# Behavioural Ecology of Sheep
# in the
# Australian Arid Zone

by

Mark Stafford Smith

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

March 1984

# Declaration

The work presented in the body of this thesis is my own, except where due reference is made in the text. The Appendix includes work that was carried out jointly, and this is made clear.

Mark Stafford Smith

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

## Abstract

This thesis describes an investigation of the ranging and grazing behaviour of merino sheep in the South Australian arid zone. The information that was obtained from this study is used to build a model of sheep behaviour in very large arid zone paddocks.

The positions, activities and movements of sheep in three paddocks were mapped for several days at ten times during 1980-83; these years corresponded to increasing drought and declining forage availability. Patterns of movement were dominated by the influence of three 'foci of non-grazing activity' - the waterpoint, night-time campsites, and shade sites on hot days. The use of each of these was investigated.

A simple water balance model for the sheep adequately predicts the times at which they water. Night-time campsites were few, and choice between them was affected by prevailing wind directions. A physical model of the energy balance of the sheep is developed; this predicts a respiration index which correlates very well with observed respiration rates. This index is shown to predict the use of shade by sheep in the open paddock, and some interactions between heat, hunger and thirst are investigated. Choice of shade locality seems to depend on similar factors to the use of sites for the unstressed activity of resting in the open; this may be partly because of the common availability of shade trees throughout the study paddocks.

The location of both shade use and resting is dependent on movement in grazing since the previous non-grazing activity. 'Directed grazing', towards a destination, occurs mostly in stressful conditions. Otherwise movement in grazing is little affected by wind direction. It is inferred that movement to foci of non-grazing activities is the dominant determinant of the area of the paddock in use.

The details of grazing behaviour and diet selection were studied in small enclosure trials. The proportion of active time spent moving by sheep does not vary consistently during a grazing period, but speeds of movement increase in enclosures containing poor forage quality, probably as a result of increased distances between acceptable food items. It is shown that there is a dramatic and consistent switch in diet preferences during a grazing period, from eating shrubs when hungry to eating ephemeral material when sated. This is interpretable as a switch from foods of high potential intake rates to foods that are normally highly preferred but of low availability. The significance of these findings in the open paddock, and to grazing trials, is discussed.

Finally, a model of sheep ranging behaviour in large paddocks, and their resultant grazing impact, is described and tested. The model predicts general activity patterns and the use of water over the years of this study very well. In good vegetation conditions, it predicts ranging behaviour well in two paddocks of very different layout, even on a day-to-day basis. The model's weak points seem to lie in selection of campsite locations, and in the learned response of sheep to locally poor vegetation quality; in drought years, it consequently under-estimated the ranging of sheep over the paddock.

The model was used to predict the outcome of two future management options at the study site. Despite its limitations, it predicted results which are sensible in retrospect, but which might not have been foreseen without this approach.

-----------------

## Acknowledgements

This study was carried out whilst I was a post-graduate scholar in the Department of Environmental Biology, A.N.U., and was supported under the Commonwealth Scholarship and Fellowship Plan. I am grateful to the Association of Commonwealth Universities for this opportunity to come to Australia, and to Professor C.B. Osmond for the opportunity to study in this particular department, which I have found both stimulating and friendly.

The learning experience of a Ph.D. study is very dependent on the direction of a supervisor, and I count myself lucky to have encountered the diverse talents of Ian Noble, my major supervisor. I am also indebted to Alan Newsome and George Dudzinski for their help, although it is with sadness that I must add that George died in an untimely accident last year; the frequency with which his name appears in my bibliography reflects his great contribution to this and many other areas of science.

I owe debts of gratitude to many people in the department and elsewhere in the University for equipment, advice, help and friendship. I am especially grateful to Peter Cochrane, Bruce Wellington, Doug Abrecht and Hugh Comins for unflagging help in all manner of tasks, from chasing sheep to reading manuscripts. I also thank Greg Jones of Townsville, and Paul Jupp of the A.N.U. for help in the field, and Imanuel Noy-Meir for both fieldwork and interesting discussions. Claire Nipperess kindly typed the bibliography to this volume.

My fieldwork has been based at the Middleback Field Centre, run by the Department of Botany, Adelaide University, and I thank them and Dr Bob Lange for making these facilities available, as well as for hospitality in Adelaide. David Thompson was helpful at the field centre. I have gained greatly in discussion and friendship with many Adelaide indigenes, most especially with Nick Reid and Kym Nicolson.

At Roopena and Middleback Stations themselves, my undying gratitude goes to both the Nicolson families, Don and Penan, and Andrew and Lesley, for their advice, help, hospitality and extraordinary tolerance. Their respective offsiders, David Illman and Paul Farrell, have also been very helpful.

Last, and probably quite least, I must mention Bluebell, the rheumatic ewe, who led me many a merry chase, and who is now exercising her not-inconsiderable talents for disruption at every station muster. Fieldwork could have been much more boring.

# Contents

---

# Chapter I

## Introduction.

Semi-arid and arid lands form a large part of the world's surface. Many of these areas are occupied by man and his domestic animals, whilst others support wild populations of large mammals. In contrast to the extreme deserts and the more mesic agricultural lands, most semi-arid systems are subject to a highly variable and unpredictable climate (Goudie & Wilkinson 1977). In consequence, life for both humans and animals in these environments is often marginal.

In the Mediterranean region, man and agriculture have had an influence on semi-arid lands since ancient times (e.g. Hills 1969). These lands have often proved susceptible to degradation under his hand, as is evidenced by the former 'granaries of Rome', inland of the North African coastal strip. Cycles of degradation have resulted from intermittently increased demands on the resources of these areas. These pressures began with settlement and the discovery of agricultural methods by early man, and have been intensified since as various civilisations have flourished. In recent decades, renewed pressures on arid lands have resulted from a rapidly increasing world population; these pressures are sometimes localised to areas settled by peoples of previously-nomadic cultures.

The semi-arid and arid region of Australia (Williams 1979) is singular in that it had not been exposed to the influence of a sedentary culture until the last two centuries. Following European settlement, many areas have passed through stages of degradation that occurred pre-historically in equivalent Mediterranean regions. Today, it is estimated that at least one third (i.e. over one million $km^2$) of Australia's arid grazing lands need some conservation work (Woods 1983). In many areas, the downward trends in productive capacity, and alterations to both physical and biotic structures, have yet to stabilise at a new, lower level (Newman & Condon 1969, Perry 1973). Much of the arid-zone is managed by a well-educated population who are increasingly aware of the limitations that the variable climate places upon their management procedures. Hardship in this pastoral community is usually manifested in economic terms, which is unlike the life-and-death balance endured by occupants of many of the world's arid regions.

Changes associated with the degradation of arid lands are often slow, and there are usually long recovery times; this is largely due to the rare occurrence of suitable combinations of climatic conditions, and because of long-term alteration of resource bases. In consequence, there is a great onus on the applied sciences to provide predictive tools for determining the long-term outcome of management policies before major and undesirable changes take place. Australia is an ideal continent in which to study how these predictions should be made, both because of its recent history of degradation, and because of the ready availability of high technology.

My thesis is concerned with a study of the behaviour of sheep (Ovis aries) in the Australian arid zone, and with the application of the results of this study in the prediction of the outcome of management policies. Sheep occur in large numbers in many semi-arid and arid regions of the world, but the species is intended to be an exemplar of any large herbivore in these regions. I discuss the advantages and limitations of sheep in this respect in the next chapter, which also reviews a wide range of behavioural information and theory.

In this study, fieldwork was carried out with sheep that 'free-range' within the large paddocks typically used in the Australian arid zone. The approach adopted to prediction in this system is that of modelling, and these models often require the insensate calculating ability of a computer. Although the management systems used in the Australian arid zone are important in some areas of the world, again they are intended as exemplars of other systems; in particular, the replacement of animal movement models by the influence of shepherds (and their behaviour) would permit the modelling of herded systems, whilst the removal of fenceline constraints would allow the description of wild animal populations such as those of game reserves. Chapter III discusses the relevance of predictive models, and outlines one which I have used as a starting point in this work.

The last section of Chapter III discusses various approaches to the ranging behaviour of sheep in large areas, and the four subsequent chapters are largely concerned with my investigations at this scale. Chapter IV describes the study site and methods used; Chapter V considers which factors are important in determining ranging behaviour and flock structure, whilst Chapter VI examines these processes in more detail. Chapter VII focuses on movement in grazing in the open paddock, and Chapters VIII and IX describe the study of grazing intake behaviour. Finally, in Chapter X, I draw these lines of investigation together into a new model of sheep behaviour in the large paddocks of the arid zone, and test the adequacy of the predictions of the model.

# Chapter II.

## Ranging and selection behaviour in semi-arid ecosystems: a review.

Pastoralists and nomadic herders possess great stores of anecdotal knowledge and 'gestalt' understanding of the behaviour of man's various domestic animals. This knowledge is derived from individual experience and is transmitted culturally. There are many examples reported, such as Lott & Hart (1971) on the integration of the lifestyle of the Fulani tribal society with the behaviour patterns of their cattle; Baskin (1974) of native shepherds directing their sheep's movement in Central Asia; or the control exercised over the ranging of camels in the Sahara by manipulation of their parental attachment to their offspring (Gauthiers-Pilthers 1974). The limitation of such information, despite its fascinating insights into man and animal alike, results from its anecdotal nature.

At the other end of the scale, there has been much laboratory and small-plot research into many aspects of herbivore physiology, nutrition and behaviour. Often such research is aimed at testing the specific responses of a breed to a particular environment, but it also provides the quantitative information necessary to model the physiology and behaviour of these animals.

Large mammalian herbivores in semi-arid regions usually range over such great distances that it is difficult to quantify natural history observations, and often impossible to extrapolate from the laboratory to their normal habitat. The chasm between these approaches lay behind Tribe's (1950) review of the behaviour of the grazing animal, for example. Since then many studies have attempted to quantify the observations made in the field; this has resulted in overviews such as Schaller (1977) on Himalayan caprovids, Sinclair (1977) on African Buffalo, and Geist's (1971) classic work on North American mountain sheep, as well as many others.

Concurrently, development of the theoretical side of ethology has has begun to suggest explicit reasons based on genetic selection why certain behaviour patterns should develop and be maintained, both evolutionarily, and within an individual's lifetime. The relevance of some of these theories has only been tested in laboratory conditions; but for others, field studies (e.g. sociality, Bertram 1976; dispersal, Greenwood et al.1978; sexual competition, Hrdy 1976, Le Beouf 1974; and many aspects of foraging behaviour mentioned below) are finding support for the assumption that selection drives towards some optimal state.

Management of land systems has become, by necessity, more of a scientific discipline in our society: both as a result of the need for agricultural efficiency, and because policy is increasingly determined by people who cannot obtain a lifetime's understanding of every land system over which they may exert control (Box 1973, Lange 1973). For long-term planning, the concept of stability in plant-animal systems has become important for the prediction of limitations to growth (e.g. Noy-Meir 1975, Westoby 1980, Caughley & Lawton 1981). The ambit of these three research approaches - field studies, laboratory work and theoretical ecology - is so broad that their linking may only ever take place at the level of whole system modelling. Communication of the results of this research to policy makers may also require simulation models (Holdgate 1984).

In this chapter I establish a framework and context for the development of the rest of this thesis. The best recent summary of relevant behavioural information for domestic herbivores is to be found in Arnold & Dudzinski (1978), to which I shall refer not infrequently. It is apparent from their review that, despite considerable work on some economically-important aspects of behaviour, other areas remain obscure. These include especially an understanding of the short-term selection of food by herbivores, and the reasons underlying many of their patterns of movement. After some historical background, I shall discuss both ranging and grazing behaviour. The following chapter takes up the theory and practice of modelling.

