaria* (Anderson 1982). It is unlikely that the short period of time since the introduction of domestic stock to the Australian rangelands has been sufficient for *A. vesicaria* to form resistance to herbivory. This suggests that the deterrence of male saltbushes to sheep is coincidental.

There are at least two possible explanations for the deterrent in male saltbush. The first is based on the idea that bladder saltbush may have been the focus of attack in the past. In an arid environment, before the introduction of domestic stock, the most likely agents for attack would be insects because many of them are not constrained by the need for free water. Harborne (1988) has suggested that chemical defences in plants usually arise as a result of herbivory by insects. As early as last century, records of insect damage were recorded for both *A. vesicaria* and *A. nummularia* (Olliff 1892). Olliff noted that the larvae of the saltbush scale (*Pulvinaria maskelli*) swarmed over the shrubs soon after hatching and ate the bark, stems, younger shoots and leaves. Froggatt (1910) recorded several species of caterpillars, beetles and weevils in saltbush specimens. The most destructive insects appear to be the caterpillars which, at times, can reach plague proportions:

> *"[caterpillars] appeared in such enormous numbers that they left hundreds of thousands of acres of rich saltbush plains absolutely bare, with all the old saltbush practically dead"*
>
> *(Froggatt 1910, pg 465)*

Even in the last 20 years, caterpillar plagues have been implicated in the decline of saltbush stands in the Riverine Plain area of New South Wales (Clift *et al.* 1987). Unfortunately, there is no information available on whether the sexes of saltbush vary in their susceptibility to insect attack. As a result, the hypothesis that male saltbushes have evolved a chemical defence against insect attack remains purely speculative.

The second explanation for the deterrent is based on the differential use of environmental microsites by the sexes. In many dioecious species, including some in the genus *Atriplex*, males tend to dominate xeric sites whilst females dominate more mesic ones (Freeman *et al.* 1976, Freeman *et al.* 1980). This is because female plants require a long period of favourable moisture conditions in order to bring fruit to maturation

(Freeman *et al.* 1976). It is known that environmental stress (as defined by Charnov 1982, p. 204) does influence the concentrations of metabolites in plants (McArthur 1977, Freeman *et al.* 1980, Charnov 1982). It is therefore possible that male bladder saltbushes produce metabolites due to the stressful microsites they occupy, and that these metabolites deter sheep. Obviously, there is considerable scope for investigating the chemical deterrent further.

MONITORING AND MANAGEMENT OF BLADDER SALTBUSH

In South Australia, the principal aim of management in the chenopod shrublands is to minimise shrub loss (Lange *et al.* 1984). This means maintaining cover, keeping shrubs in a reproductive state and ensuring that recruitment occurs (Lange *et al.* 1994, Hunt 1995). Compared to many chenopod species, bladder saltbush is relatively palatable, short-lived and susceptible to grazing and trampling (Graetz & Wilson 1984, Lange *et al.* 1994). For these reasons, it is considered to be a sensitive (early warning) indicator of range condition and trend (Lange *et al.* 1994, Hunt 1995). At the present time, the density of bladder saltbushes is often used to assess condition and trend (Lay 1979, Lange *et al.* 1994). Unfortunately, changes in shrub density may take many years to occur and may be difficult to detect (Lay 1979, Andrew & Lange 1986b). As a result of this study, I propose that the use of bladder saltbush as an early warning indicator could be refined. In areas where bladder saltbush is the principal indicator species, the following aspects could be readily incorporated into a monitoring program:

- The ratio of grazed to ungrazed shrubs.
- The ratio of vegetative to reproductive shrubs.
- The ratio of male to female shrubs.
- The number of recruits.

The first two aspects offer fine-scale measures of grazing pressure and could be quickly assessed several times a year. My results have shown that sheep tend to regraze plants that they have grazed previously and rarely graze plants that have not been grazed before. Any large increase in the number of grazed plants at a site would therefore be a sensitive indicator of inappropriate grazing pressure. Likewise, any measurable increase in the ratio of vegetative to reproductive shrubs (especially in conjunction with climatic conditions favourable for reproduction) would indicate a problem requiring attention. The ratio of male to female shrubs could be assessed annually and would indicate the relative 'health' of a grazed population. A ratio greater than 2:1 in a grazed population may be indicative of poor recruitment potential (Williams 1972). The number of recruits in the population could be used to verify this.

It must be emphasised that saltbush populations chosen for monitoring must be capable of showing the effects of grazing. Bladder saltbush populations which receive moderate to heavy grazing pressure should be used to monitor the effects of grazing over time. In most cases this will mean using saltbush populations close to waterpoints, although there are other areas away from waterpoints which may be preferentially used by sheep. In order to fully assess the effects of grazing and climate, it would be useful to have control plots (exclosures) in many of the monitored populations. This would allow parallel comparisons of grazed and protected populations and would help managers to understand how grazing and extreme climatic conditions (such as drought and large rainfall events) affect bladder saltbush. Unfortunately, the erection of exclosures adds further expense and complexity to a monitoring program and may not be a viable option in most cases. Whilst the use of exclosures would be ideal, the monitoring process could still occur without them.