## (a) Prehistory and history.

### (i) Evolutionary background.

The behaviour patterns of today's herds are constrained by their evolutionary history, and have been altered by the imposition of domesticity. Grasses form a major component of the diets of modern mammalian herbivores. On a geological time-scale, grazing became widespread as the great savannas, pampas, prairies and other grasslands of the world developed during the Tertiary Period. In the fossil record, many parallel lines of evolution derived from differing stock (such as the palaeotheres in South America which so strikingly resembled the equid line in tooth and leg development) suggest that there were extensive opportunities for small herbivores to increase in size (e.g. Simpson 1951, Romer 1959). An increase in size permitted greater energetic efficiency in movement over large areas (e.g. Taylor et al.1970). Whilst becoming larger, however, these animals had to develop new methods of predator-avoidance, for it was no longer so easy to hide - both because of size and because of the open landscape. For many species, the wide-spread appearance of socially-tied groups enhanced their ability to avoid predators (e.g. Hamilton 1971, 'the selfish herd'; Bertram 1978, warnings), as well as improving foraging (e.g. Pitcher et al.1982). This in turn demanded modifications to searching and grazing habits; for instance, some needs of the individual were subjugated to the instinct to stay together.

The evolutionary background of herbivores is important, for it has left domestic animals with a legacy of behaviour patterns that persist despite possible irrelevance to present conditions. Knowledge of these patterns is essential for the shepherd's control of native flocks, but is also important in the management of stock that have been distantly removed from their native pastures. These animals may be artificially segregated and submitted to conditions very different to those which originally moulded their behaviour patterns. Examples of domestic animals finding highly poisonous plants palatable (the deadliness of which presumably implies that no equivalent commonly-occurring plant would have been eaten in their homelands) are well-known and documented (e.g. Mitchell 1979) and can be useful in understanding the cues used by animals in dietary selection.

On the other hand, many animal species have changed during their long history of domestication by man. Primitive herders could easily select for some physical attributes; for example, domestic cattle initially tended to be smaller than the original wild aurochs in Europe, but increased in size again from the Middle Ages as herders learned greater control, and, perhaps, greater docility was bred in. Less physical differences are apparent in the degree of permanency of flock structure between Geist's (1971) mountain sheep or the long-time feral sheep of Soay (Grubb & Jewell 1974), and today's free-ranging herds. Changes such as these must be carefully considered before any attempt is made to extend observations from the more-easily observed domestic animals to their wild counterparts (cf. Fraser & Herchen 1979).

### (ii) Sheep in recent times.

Sheep husbandry in the world today may be loosely divided into three categories. In mesic areas, free-grazing occurs in small pastures usually dominated by grasses and herbs, in which the animals rarely move out of sight of most of the land available to them, and are entirely constrained by fences. In lands of lower productivity, animals may free-range in much larger paddocks, fences are encountered relatively infrequently, distances are large enough so that special features such as waterpoints are not always in line-of-sight, and the fodder available tends to be very variable and often depauperate for at least some part of most years. Thirdly, there is active shepherding, in which a shepherd takes the place of fences and directs the movements of the flock; this often occurs in areas where the vegetation is not very productive, if only because other areas have been sufficiently productive to pay for fencing.

During the last few decades, Australian practices have been almost exclusively of the former two types, except in the special case of stock route usage. Much of the investigation of sheep husbandry has been carried out in small, easily-observed paddocks, but it is in the larger paddocks that behavioural adaptations are more critical to sheep survival. Here the sheep must range over much larger areas for their food and water. Research in these pastures is more relevant to the low productivity sheep-lands of the 'third world', in terms of the survival of the fragile vegetation, as well as the animals themselves. Such rangelands also often contain open vegetation which is more easily observed for studies of selection and movement patterns than are high-density grasslands.

Sheep in Australia provide an extreme example of animals removed from their original environment. In the semi-arid lands, however, the management policies used in this century have allowed far more free-ranging behaviour than does any shepherded system, by the fencing of very large paddocks. The hardy Spanish Merino breed, and its modified descendants, survive in chenopod-dominated vegetation and native grasses: in many places the perennial shrubs and longer-lived ephemeral chenopods have become their main drought reserve. Management may involve mustering no more than twice a year (at shearing and crutching), and the sheep usually have areas of more than 1000ha in which to roam.

On the other hand, the animals' ranging is severely limited by the necessity for regular recourse to the man-made waterpoint for much of the year, and they are artificially segregated into single sex (and often limited age-group) flocks with controlled access for mating. In fact these single-sex flocks may be less 'unnatural' than they seem, since both the mountain and wild Soay sheep spontaneously maintain discrete male and female groups for all the year except in a well-defined rutting season, and lambing may consequently be no less synchronised than under management. Domestic flocks may differ mainly by the reduced inter-male competition between domestic rams, so that the range of differential reproductive success is much smaller than in the wild. The history of sheep in Australia is variously well-documented from Dixon (1892) and Davidson (1938) to, for example, Peel (1973), Reeves (1973) and Squires (1976b).

## (b) Ranging behaviour.

### (i) Introduction.

There are many studies of open-ranging in the wild by herds in Africa (summaries in Leuthold 1977, Eltringham 1979) and elsewhere (e.g. Geist 1971, mountain sheep; Jewell & Grubb 1974, Soay sheep; Klein 1970, deer; Caughley 1964 and Newsome 1975, kangaroos); other work has been carried out on domestic animals, such as Hunter's (1962) Scottish hill-sheep. These studies use a variety of observational methods including aerial counts or photography (e.g. Dudzinski & Arnold 1967), mapping from ground vehicles (e.g. Jarman & Jarman 1973), following groups on foot (e.g. Harrington & Pratchett 1973), and watching from fixed vantage points (e.g. Kilgour et al.1975); others have examined dung distribution as an indicator of activity (Riney 1957, Lange & Willcocks 1978, Welch 1982).

In Australasia, work on domestic herbivores has used all of these methods, with most of the results coming from relatively few authors. For example a considerable amount of data has been obtained on free-ranging short-horn cattle near Alice Springs, N.T., summarised in Hodder & Low (1978) and Low et al. (1981a,b,c), from which they provide detailed transition matrices for activities, as well as data on vegetation community usage (eg. Low 1972).

As Lynch (1967) put it, most studies of sheep had until then been of less than 30 sheep in less than 3 acres, and very little had been published about Merino ranging behaviour under extensive conditions. In large arid paddocks, this behaviour must be more important to survival, and studies in these areas may shed light on the less obvious expression of behaviour in smaller paddocks. The situation has now improved with various general studies being published such as Arnold & Pahl (1967), Dudzinski et al. (1969), Lynch (1974), Squires (1974) and Noble (1975) in Australia, and New Zealand hill-country work such as Kilgour et al. (1975) and Harris & O'Connor (1980). A study of feral animals in unmanaged conditions - the information on the Soay Island sheep summarised in Jewell et al. (1974) - is also useful for comparitive purposes.

Most ranging behaviour of herbivores is determined by, and composed of, the primary activities of grazing, watering and resting, intermittently affected by interruptions associated with reproduction. Resting at night seems to be qualitatively different to that in the day and is referred to as 'camping' herein. The additional activity of walking - the proximate mechanism of ranging - may be associated with any of the other activities. The ranging behaviour of individuals may also be strongly dependent on social interactions.

Many studies (e.g. Arnold 1962, Bowns 1971, Squires 1974b, Harris & O'Connor 1980) have described the general patterns of daily activity, which seem to be as common to domestic sheep in Australia as the feral Soay Island sheep. These patterns are summarised by Arnold and Dudzinski (1978). Morning and evening grazing periods are usually separated by rest periods in the middle of the day (spent in or out of shade) and at night (at regularly-used campsites). In hot weather, the period spent in shade in the afternoon may considerably exceed the camping period at night. In cool weather, there is often a pause in grazing in the mid-morning, effectively creating a third period of grazing; a similar extra grazing bout probably occurs at night in hot weather, before the campsite is occupied. The time of watering in

Australia is usually strongly bimodal, in the first and last few hours of daylight; this bimodality of behaviour is even evident in feedlot lambs (Shreffler & Hohenboken 1980). Some of these activity patterns can be related to seasonal and climatic conditions (Dudzinski & Arnold 1979, Bueno & Ruckebusch 1979).

The spatial use of pastures by herbivores is important not only for the animals' livelihood (McBride et al.1967, Lynch & Alexander 1973, Kilgour 1974), but also with regard to the resultant effects on the vegetation (Squires 1974a, Taylor 1980). The most dramatic effects are the patterns imposed on the vegetation around waterpoints, which Lange (1969) has termed 'piospheres'. The concept describes a zone which is depleted of palatable forage species in a regular fashion (Barker & Lange 1969, Graetz & Ludwig 1978). Such centres can be seen as a form of 'refuge' in the sense of Hamilton & Watt (1970), and the waterpoint is not the only one to affect pattern development (Foran 1980); for sheep, the location of shade is also important (Squires 1975).

A great amount of work has been done on aspects of sheep ranging behaviour and physiology. I now examine some of these aspects; studies of particular relevance will be mentioned here, and others appear in later chapters, but I do not attempt to review the whole gamut of previous work.

### (ii) Watering.

The ranging of sheep in the Australian arid zone is most singularly constrained by their need for water. This dependence may be greatly reduced in winter as a result of lower heat stress, the occasional presence of ground-water and greater succulence of vegetation. Because it has considerable direct economic importance, watering itself has been studied in relation to frequency, quantity and the effects on these of climate and vegetation.

Macfarlane et al. (1967) described the water metabolism of sheep grazing halophytic chenopods. They found significant breed differences between Border Leicesters and Merinos, and wide inter-individual differences. The presence of some grass greatly reduced water requirements. Interestingly they concluded that "the tolerance of animals for the taste and effects of sodium and potassium salts in the body may be determined more by behaviour than the ability of gut and kidney to remove the salt ingested".

Wilson (1966), on generally similar pastures, found that by varying their water and food intake according to the salt concentrations in available fodder and water, sheep would maintain a NaCl:total water ratio in the narrow range 1.82-2.17% whilst water intake varied up to 11.3 l/day. Intake of Atriplex nummularia dropped by over a half when the water available was changed from fresh to that containing about 1% NaCl. Dietary salt intakes were apparently more important than temperature in determining water intake, although both would be correlated with time of year.

Further work by Wilson (1974) showed predictably higher water requirements on halophytic vegetation than on pure grass communities; on the latter, water might not even be needed for as much as five months per year, especially after rain. On the chenopod-dominated communities (with some grasses only in winter) intake was as high as 12 l/day for several months during one particularly dry period, and some watering continued through winter, except after rain. Provision of shade generally reduced water turnover by no more than 10% during summer (e.g. 0.4 l in 4 l/day), suggesting that it was of little importance for woolly sheep. On the other hand, Lynch (1967) found that temperature correlated with watering in a 2400 ha paddock near Ivanhoe, N.S.W.

The watering behaviour of sheep is constrained by the distances over which they must range. Squires et al. (1972) examined the distances sheep are prepared to walk between food and water down a long race, and found significant breed differences associated with speeds of walking. The food was easily foraged for, but, if the length of the experimental race became too great, the food and water intake dropped. As distances increased, the sheep reduced their watering frequency from twice daily to three times in two days, and then only once per day (Squires 1970): the sheep could not take more than about six litres in a single drink. An average walking speed for merinos not engaged in any other activity was about 2.5 km $h^{-1}$, corresponding to values estimated by Noble (1975) in the open paddock.

In open paddocks of the order of 1000 ha in area, Squires (1976a) found differences in watering between sheep on <u>Danthonia</u>-<u>Stipa</u> grassland and <u>Atriplex vesicaria</u>-dominated communities; two waterings per day were common on the latter in late summer, compared to only one watering per day on the grassland, and a third the water consumption. Correspondingly the saltbush sheep walked an average of twice the distance (up to 14 km/day) that the others did, even in late summer when forage levels became low on the grassland: these distances are equivalent to the maxima that he found in his long-race experiments. The spatial arrangement of communities within the paddocks was found to be important (and the saltbush paddock was 30% larger).

The movement distances described by Squires seem to be maximal: a survey of daily movement distances recorded in the literature appears in Arnold & Dudzinski (1978, p41), although without comments on numbers and distributions of waterpoints, or on climate. There is no doubt that this focus of activities, the waterpoint, is very important in flock dispersion and the general patterns of movement over the whole paddock, which I now address.