Populations which are consistently identified as having declining condition are likely to be at risk of local extinction unless some active management is applied (Hunt 1995). In the study area, most of the saltbush populations close to established waterpoints are probably in this category. It is now accepted that bladder saltbush is grazed almost all of the year and that the natural 'inbuilt rotational grazing system'[5] rarely operates on northern Eyre Peninsula (Hunt 1995, D. Maywald, pers. obs.). This means that active spelling or physical protection will be required to allow grazed bladder saltbushes to recover their sizes and reproductive output. As the time-scales for recovery appear to be at least several years, active seed casting inside of the exclosures may be needed in order to establish a seed bank. Unfortunately, the optimum population size for

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[5] proposed by Graetz & Wilson (1984).

seed bank establishment and the effects of plant competition on protected populations remain unknown. In addition, these management options are labour-intensive and are likely to be economically unfeasible in many cases. Without them, however, large areas of bladder saltbush will be seriously threatened and populations close to waters may die out (Hunt 1995). In the long-term, this will become more difficult (and more expensive) to rectify. Conservative stocking practises alone will not guarantee the survival of many populations because repeated grazing at any intensity is still detrimental to bladder saltbush (Hunt 1995).

FURTHER RESEARCH

The most obvious area for further research is to identify and characterise the chemical deterrent present in male saltbushes. On a world-scale, the genus *Atriplex* is considered to be relatively benign in terms of chemical defences (Sanderson & Stutz 1994, M. Ralphs, pers. comm.). This suggests that any further research in this area should begin with the simplest of chemical groups. Some Australian species of *Atriplex* are known to contain unpalatable concentrations of salts, saponins, triterpenes and steroids (Simes *et al.* 1959). Some chenopod shrubs, including *A. vesicaria*, are also known to contain oxalates (Osmond 1963, Sanderson & Stutz 1994). The most common salts in *A. vesicaria* are sodium and potassium chloride, which can make up 24-38% of the dry weight of the plant (Beadle *et al.* 1957). In combination with saline drinking water, the salt content of *A. vesicaria* may be harmful to sheep (Wilson 1966). Saponins can be bitter and toxic to livestock and are usually most concentrated in rapidly growing shoots (Simes *et al.* 1959, Askham & Cornelius 1971, Oakenfull & Sidhu 1989). Oakenfull & Sidhu (1989) also noted that saponins often occur in plants which are prone to attack from insects. Oxalic acid and its derivatives are widespread in *Atriplex* species throughout the world (Mathams & Sutherland 1952, Davis 1981). *A. vesicaria* does contain relatively high levels of calcium oxalate in crystalline form (Osmond 1963). Calcium oxalate crystals irritate the mouths and throats of livestock and can abrade the kidneys (M. Ralphs, pers. comm.). Wilson (1966) believed that oxalate poisoning was possible for sheep consuming *A. vesicaria.* It should also be noted that some species of *Atriplex* also contain more complex metabolites such as tannins and alkaloids (Webb 1949, Davis 1981).

This project has revealed that male saltbushes contain both physical and chemical cues which deter sheep. The male flower spike is involved in both cases. Flower densities probably influence the ability of sheep to detect the visual cue. More research is required to determine which combinations of flowering density and spike size influence the dietary behaviour of sheep.

The piosphere studies conducted in western New South Wales gave the first indication that the sexes of *A. vesicaria* varied in their palatability. This project has confirmed those findings and demonstrated that the phenomenon also occurs in South Australia. Given that *A. vesicaria* is such a widespread species, further investigation would reveal the generality of the phenomenon. One way of achieving this quickly and inexpensively would be to infer palatability from surveys of cross-fence comparisons over the entire range of the species. This would determine whether male-biased sex ratios are a common feature of grazed bladder saltbush populations throughout southern Australia.

Finally, more information is needed to determine the effect of selective grazing on population dynamics. This project (along with several others) has demonstrated that grazing does influence the fitness of grazed individuals. The selective (and repeated) grazing of female shrubs appears to be of particular seriousness to the population. The results of this study and that of Hunt (1995) leave no doubt that chronic grazing reduces the numbers of seeds entering the seed bank. However, the minimum level of seed input necessary to maintain populations remains unknown. Research is also required to determine whether grazing further threatens the seed bank by reducing seed weight and seed viability. Only when these things are known can we identify the critical grazing pressure which ensures the longevity of grazed populations.

CONCLUSION

As noted by Petrides (1975) the study of food preferences is of widespread ecological significance and is basic to the concept of range management. When Graetz (1978) presented piosphere evidence for the selective grazing of the sexes of bladder saltbush, he concluded that "its net outcome [had] no ecological significance for the shrub population as a whole or for rangeland management". The results of this project leave no doubt that the selective grazing of the sexes does have substantial ecological significance and that knowledge of the phenomenon can now be used to improve the management of chenopod rangelands.

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