### (iii) Flock structure and sociality.

Flock usage of large paddocks is affected by flock dispersion and sub-group movement. The function of differing group sizes between species that have different foraging habits has been discussed by Jarman (1974) and Estes (1974), both approaches being supported by Wirtz & Lorscher (1983). However, group sizes can also vary greatly within a species.

Arnold & Pahl (1967), Dudzinski & Arnold (1967) and Dudzinski et al. (1969) have used aerial techniques to describe the statistics of group patterning, and found in general that, with scarcer feed, flocks tended to break in smaller subgroups. A major limitation in the application of aerial techniques to large paddocks with bush was the small percentages of sheep actually located (e.g. 5%), although useful statistics were still obtained. Dudzinski et al. (1978) were able to develop this approach to the point of predicting a measure of range condition from the observed flock dispersion.

Noble (1975, p168) suggests that increased subgrouping and inter-group distances is a mechanism to allow more complete searching for scarce palatable ephemerals. Alternatively, this scattering might be regarded as an incidental result of patterns of search in poor forage contitions which over-rides the forces of sociability, rather than a change in the patterns themselves. Squires (1976a), observing sheep in large paddocks from a 10m tower, saw few, large groups with a mean inter-individual distance of 2.9m in saltbush vegetation, but many, smaller subflocks on dry grasslands where there was a mean inter-individual distance of 4.4m, and inter-group distance of 187m. Lynch (1974) also found greater scattering in times of feed scarcity, and Gardiner et al. (1978) found that lower pasture productivity correlated with lower live weights, smaller group sizes and more groups; they commented on the relevance of this to mating efficiencies - mainly that more rams may be needed if conditions are bad.

These studies show that environmental conditions affect subflock numbers more than inter-individual dispersion within groups, and this suggests that there may be some social cohesiveness within these sub-groups. The mechanism for this was proposed by Crofton (1958) to be the maintenance by any individual of at least two other objects (sheep or landmarks) within their visual ambit for orientation during grazing. However, chenopod shrublands can become relatively high, and it seems unlikely that this mechanism can predominate in them (Noble 1975, p162). Presumably a mixture of audible and visual cues maintains flock contact in these pastures, and it is not uncommon to see a subflock appear to simply diverge into two sections in high scrub, nor to hear isolated individuals bleating loudly.

The longer-term cohesiveness of domestic subflocks is a matter for interest - for example, Noble (1975) found that movements between subgroups, and regroupings, were not unusual. Amongst other ungulates, Lott & Minta (1983) have found almost random associations amongst American Bison, once the parent-offspring bond is broken. Conversely, Bighorn and Soay sheep under 'natural' conditions show total stability in the group structure of the females (Geist 1971; Grubb & Jewell 1974). This stability is paralleled by the occupancy of a definite, small home range, although the location of this changes seasonally in the Bighorns. Hunter (1964) found that Scottish hill-sheep subflocks also used definite ranges.

Inter-individual dominance behaviour is not obvious in domestic sheep, although such interactions become more visible under conditions of stress associated with restricted food, and perhaps at waterpoints (Collias 1956, Squires & Daws 1975). Squires & Daws found that in long experimental races, certain sheep always tended to be in the same position in the flock during movement to and from water, and there was a high correlation between position and social dominance as ranked when limited access to a self-feeder was allowed. They do not indicate whether there were differences between orders of movement to water on the one hand, and food on the other (i.e. whether the leader was dominant in all activities, or was only the animal that, for example, became water-stressed most easily). Thus Arnold & Maller (1974), studying competition at supplementary feed troughs, also found certain sheep to be regularly first to the trough, but there was no correlation with competitive ability once there. Arnold (1977) observing groups of six sheep in small fields found that flock movement was stimulated by individuals who tended to be less gregarious and graze at greater inter-individual distances; less independent sheep would then follow them, but active 'leadership' was not involved.

### (iv) Movement and grazing.

The question of which areas of a paddock are used for grazing is a complex one, evidently involving the positions of waterpoints, shade and camps, social factors, vegetation distributions and the effects of some climatic variables, all of which interact (e.g. Squires 1978). Knowledge of the form and extent of the interactions would have considerable potential value in solving managerial problems such as determining best paddock sizes, waterpoint positions, flock sizes and other parameters (Lynch & Alexander 1973, Squires 1976).

There can be a huge differential in density of grazing activity across a paddock, making the mean stocking rate irrelevant as far as the localised impact on the vegetation is concerned. This has been shown using dung densities by Lange & Willcocks (pers.comm.), and Lynch (1974) found that half of his study paddock was unused during one summer. On the other hand, at least some sampling of most areas in a paddock does occur from time to time, and the factors that influence this ranging are important for the survival of palatable minority species (Lange & Willcocks 1980).

The influence of some extrinsic variables on the patterns of sheep movement are known in general terms. For example, in moderate winds, it is well-known that sheep tend to be in the upwind portion of a paddock. Examination of aerial photos often emphasises this positioning, and distinctively different vegetation conditions may be found in the corners of the paddocks into the prevailing wind direction, with strong cross-fence contrasts to adjacent under-used areas. In stronger winds, especially if cold, sheep tend to move with the wind (e.g. Arnold & Dudzinski 1978, pp38-9).

Despite these general observations, however, wind is certainly no more than one of a suite of cues that may determine direction both in grazing and movements on a larger scale. In many animals there is evidence of habitat selection (e.g. Hodder & Low 1978, cattle, Belovsky 1981, moose, Duncan 1983, horses); movement may be affected by slope (e.g. Mueggler 1965, cattle); and it can certainly be altered by predators or a human presence (e.g. Berger et al.1983, pronghorns). For sheep, Crofton (1958) discussed factors that may be important in orientation, such as landmarks and the location of other individuals. In the arid zone especially, previously-developed sheep tracks may also be important (Lange 1969).

Lynch (1974) stated that sheep in a 2000 ha paddock tended to graze in preferred areas, limited only by fences, and by distance from water when watering became a more frequent necessity. Squires (1976) compared sheep usage patterns in two paddocks with different vegetation subunits and forage availabilities, but was unable to find any particular correlation. In one of his paddocks, the area used correlated well with prevailing wind direction, whilst in another the movement pattern was entirely contrary despite three days of consistent winds; forage distribution probably had an effect here. Harris & O'Connor (1980) observed sheep over a period of three years on part of their high country summer range in the South Island of New Zealand. They related distribution to forage conditions and various other attributes of nineteen land units, finding a general preference for damper sites (with more persistent forage) especially towards late summer. Similar trends in the relative usage of different landunits for each year indicated consistent non-random behaviour, but only to the extent that sheep stay in areas where the forage lasts longest.

Sheep sometimes 'trek' (i.e. move without any significant grazing for 2 to 3 km) in a definite direction out from the waterpoint in Australian arid zone paddocks (Squires 1974b). The large movements involved must be important in determining which part of a large paddock is occupied for grazing. No study to date has been able to offer any real clues as to the combination of factors which is specifically determining these movements.

Shade sites used in hot conditions are usually individual trees, of which there may be many. However, in a paddock of the order of thousands of hectares in area, there are usually only five or six sites used regularly for night-time camping. Camping is restricted to these sites even in summer when less time may be spent in rest during the short nights than in the day. The areas used for camping tend to be less well-delineated than day rest-sites, in the open, and often up hills (cf. Figure 1.23, Arnold & Dudzinski 1978). Initial selection of sites can be influenced by social factors such as the presence of sheep in an adjoining paddock which may cause camping on the common boundary (Whalley pers.comm.).

Little work has been carried out on learning of the layout of large paddocks, nor to examine the effects of changing paddock configurations on the long-term patterns of movement. In small enclosures, sheep can learn changes in the position of gates to a waterpoint rapidly, but they are notoriously slow to learn the position of a new waterpoint in the open paddock. When moved by graziers, young sheep especially tend to return to the old waterpoint. Arnold & Dudzinski (1978) quote some information on exploratory behaviour in smaller paddocks (100's ha), but its importance to productivity in large paddocks is unknown. Rapidity of learning could be important in a management scheme which does not return the same sheep to the same paddock each year, since the location of shade, camps and preferred vegetation might have to be re-learned annually. Experience is known to affect the foraging efficiency of sheep, and their expectations in grazing, to which I now turn.

## (c) Grazing behaviour.

### (i) Introduction.

A major portion of an herbivore's active hours is spent amassing the relatively large quantities of plant material that must be processed for its nutritional needs. Arnold (1964a) has provided a summary of the intrinsic and external factors which combine to determine a herbivore's diet. These include the plant species available (influenced by their physical, microclimatic and macroscopic environments, and their position relative to biotic factors such as established patterns of animal movement), which interact with the individual animal in its particular physiological state and social situation (modified by previous experience - both long- and short-term) to resolve the diet composition.

There have been many studies of the specific selection of diet by sheep in particular environments. Much of this is reviewed in Arnold & Dudzinski (1978). Techniques have included oesphageal fistulation (e.g. Arnold & Bush 1963, Leigh & Mulham 1966), rumen fistulae (Thornton & Minson 1973), dung cuticle analysis (Croker 1959, Peden et al.1974) and determination of net biomass change (Andrew et al.1979). In a few instances (e.g. Harrington & Pratchett 1973), direct observations of animals have been made. Each technique has its problems (e.g. Monro 1982). Fistula techniques sample what has definitely been eaten, but omly over short sample periods, which may not be representative; significant veterinary attention is usually needed. Dung samples can only be taken after the process of digestion. Vegetation biomass change needs a non destructive estimation technique, and then measures the effect on the vegetation, but not necessarily what has been eaten; significant losses can occur due to trampling and wastage, which are not easy to quantify. Direct observations measure effort rather than intake, and are often limited by restricted visibility and the need for minimal disturbance of the animal. Some methods require that the animal be penned for a period before the trials. None has been used in large open paddocks. Combinations of methods are probably best (e.g. Peden et al.1974), but involve great manpower costs.

Dietary selection undoubtedly occurs in sheep. Numerous studies have shown that a diet is selected with higher contents of nitrogen, phosphate, and gross energy, but lower fibre than is available on average in the herbage on offer (see summary of references in Arnold & Dudzinski 1978, p100). The proximate explanation for this may be that, on a given plant, sheep tend to select leaf material in preference to stem, and young tissue in preference to old or dry (ibid., and Hamilton et al.1973). The majority of the plants eaten may be chosen from a very small proportion of the forage species on offer; for example, Leigh & Mulham (1966a,b) found that at one time of the year, 80% of forage was selected from plant species representing only 1% of the herbage available, by weight at least. Such extremes cannot occur where there are few species to choose from; then diet changes may be more constrained by relative abundances of moderately-acceptable species (e.g. Arnold et al.1966).

Foraging selectivity which is apparently this sensitive might be expected to be strongly affected by physiological status, breed and age, but there is little evidence to suggest that this true. Arnold & Dudzinski (1967a) found that there were differences in grazing times and intake rates between dry, pregnant and lactating ewes but there was little effect on diet composition or total digestible organic matter intake; much of this variation could be accounted for by changes in fodder availabilities. Graham (1980) found some changes in the use of energy and nitrogen by sheep between weaning and maturity in the laboratory, but the partitioning of digestible energy between nitrogenous losses and metabolisable energy varied with level of feeding rather than age; furthermore, effects of increasing intake lessened as the sheep grew. Hodge & Doyle (1967) found that young lambs and yearlings ate similar proportions of grass and clover. Although these are only a few of the studies available, representing little variety of environment, they suggest that grazing trials should be robust to some age and physiological variability in experimental animals.

Variation between individuals may outweigh other effects, since individuals can be much more selective than is apparent from mean flock data. Arnold (1964c), quoted in Arnold & Dudzinski (1978), found that the variability in the percentage grass content of the diets of different individuals within a day was of the same order as the variation between groups of sheep from day to day. This result shows the importance of being able to analyse individual and summed data separately. Differences between breeds have also been found (e.g. Langlands 1968), some of which may be accounted for by documented differences in taste preferences (Arnold & Hill 1972).

Dietary selection clearly occurs: what are the mechanisms, and how do they operate ?

### (ii) The senses.

An herbivore selects its diet at two crudely-separated scales. First it chooses an area in which to graze - the ranging aspect of behaviour discussed above - and then within that area it selects individual plants and plant parts. For the latter activity, the mechanisms employed are the various senses, and these are interpreted into behaviour. The patterns of this interpretation are established by the existence of the senses, and 'innate' instinct; they are modified by learning, other forms of experience (including losing a leg, for example), and probably in the short-term by feedback from internal organs regarding cues such as nutritional status or rumen fill. From the point of view of the plant, there is an important distinction between remote sensing (sight and smell) and sensing that requires at least some sampling (taste, and perhaps texture).

Fontenot & Blaser (1965) reported that colour vision had no influence on sheep grazing behaviour, and that smell was unimportant in selection. Arnold et al. (1980) found that there was little effect caused by odours added to chaffed hay on intake, though a few were consistently avoided. Arnold (1966) and Kreuger et al. (1974) used impairment techniques to come to broadly similar conclusions regarding the importance of smell, taste and touch to diet selection. Arnold found that these senses each had a qualitatively similar effect of changing the preference ranking of about a third of twenty different strains of each of seven species in an Australian grass-clover pasture. Inability to taste was more likely to improve acceptability than to depress it, whilst smell and touch had about equal partitioning of effects. Combined impairment of all three senses had no significant effect on animal productivity under these good pasture conditions.

All authors considered sight to be of minor importance except in gross orientation and recognition of some conspicuous food plants. It would be surprising if sight were equally unimportant in arid areas, where more movement is often necessary to locate forage.

The interpretation of these sensory inputs gives rise to the actual selection of forage by the animal. The first stage involves the differential use or filtering of the available senses as above: and the final result is a specific diet composition. It is the latter that has been given most attention in the literature, and there are many examples of the preferences of particular breeds of sheep on particular pastures. It is clear, however, that better understanding of the intermediate stages is needed before this data can be more generally applied. Genetic background and previous grazing experience are also important, both of which have been largely neglected for large domestic herbivores. It may be that genetic factors largely determine the general strategies of searching, and the responses to internal stimuli, as well as the form of the filter which specifies which sense is important in a particular context.

Experience early in life is important in influencing grazing preferences, efficiencies and expectations, in a fashion perhaps analogous to imprinting (e.g. Bateson 1976). As the animal gets older, learning seems to become slower. Arnold & Maller (1977), following Arnold (1964b), found that sheep which were experienced in a limited range of grazing environments performed worse in new environments than sheep previously conditioned to a wider range; this effect was more significant in animals which were treated when younger. Differences in preferences for normally-palatable plants persisted for two years despite attempts at 're-education'. Lobato et al. (1980)

state similarly that early (pre-weaning) familiarisation with dietary supplements greatly increased later ingestion of them (a fact of evident commercial significance).

Arnold & Maller (1977) showed that experienced animals were able to obtain food at a much faster rate than sheep which had been raised without grazing experience, when put out to pasture: this presumably involves experience other than just the establishment of preferences. Dudzinski & Arnold (1979) found consistent behavioural differences in response to temperature, relative humidity and daylength, in merinos raised in a dry tropical climate compared to merinos raised in a Western Australian Mediterranean climate, when they were grazed together for three years; these differences decreased with time. Gluesing & Balph (1980) showed that the expectation of alfalfa by sheep which had been in a pasture containing the plant led to greater time being spent searching for it in a new pasture.

Diet selection thus rests on a genetic base which may be modified by learned behaviour during an animal's life. Some genetically-determined aspects of selection are purely physical, though nonetheless important. These include the forms of the sheep's jaw, lips and teeth, which enable, for example, sheep to be potentially more selective in eating than the larger-mouthed cow or horse. They determine certain constraints on grazing, such as the greater accessibility of the higher layers of vegetation. Although these constraints may reflect preferences on a genetic timescale, they should not be described as behavioural selection. Such genes also circumscribe the the variety of senses available, although conversely the availability of a sense does not imply its use. Such long-term attributes as these are usually not behaviourally flexible and need only be borne in mind as precursors in diet selection. The behavioural aspects have been considered as part of foraging theory.

(iii) Foraging theory.

Although the recent development of ethological theory has placed considerable emphasis on how animals locate and select their diet - foraging theory (e.g. Emlen 1966, 1968, Schoener 1971, Pulliam 1974, Estabrook & Dunham 1976, Ellis et al.1976, Zach & Falls 1976, Pyke et al.1977, Krebs 1978, Hainsworth & Wolf 1979, McNair 1979, etc) - few attempts have been made to extend it to herbivores (but see Freeland & Janzen 1974, Westoby 1974, 1978, Belovsky 1978, Owen Smith & Novellie, 1982). Location and patchiness of prey have also been considered at length (MacArthur & Pianka 1966, Gill & Wolf 1977, Bobisud & Voxman 1979, Morse & Fritz 1982), as has optimal habitat use and predation risks (Belovsky 1981, Werner & Mittelbach 1981, Werner et al.1983). The trend in foraging theory in recent years has been to try to include more realism in models, which has involved greater complexity, and often made testing less easy. These complications include a number of aspects that may be relevant to herbivores, including prey switching (Murdoch 1969), the differences between sequential and simultaneous encounters (Houston & McNamara 1982, Waddington 1982), substitutable resources (Rapport 1980), stochastic models (Green 1980, Stephens & Charnov 1982), competition (Milinski 1982), partial consumption of prey (Sih 1980) and the effects of hunger (Richards 1983), amongst many others.

The basis of foraging theory is that (genetically and/or behaviourally) animals are equipped to optimise their diet in some fashion. The 'currency' being optimised, the relative 'values' of different 'prey' at different times and the predator's perception of relative and absolute abundances must all be determined or assumed (Estabrook & Dunham 1976, Pyke et al.1977). The currency may be any of a variety of absolute or perceived measures, generalised by Estabrook & Dunham (1976) to the intake of food 'value' per unit time such that this 'value' may maximise the expected genetic contribution to subsequent generations. whether the 'value' (as total energy, or specific overriding nutrients, or sometimes particular trace chemicals), or the time is more significant may depend upon forage type. Thus, for herbivores with an approximately fixed bulk or time of intake, food quality may need optimising rather than, for example, time in an animal that is subjected to higher risks whilst foraging, or bulk in animals with a limited capacity; plainly all these factors may interact. Krebs (1978) lists the possible failures of the theory which arise when data do not match model predictions.

To what extent may these theories be applied to domestic herbivores, and in particular, the sheep ? There has been little critical discussion of whether ruminants optimise their diet and there is almost no evidence as to how much 'nutritional wisdom' may be involved in their diet selection. Few studies have been interpreted in terms of optimal patterns of movement.

In a broad sense, if there is any biological mechanism by which a ruminant can optimise its foraging behaviour, then selection should have occurred to enable it to do so; the continued presence of the species is evidence that they can usually obtain adequate nutrition. However, any large, generalist herbivore may have difficulty in developing viable foraging mechanisms, and domestic animals have added problems imposed by pastures alien to their genetic history. Westoby

(1974) points out that the size and mixing of consecutive 'meals' in large herbivores may mean that it is almost impossible to correlate bad after-effects with particular foodstuffs. There is no evidence of such 'long-delay' learning in herbivores: indeed, the only reliable evidence is for rats (e.g. Revusky & Garcia 1967) who may take a very varied diet but are extremely conservative in their approach to new foods.

Belovsky's (1978) study of the moose is one of the few to show a clear correlation between reality and optimal predictions in an herbivore, and it may be that it is unusual to have a system in which animals are constrained simply between two main requirements (sodium and energy), with food plants falling clearly into one or other supply category. In these circumstances, Belovsky could predict daily consumption of the three main food-types well on the basis of an energy-maximising strategy. As a result, he could also predict optimal body sizes, and habitat use (Belovsky 1981). He concluded that "the situation faced by some herbivores in selecting a diet is not as complex as has been previously supposed": 'some' may be the operative word, although Owen Smith and Novellie (1982) have had some success with diet selection in kudu.

There is limited evidence (Allden & Whittaker 1970) to suggest that intake in sheep may be related to available pasture 'quality' in such a way that a certain level of digestible intake is maintained, but that this level cannot be attained below a certain threshold of forage availability. Their approach was based on Holling (1959), and was not supported in findings for microtine rodents (Batzli et al.1981). Other studies of sheep (e.g. Arnold & Dudzinski 1967a,b, Thornton & Minson 1973, Arnold 1975) have also failed to show the effect;

however, some fixated preferences undoubtedly cloud the issue (cf. Arnold & Dudzinski, pp121-4), as well as previous experience (Allden & Scott Young 1964 and Langlands 1964 found increased compensatory intake after undernourishment in young sheep).

To be detected, quality of food must be correlated with some sense-susceptible attribute. As Janetos & Cole (1981) suggest, there may be no adaptive advantage in being perfectly optimal, if the costs of the perfect sensors outweigh the small improvement in return rates. Westoby (1974) has put forward the concept of 'fallible nutritional wisdom', wherein a general tendency to optimise is rendered deficient in practice both by the imperfect correlations between sensible attributes and food quality (including particular toxins), and by the continual need to sample other plants in small quantities in order "to keep up with seasonal changes in what the nutritionally optimal diet is" (Westoby 1978; also Freeland & Janzen 1974). These imperfect correlations are likely to be worse for domestic herbivores (and introduced feral animals) since their available fodder is not necessarily similar to that on which the required senses evolved. This phenomenon presumably explains the cases of palatable poisonous plants, such as the instance quoted by Arnold & Dudzinski (1978) where sheep but not kangaroos in Western Australia will ingest lethal doses of fluoroacetate from Gastrolobium and Oxylobium species.

Domestic animals may be good experimental subjects for examining foraging theory in regard to herbivores, since a great deal is known about their physiology and general behaviour. Against this, however, is the fact that they are usually translocated from, and no longer under the influence of, many of the selection pressures of their past. Some aspects of foraging behaviour should still tend towards optimality, but most previous work has not been interpreted in these terms.

Ultimately, some all-encompassing diet selection theory will be needed to model the quantity and quality of dietary intake on new pasture combinations. Recent work in the very early parts of grazing periods using artificial foods by Kenney & Black (1983) has moved towards predicting these factors on the basis of rate of intake alone. For reasons that will become apparent (Chapter IX), this approach is unlikely to explain more than part of the whole. There is, however, considerable data available on which to base a model of sheep behaviour, and it is with this that the next chapter is concerned.

### (d) Overview.

A model of the behaviour of an animal necessarily includes information from a wide spectrum of sources. In this chapter, I have described some of the evolutionary and historical processes which delimit how herbivores, and sheep in particular, can behave and adjust their non-reproductive behaviour in the short-term. I have then examined the literature available on ranging behaviour and grazing behaviour in more detail, since these two aspects of the sheep's activities broadly determine where and how great will be its impact on the vegetation. In doing this, I have dealt pre-emptively with some areas of the literature which will turn out to be important in later chapters.

# Chapter III.

## Modelling, and approaches to open paddock ranging.

Chapter I has outlined how both domestic and wild herbivores use semi-arid and arid regions for extensive pasturing. The long-term changes that herbivores can cause in vegetation, especially when mismanaged by man, result in the need for a clear understanding of interactions between plants and animals. Models of grazing behaviour not only help clarify these interactions, but also provide a basis for management decisions. The long turnover times of arid zone ecosystems mean that these systems require a modelling approach which can predict the results of management strategies well beyond a manager's lifetime.

In Chapter II, I examined some of the background biological knowledge that is available to such an approach, and delineated some problem areas. In this chapter, I describe the requirements for whole-system models which are intended to be useful in management, and I critically examine the model of Noble (1975) upon which much of my work has been based. Although one ultimate aim is to validate this model and redress its inadequacies, certain areas need further study in order to determine the best modelling approach. In the final section of this chapter, I outline the framework within which my work has been structured.

### (a) Systems and management-oriented modelling.

The objectives of model design are often described as a balance between realism, precision and generalism. There are three categories of reasons for building a model of an herbivore's interaction with its biotic environment; each type of reason emphasises a different objective.

Firstly a model may be developed primarily for its scientific value. The explicit coding of a model exposes gaps in our scientific knowledge, since it requires a clear statement of all assumptions underlying the model. Most competent managers, and scientists, possess many of these assumptions as part of their 'gestalt' understanding of a system, but these may not be communicable, and may be inapplicable in different situations. The infilling of gaps in our knowledge, and the disclosure of underlying assumptions often results in significant contributions to scientific theory. Model-building for such purposes tends to emphasise realism in describing process, and often requires great detail in the input variables. Many ecosystem models have been built using this approach.

A model for local management, on the other hand, is intended to predict the impact of particular events on a given system. These events may be management procedures, such as stocking rates, or less predictable phenomena, such as fires. In order to be practicable, such a model must operate on a bare minimum of reliably-available input information. It may be used to test between management options which are as yet unimplemented, or to predict the course of a particular event so that appropriate management action can be taken. The realistic modelling of process is not usually important, but precision is needed in suitable output indices. Modelling approaches of this type have been implemented, for example, in planning for the management of National Parks in the U.S. (e.g. Shechter & Lucas 1978).

The third use of complex models involves an increase in generality at the expense of both realism and precision. This occurs when a wide range of conditions are to be modelled at the same time - for example, a model to summarise patterns of production over large areas such a whole properties, game reserves or climatic regions, or a model of fire intensities in many vegetation types under many climatic conditions. Often such models may best be derived by running more detailed models for a large range of conditions, and using simplified regression relationships between input variables and relevant output parameters to substitute for the realistic modelling of process. The approach of regional models is well illustrated in Freeman & Benyon (1983).

These different approaches result from changes of scale between explanatory and descriptive models. I emphasise this point since choice of scale is an essential part of model-making that is not always acknowledged, and is frequently the reason why models fail when they are unjustifiably applied to situations for which they were not designed. For example, a transition matrix of daily activity changes for animals may serve to describe statistically what an animal is likely to be doing, and therefore may predict the effects of long-term grazing on a pasture. However, such a transition matrix offers no information about the 'decisions' that underlie the changes in behavioural state associated with particular conditions, and it may not apply under conditions other than those in which the data used to build it were collected.

Such a model could include more detail, and determine the physiological state (say heat balance) of the animal, and consequently predict a movement to shade on the basis of specific external conditions which combine to cause some internal index to exceed a threshold level. In this case, the explanatory level has moved down from the transition matrix to a physiological level, and this change in activity has been distinguished from one due to rumen fill or thirst. The model is now likely to be applicable under most combinations of external conditions because, if the correct index has been used, some degree of process has been explained realistically. However, the model is still at the descriptive level in establishing the threshold of the physiological index to be used. This threshold in turn might be modelled by detailing the heat tolerances of cells, movement and temperature of blood in the brain, and so forth: but each deeper level will be constrained by some descriptive parameters (as well as requiring more computational time), until the Laws of Thermodynamics are finally reached.

My study has aimed to elucidate some of the processes involved in sheep's ranging and selection behaviour, with the intention of going beyond the level of detail that is essential to a management-oriented model. By a process of simplification, it is then possible to pare the model down to the level of detail which is relevant to the required scale of modelling.

## (b) The Noble model.

I began this study using a model of sheep behaviour and vegetation dynamics which had been developed for a paddock near Middleback (see Chapter IV(a)) called 'Wertigo'. This model was conceived and written by Ian Noble. Much of my study has been aimed at validating and complementing the approaches of this model, as well as extending it in certain areas. I therefore present here a brief description of the structure of Noble's model (usually termed 'the model' hereafter), before examining some of its weaknesses. While I have modified the model considerably, and extended its application to other paddocks, I stress that the original structure and approaches are those of its author. A detailed description of the original model can be found in Noble (1975, 1979).

### (i) Description.

Figure III.1 is a simplified schematic outline of the structure of Noble's model. Briefly, a small number of climatic inputs operate on a daily basis to drive a soil moisture budget submodel. This in turn drives the germination, growth and death of several classes of vegetation. Some structural information about the paddock being modelled is necessary, including the spatial patterns of run-off, soil characteristics and the initial vegetation distribution over the paddock. Figure III.2 is taken directly from Noble (1975) and illustrates his view of the detailed interactions involved. The vegetation component of the model was perhaps the part best validated, drawing considerably on the records of the Koonamore Vegetation Reserve (see Noble & Crisp 1980, Noble 1977). I do not deal much further with the vegetation growth model in this study, but it is worth noting here that it is the

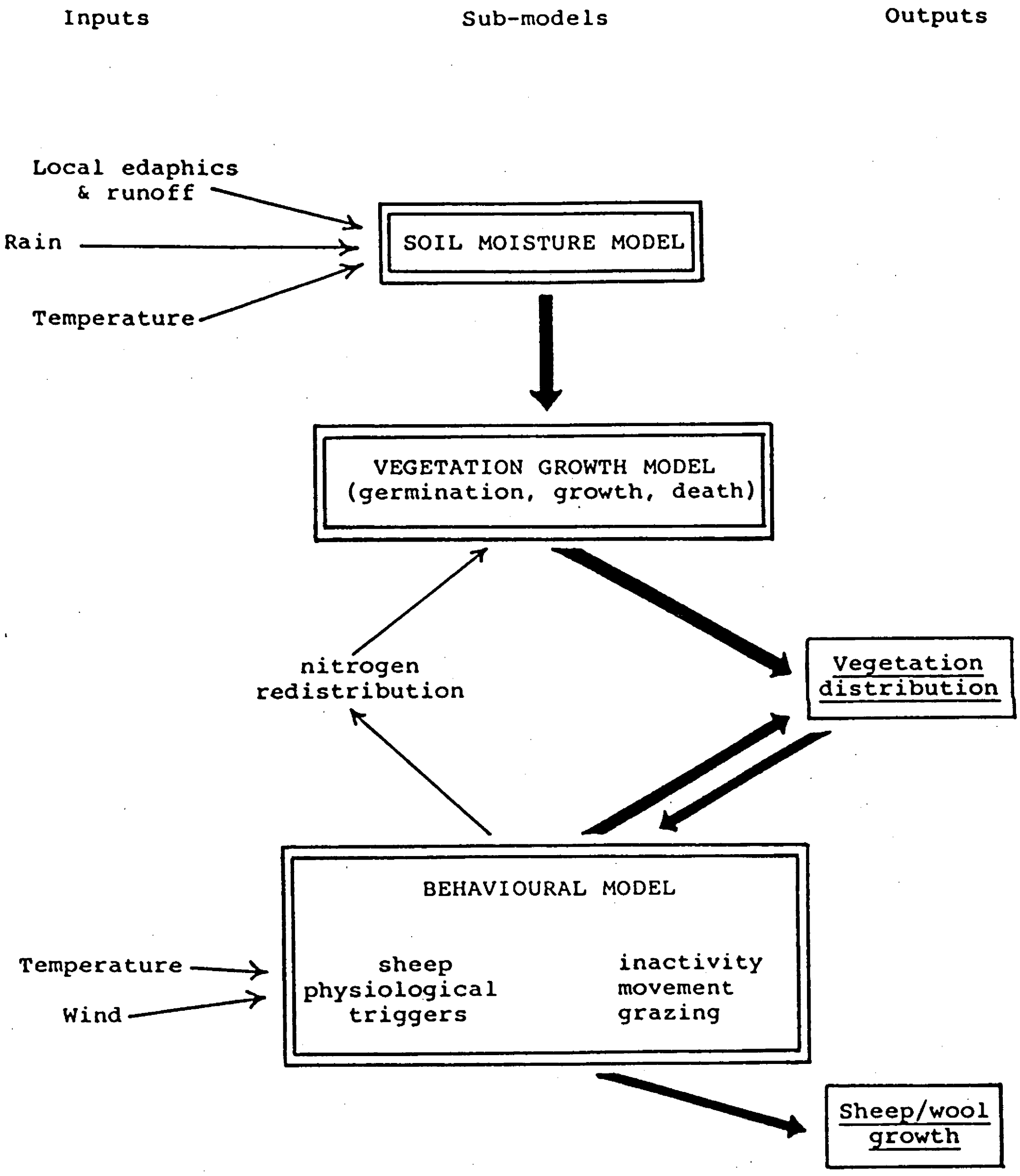


Figure III.1: A simplified outline of the overall structure of Noble's paddock model. The 'black box' of the behavioural sub-model is expanded in Figure III.3.

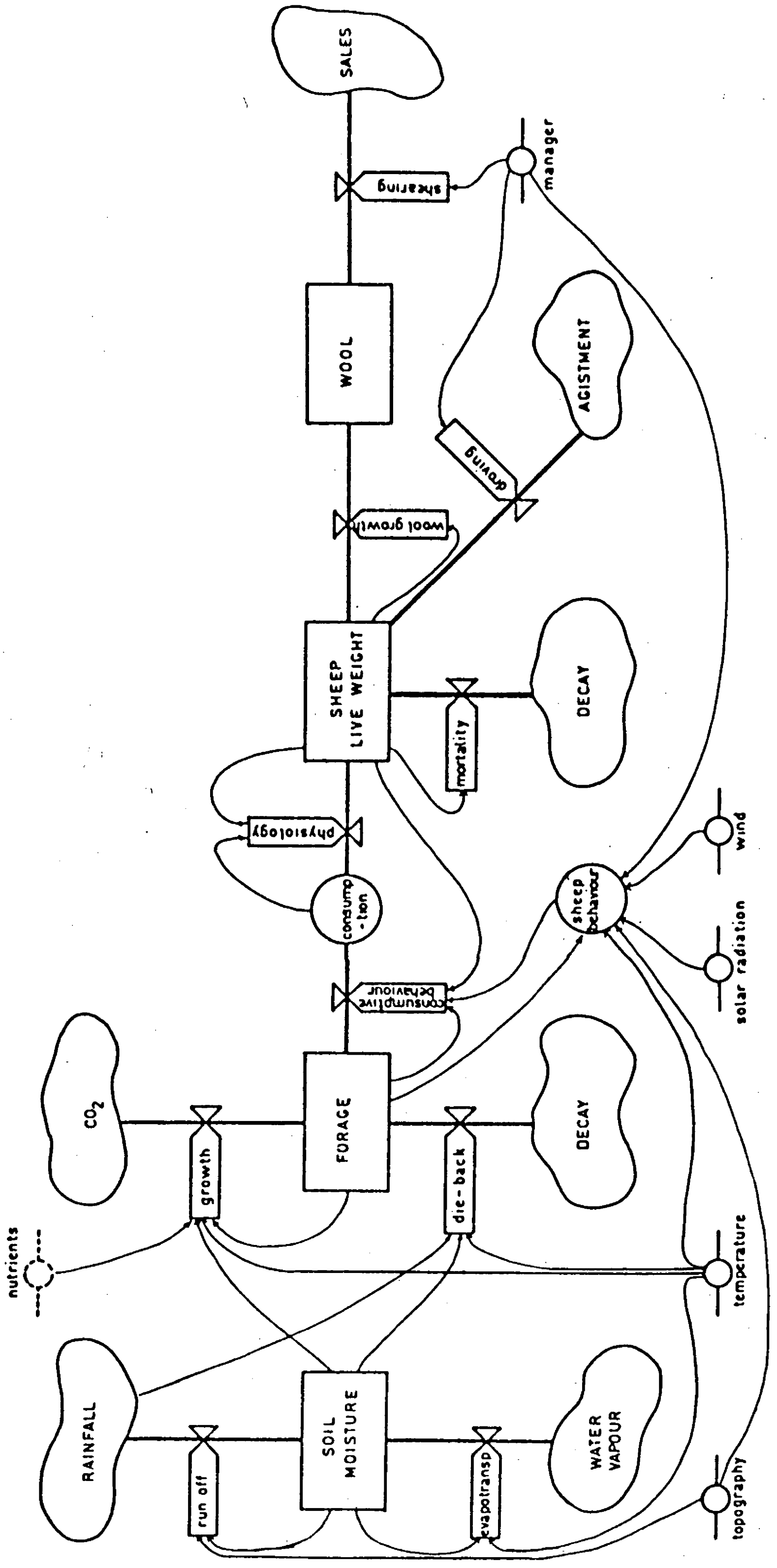


Fig. 4.3a. A diagram of the complete model using notation similar to that of Forrester (1971). The heavy lines represent the flow of water (left hand side) and carbon products (right hand side).

Figure III.2: Figure 4.3a from Noble (1975), illustrating his view of his model.

section that requires most information before the model can be applied to a new paddock.

As Figure III.1 shows, the behavioural model interacts with the distribution and condition of the vegetation, with feedback resulting directly from grazing impact and indirectly by nitrogen redistribution. Goodall (1969) and Noy-Meir (1981) stressed the need to incorporate spatial heterogeneity in this type of model. It was the clear intention of Noble's study, therefore, both to model the mean effect of a herbivore on its pasture, and to determine the spatial distribution of this effect (Noble, 1975, p18).

A spatial component was included in the model by dividing the paddock into a number of adjoining cells using a regular grid system. Each of these cells had its own run-off and soil characteristics, and the growth and condition of the vegetation in each is modelled separately. In the behavioural model, each group of sheep in the paddock has a position in one of these cells, and the modelling of their movement between cells locates the impact of their grazing.

The definition of both spatial and temporal scales is fundamental in all ecology. For the model, these definitions depend upon the detail of the processes that are to be modelled. Vegetation growth was modelled on a daily timestep, but this could probably have been done less frequently. On the other hand, animal behaviour and movement was modelled on an hourly timestep so as to be realistic in relating them to actual activity and spatial position. In the original model, the paddock cells were defined as 800x800 $m^2$, an area comparable to that over which a sheep may graze in an hour, as well as for other practical reasons. These choices immediately constrain both the detail required on input, and the detail available on output. I have used a smaller cell size of 500x500 $m^2$ for much of my study, in an attempt to increase the realism of the spatial aspects of grazing.

The behavioural portion of the model is outlined in Figure III.3. This submodel centres around an hourly selection of activity for each subflock being modelled. Activity selection is controlled by a series of 'trigger conditions': these are the evaporative load on the sheep (its 'heat stress'), its thirst, hunger, and the fall of darkness. The threshold levels of these trigger indices which cause an activity transfer are more-or-less directly heirarchical (see Table III.1). There is some interaction, so that, for example, a hot and thirsty sheep will not try to leave shade for water, unlike a hot and severely dehydrated animal.

Table III.1

Abbreviated version of Table 8.2 from Noble (1975), listing the trigger conditions that cause activity transitions. The heirarchy is indicated by the number, 1 being dominant.

| | Trigger | Description and result |
|---|---|---|
| 1<br>3 | dehydrated<br>& thirsty | Two levels of water deficiency. Thirsty sheep may not travel in the hottest period of the day, but if they lose more water and become dehydrated, they will seek water despite the heat. |
| 2<br>4 | body temp.<br>rising & hot | Two levels of heat stress. Hot sheep will stop grazing and seek shade, but move to water if they become thirsty. In more extreme heat stress they will not leave shade unless they are suffering from dehydration. |
| 5 | night | No grazing occurs from late evening until an hour before dawn. |
| 6 | hungry | One level of hunger stress (rate of consumption is varied with hunger in the intake sub-model). |
| 7 | no stress | Resting occurs wherever the sheep happen to be. |

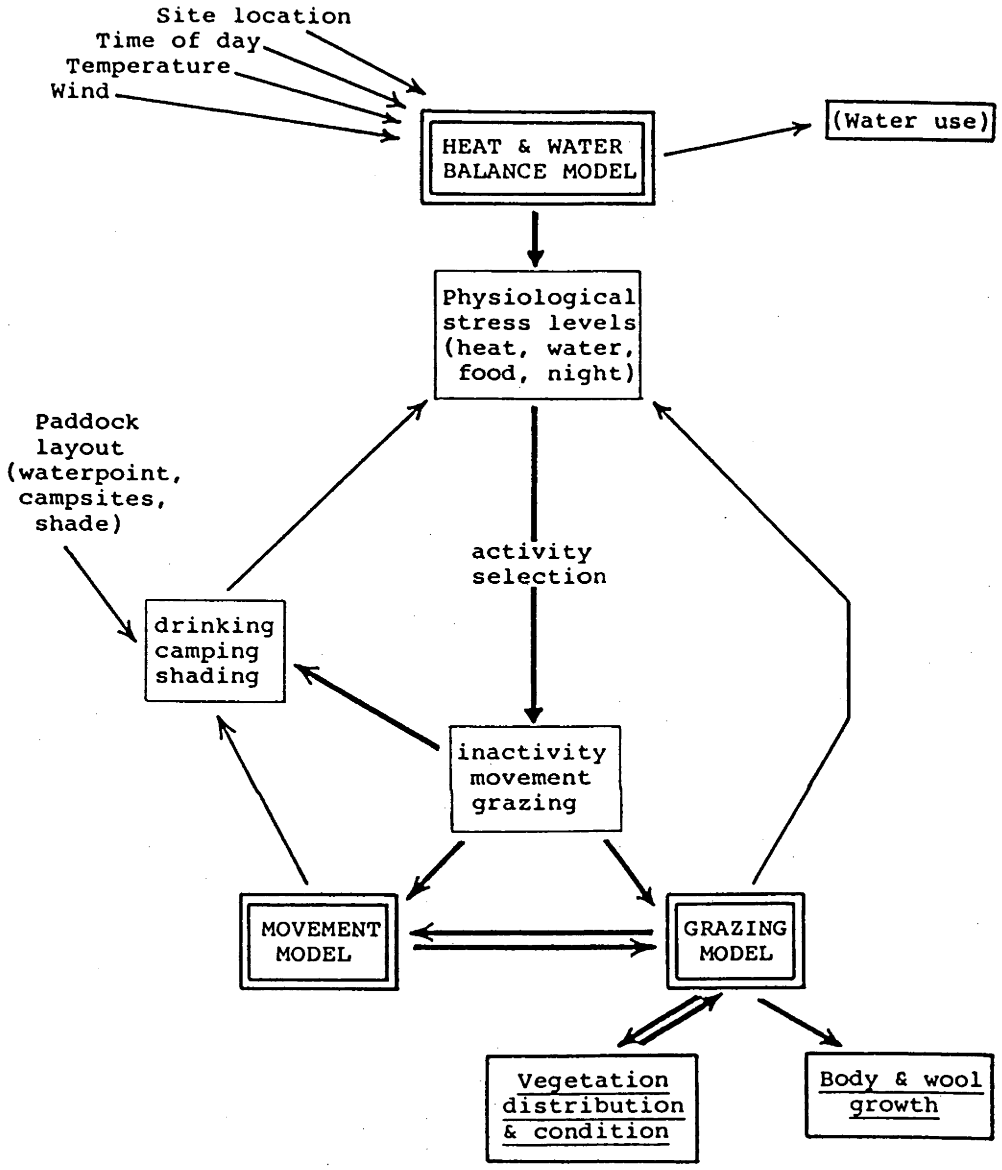


Figure III.3: Outline of the behavioural sub-model of Noble's model. Underlined items are outputs of potential interest to a manager. Inputs are shown on the lefthand side of the diagram.

As a result of the hourly choice of activity, a sheep may move to water, shade or camp at night, or graze, or do nothing if no index passes its threshold level. Movement may thus occur for two purposes: either in the course of moving to shade, camp or water, or during grazing. The former involves a choice of destination, and is then assumed to occur at 2 km $h^{-1}$ with no grazing en route. The latter is the least deterministic event in the model, involving a probability function which describes the likelihood of moving in a given direction relative to preceding movement direction and wind direction. The speed of movement in grazing is 0.5 km $h^{-1}$, but is increased in low quality or unpalatable pasture.

Finally, the actual effect on the vegetation via grazing is modelled by a simple intake model, in which pasture availability in a cell determines how much may be eaten from that cell during each hour. The total intake is apportioned between the various forage types present by constant preference indices for each. Consumption per hour is reduced as satiation is approached. The salt and water obtained from plants during grazing affect water usage.

(ii) A critique.

To quote the summary from Noble (1975),

> 'Separate validation of each submodel has been attempted. No data of sufficient detail were available to validate the paddock model as a whole but the output agrees with our present understanding of the system in all important aspects.'

The model in Wertigo paddock functions quite well. It satisfied reasonably the requirements for minimal input - the most significantly time-consuming section would be creating a vegetation map of a new paddock, and perhaps locating the sheep's campsites, since most other information could be obtained from topographic maps and stereographic aerial photos, providing the soils were reasonably uniform. Climatic input was modelled, but the model may be run under real conditions with only meteorological station variables. The outputs generated included the amount of wool cut, and animal condition as measured by live weight, and the state of the vegetation in each cell in the paddock. Water consumption could be estimated if desired, and details of many other variables could be obtained.

Long-term output seems to match 'reality' for 'normal' conditions in Wertigo. The model predicts that, under average conditions and stocking rates, the effects of rainfall on vegetation growth will dominate in most of the paddock except for the area around the waterpoint. However, the model appeared to overpredict the rate at which a piosphere would develop, even in a paddock such as Wertigo which was supposedly in a relatively stable condition after many decades of similar stocking. The original justification for looking further at the model, indeed, was that in a paddock of very different structure (Jervoise, see Chapter IV), a major overprediction of the use of the area close to water was also obtained; this area is the most important zone of impact. It was apparent that there might be serious flaws in the movement model in particular.

I now examine aspects of the behavioural model which were not validated, and identify areas which need further study in order to replace them or justify their presence in the model. In the next section, I will place the areas that require further study into a more theoretical framework.

Three sections of the model of sheep behaviour warrant discussion.

Firstly, the 'decision' to move to water or shade is based mainly on a heat and water balance submodel for the sheep. This submodel is developed in considerable detail, but is not validated and has not been related to open paddock behaviour. Amongst the assumptions of the original model are the relationships between the 'heat' index threshold levels and other indices. These relationships are important in determining the use of shade in relation to other activities, and are also unstudied in large paddocks. This section of the model is quite modular, and is discussed in more detail in Chapter VI(b) and the Appendix.

Secondly, the movement aspects of the model were based on relatively few paddock observations. Movement other than that associated with grazing involves two factors - the choice of a site and the form of movement to it. Selection of camp and shade in the model is assumed to be selection for the nearest available; choice between multiple waterpoints does not occur. The locations of camps, shade and waterpoints all represent sites from where the next grazing period is likely to begin, so that justification of this selection is necessary. No grazing is permitted during non-grazing movements in the model. In reality, such committed movement rarely occurs except close to the waterpoint. Rates of movement in grazing are crucial in determining the degree of localisation of grazing impact. If significant 'directed grazing' is occurring (i.e. grazing towards a destination, as discussed by Noble, 1975, p172), it is necessary to know whether directional movement is being determined by influences in grazing, or by selection of a destination.

The prediction of movement directions in undirected grazing could valuably be made more deterministic. The model predicts these by using a probabilistic function biased only by wind direction, although speed of movement is also presumed to be affected by vegetation quality. Further validation is necessary if the model is to be useful under 'abnormal' conditions which may bring about critical changes in the pasture. It is necessary to demonstrate that other possible influences are not important, or, if they are, to include them. Such influences could include a much greater responsiveness to vegetation distribution (with or without learning) or fencelines, which are assumed in the model to have a simple reflective effect on movement. Factors relating to movement in general seemed to be a major reason for the failure of this model in paddocks other than Wertigo.

The third major area of the behavioural model is that of diet selection during grazing. A considerable amount of work was done to show that a simple submodel is adequate to predict diet selection, and that further complexities were unwarranted. This is likely to remain the case until much more is known about foraging in herbivores, and whether their habits can be fitted into the 'classical' mould of optimal foraging theory. However, a number of unvalidated factors, such as reduced intake rates, both during satiation, and after moving from a good area to a worse, were included; there was no examination of whether diet preferences vary with satiation. The scales at which animals are supposed to select their diets, and which determine their preferences for different food types, are also important. One (clearly acknowledged) weakness of the model is that its preference indices do not change with season.

In summary, the behavioural model is a major part of the overall paddock model of Noble (1975), and it determines the spatial distribution of the predicted impact of grazing on the paddock. It overpredicts the use of centres of activity, particularly the area around the waterpoint. This failing is likely to result from the lack of validation both of the trigger conditions which determine the occurrence of the various activities, and of the criteria used to determine directions of movement in the open paddock. Additionally, the grazing intake model contains a number of weak points which are unvalidated, and might be better approached in ways that avoid the need to predict the hourly intake independently of the diet selection model. Grazing selection is taken up further in Chapters VIII and IX; in the remainder of this chapter, I discuss movement in the open paddock.

## (c) Conceptual approaches to movement.

### (i) Background.

As has been mentioned in Chapter II, wind certainly affects the area of the paddock being used by sheep. On the other hand, there is evidence for sheep (Harris and O'Connor 1980), and much more for cattle (Hodder & Low 1978) and other large herbivores, that animals select preferred vegetation types in which to graze. It should be borne in mind here that the divisions between vegetation types which are discussed in the literature are often much more coarse or extreme than may be found in the comparatively homogeneous vegetation of a chenopod shrubland paddock, and the criteria that are used for defining taxa supposedly relevant to animals are particularly prone to anthropomorphic presumption. However, the influence of vegetation communities may also be significant.

If animals sense that they are going to need water later, or shade on a hot summer's day, or require to move to one of the limited numbers of available campsites on a cold winter's evening, then they might start to seek out a particular target before finishing grazing. Observations of sheep often show such apparently 'directed' grazing movement, indicating that the locations of these sites may also be important. In this respect, one might argue that on a stressful day, or late at night, all movements ought to be directed.

It is difficult then to propose a universal deterministic theory of movement which can be tested in a straightforward fashion. An example will serve to illustrate this, and to indicate some of the conditions that must be fulfilled by an appropriate solution. My main study paddock, Jervoise (see Chapter IV for details), has its waterpoint in its northeast corner. As will be shown, there was certainly a greater tendency for the sheep to move south in southerly winds than in northerlies. In north winds, they would usually graze within a 1500 m radius of the waterpoint. Often in south winds, however, they could be observed to walk with very little grazing through the same area as used previously to graze further south. Two days later, they would be grazing in the north again. Clearly a theory so simple as to suggest that the sheep walk out from the waterpoint until there is sufficient feed to eat, and then stop and graze, is inadequate.

A more complex model is essential; it is necessary to allow for interaction between factors, with different outcomes for different subflock histories and positions. Some components of such a treatment can be tested, and its overall predictions can be compared with reality; but the variation to be found in simple parameters of flock activity is not likely to be more than partially explained by simple criteria such as wind direction or vegetation type.

### (ii) A framework.

All grazing begins after a period of inactivity. The four conditions of non-grazing activity that I have mentioned are watering, camping, sheltering in shade or resting in the open. Watering occurs at the definite focus of one or more waterpoints. Camping is restricted for the majority of the flock on any night to one or two of a handful of larger sites. Shade sites are usually much more numerous, but not every tree will be used, and they are often spatially concentrated. Resting seems to take place at any site in the paddock, although local areas that are devoid of vegetation may be slightly preferred.

Shade, camps and waterpoints are thus all foci for the beginning of grazing periods. Areas around them are likely to be over-utilised relative to the rest of the paddock. The effect of the waterpoint on the development of pattern in the vegetation has been identified with the piosphere. Goodall (1967) emphasised only distance to water and from fencelines in his model of a hypothetical arid zone paddock, and Noble's (1975) prototype model 'GRZMOD1' operated on annuli around a waterpoint. The impetus to include more spatial information about a paddock is a result of the fact that these other locations of inactivity will act as similar foci in vegetation pattern development. Any vegetation types which cause particular foci to be used may themselves act as concentrating foci.

To a considerable extent, the problem of how sheep influence the vegetation of their range may be broken down into the following questions. Under what conditions will they need to use one of these foci ? What factors determine which particular site is in use ? Where will they graze when they leave it ? And, of course, what diet will they select in the area that they are grazing ? The 'selection' of a particular shade or campsite may in turn depend upon previous grazing movement.

The first stage in the process of answering these questions is to delineate what variables (such as distance from water, vegetation type, etc.) may be of significance in affecting the patterns of activity over the paddock (Chapter V). It is then possible to assess the impact of these factors on the activities of resting, using shade, watering and camping, and to determine when these activities occur (Chapter VI). The other major activity, grazing, in which movement is crucial is discussed in Chapter VII. Finally, diet selection in grazing, in which the spatial element is still very important, must be considered. In particular, if grazing regularly starts from a limited number of foci, then changes in behaviour with time through the grazing period will be important (Chapters VIII and IX). Throughout, I keep the model in mind as a focus, and finally return to it to draw these factors together in Chapter X.

# Chapter IV.

## Sites and methods used in the open paddock work.

The last chapter has laid a theoretical background to the study of of sheep ranging behaviour in the open paddock. This chapter presents the practical aspects. In it, I describe the general site, Middleback, as well as the particular paddocks that I used. I summarise the weather experienced during the study, and how this related to the fieldtrips and observation periods. After a brief discussion of methods available for the study of large-scale ranging behaviour, I describe the collection of open paddock data, both by mapping, and by other techniques.

(a). Location and conditions of fieldwork.

(i). The property, Middleback.

The fieldwork of this study was carried out from Middleback Field Centre on two South Australian stations, 'Middleback' and 'Roopena'. These are situated about 30 km west of Whyalla, on the Eyre Peninsula. This location was selected because of an existing field station, with laboratory facilities and close proximity to a major town; because of the good condition of the shrub vegetation storey; and because of well-established working relationships with the owners. Figure IV.1 is a location map.

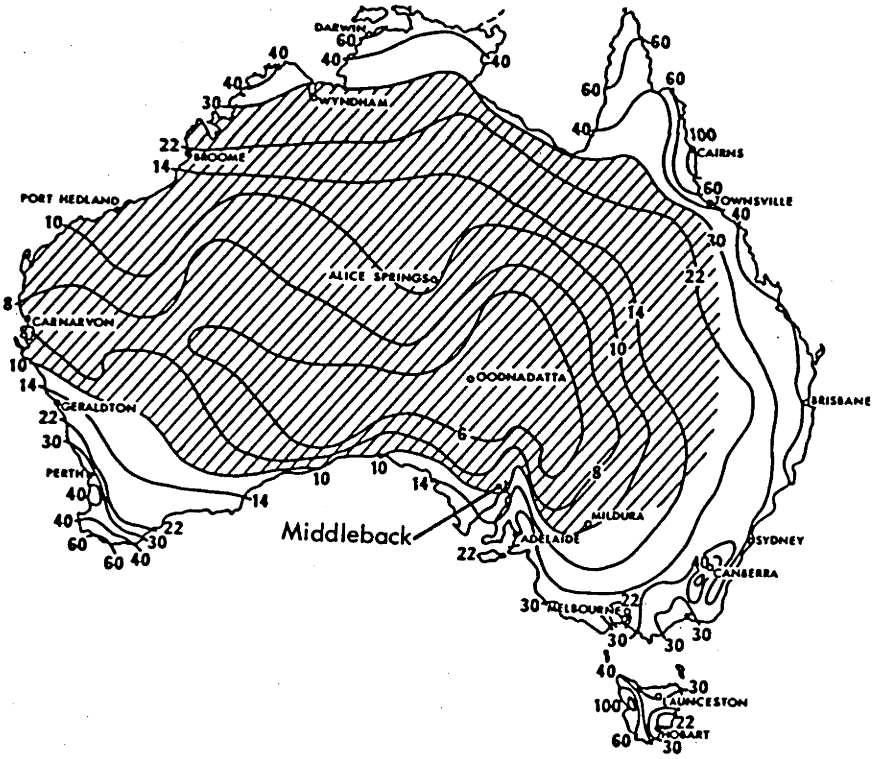


Figure IV.1: A map of Australia showing median annual rainfall (in) and the approximate extent of the arid zone. The location of Middleback is marked. (Modified from Gibbs 1969.)

Study areas were located on both Middleback and Roopena stations, but I shall refer to the whole area as 'Middleback' except where more accuracy is required. The Middleback Field Centre is a small but well-equipped field station, run by the Department of Botany of Adelaide University, under the direction of Dr. R.T.Lange. I was able to use various of its facilities and equipment: in particular, its basement provided a cool, dust-free environment in which to run a micro-computer (see Chapter VIII).

The property is run as a commercial concern and owned by the two brothers Don and Andrew Nicolson. It carries about 10,000 merino sheep, primarily for strong wool production. The two stations total about 624 $km^2$ in area, and are fenced into about 43 paddocks ranging in area from 500 to 5000 ha (Figure IV.2). Due to lack of surface water, land in the vicinity of Whyalla was not taken up until the 1870's. The Nicolson family first acquired an interest in the area in 1919. Since then, they have developed a substantial network of water-pipes from a well near the Roopena homestead. These now supply at least one waterpoint in almost all paddocks, and supplement the ephemeral water supplies of surface dams. In dry summers, over 100,000 litres of water may be pumped around the property each day.

The family's policy has been to subdivide paddocks, with the aim that no waterpoint should used by more than about 250 sheep. A similar policy was advocated independently by Waite in 1896 (see Macfarlane 1968). Although the process is not quite complete, Middleback generally has smaller paddocks and more waterpoints than surrounding properties. A fixed stocking policy is pursued, with little movement of stock except at shearing.

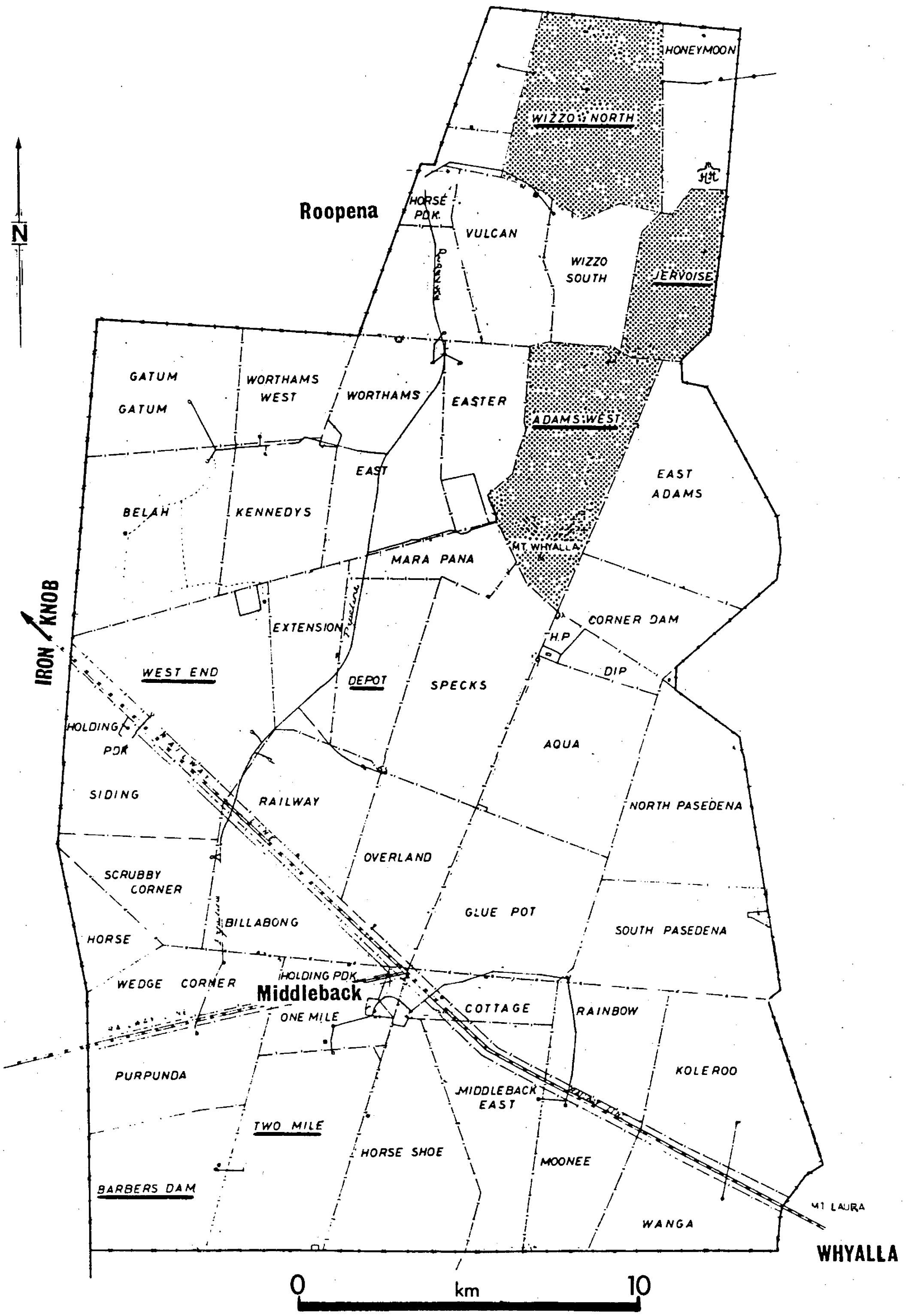


Figure IV.2: Pastoral map of Middleback and Roopena stations, showing study paddocks (stippled) and other locations mentioned in this thesis (underlined).

The normal sequence of management procedures at Middleback is: shearing (and weaning), late February; lambing, June-July; lamb-marking, July-August; crutching, September; and rams into ewe paddocks, December until shearing. Wethers comprise about half of the flock. Many sheep are not mustered more than 2 or 3 times a year (mainly for crutching and shearing), and do not see humans much more often than this.

### (ii) Physical structure.

Both stations have little topographic relief, although some hills around 'Mt. Whyalla' on Roopena soar to over 200 m. These hills are composed of coarse sandstones, grits and conglomerates, which protrude through Quaternary 'mallee soil plains'. The area is situated on the western edge of the Adelaidean Geosyncline, and much older rocks outcrop to the west of the faultline that runs down the centre of the property. The soils overlying this geology are most commonly red calcareous earths with good drainage, often gravelly and capped by travertine limestone or calcrete. More locally, there may be solonized, heavy brown loams, and sands. Rock outcrops through skeletal soils on many of the hills. There is no permanent surface water, although many sandy river-beds carry water briefly after heavy rain.

### (iii) Vegetation.

The vegetation of the area consists of both chenopod shrub steppe and open low woodland with chenopod shrub understorey (Specht 1972, Jessop 1981). Although appearing quite dense from ground level, the total ground cover of the perennials does not usually exceed 10-15%.

The dominant chenopod shrub species are Maireana sedifolia (F.Muell.) ('bluebush'), M.pyramidata (Benth.) ('blackbush'), and Atriplex vesicaria Benth. ('saltbush'). Many other Maireana spp. and Atriplex spp. occur subdominantly or locally dominant.

Acacia papyrocarpa Benth. ('western myall') is the dominant overstorey species, although several other tree species are dominant over significant areas or important to stock, including Casuarina cristata Miq. ('black oak'), Heterodendrum oleaefolium Desf. ('rosewood') and other acacias (A.burkittii F.Muell.ex Benth., A.ligulata A.Cunn.ex Benth., A.aneura F.Muell.ex Benth.). Myoporum platycarpum R.Br., Santalum acuminatum (R.Br.)DC., and Pittosporum phylliraeoides DC. are other notable tree species. Eucalypts are rare. Other common perennial shrub species include many Eremophila spp., Cassia spp., Dodonaea spp., Sida spp., Rhagodia spp., and Exocarpus aphylla R.Br. A number of 'heath' species occur in locally high densities on the hills.

There are a large number of small perennial, biennial and ephemeral species in the ground flora. Although many of these may be palatable to sheep, especially in their earlier growth stages, I do not list them all here. Two important components are the copper burrs (previously known as Bassia spp., but now split between the genera of Sclerolaena R.Br. and Dissocarpus F.Muell.), and the dominant perennial grasses, Stipa nitida Summerh. & C.E. Hubb. and Danthonia caespitosa Gaud. These plants form the bulk of ground material biomass as the vegetation dries out or dies back into summer. Further description of the vegetation of these regions may be found in Wood (1937), Black(1965) and Specht (1972).

(iv) Climate.

Climate in this area is dominated by a series of anticlines moving from the west, parallel with the southern Australian coastline, with a mean periodicity of about 6.8 days (Specht 1972). These result in repeated cycles of cool weather with southerly winds and clear skies, changing to northerly winds with hotter weather, followed by a rapid frontal passage, sometimes associated with rain, and a return to southerlies.

The 'mean' annual rainfall of the area is 200-250 mm, and varies over the 30 km length of the property. As is common in arid areas, the rainfall has high variability: Figure IV.3 shows the monthly long-term means for Whyalla, with the 10th and 90th percentiles. There is little seasonality in rainfall at Middleback in long-term averages, but individual years vary considerably. This may greatly affect the specific germination and success of different plant species (e.g. Austin et al 1981). Additionally, summer rainfalls tend to be heavy cyclonic storm events, whilst winter rain is more likely to be light and prolonged.

Figure IV.4 illustrates the monthly range and extremes of temperature for Whyalla; temperatures at Middleback are typically 2$^{o}$C higher during the day. January is the hottest month of the year, and July the coolest. Relative humidities are low, though dews and frosts may occur in winter. Winds are dominantly northerly or southerly: typical wind speed roses for Whyalla are shown in Figure IV.5 . Cloud density tends to be strongly correlated with the passage of frontal systems. These fronts sometimes carry very energetic winds, dust and lightning. Fires never burn far in the vegetation, but other

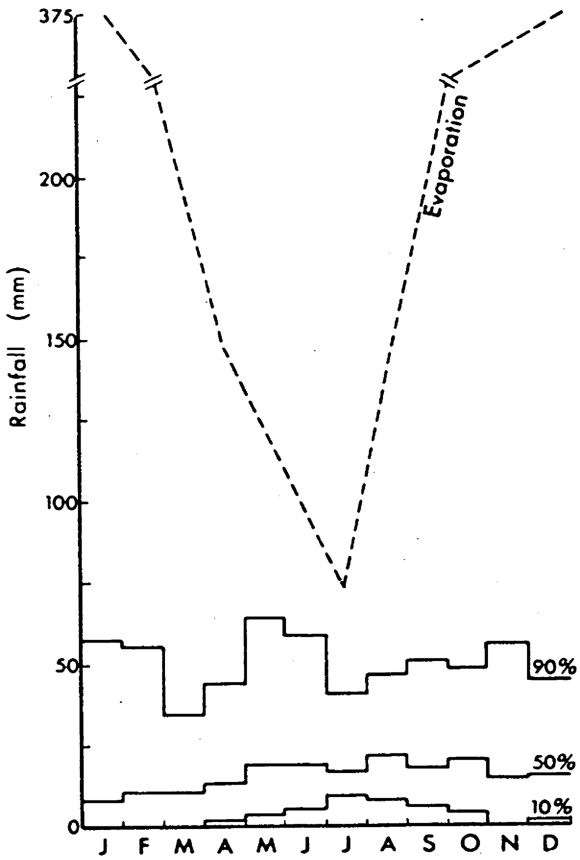


Figure IV.3: Mean and 10th and 90th percentile monthly rainfall 1931-60, and evaporation, for Whyalla (source: Laut et al.1977).

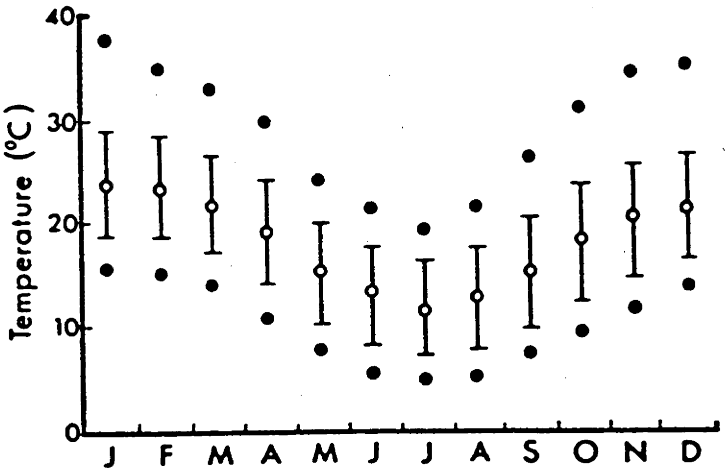


Figure IV.4: Mean monthly maximum, minimum, mean and 86th and 14th percentiles for temperatures at Whyalla (source: Laut et al.1977).

mechanical damage in these relatively rare storms may be important to plants, as well as bringing down branches which are often browsed by sheep.

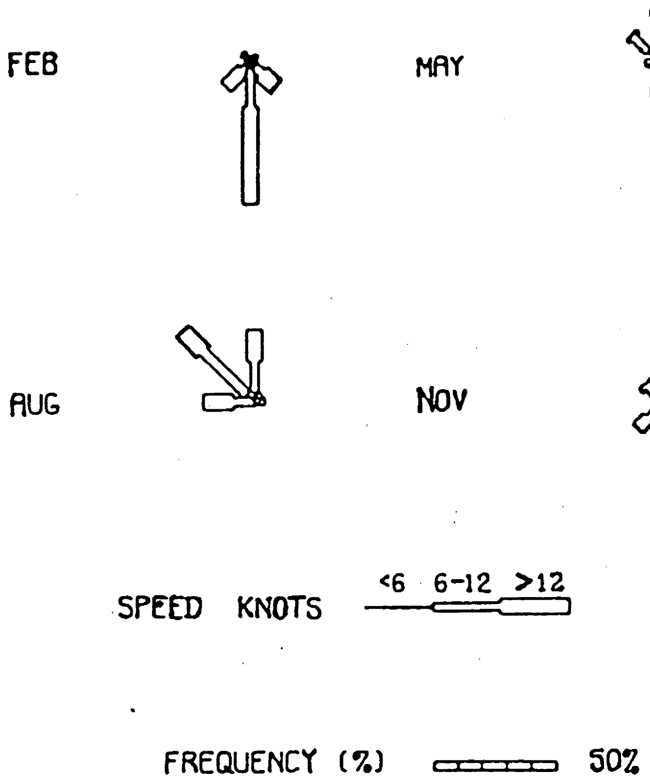


Figure IV.5: Wind roses for four typical months of the year at Whyalla, 1973-74 (source: Santos 1981).

The high variability and extremes of weather are typical of arid systems. Prolonged periods of high temperatures, including weeks over 40°C, or years of very low rainfall, occur intermittently and may be critical for plants and animals. Rare very wet years may be equally important for seedling establishment by some plant populations. These extremes of climate are just as important in modelling as 'normal' conditions.

## (v) Timing of fieldwork.

It is important to place any sampling period into the context of the conditions under which it was carried out. I made four fieldtrips a year of approximately one month duration each from early 1980 to mid 1983 (Table IV.1). Two trips were concentrated around summer, since this was the time of year that I expected to be most behaviourally critical for the sheep. Summer was also often more suitable for small enclosure work (see Chapter VIII), since there was relatively less ground material around. Further trips were made in autumn, and in late winter.

Table IV.1

Dates and primary activities of all fieldtrips.

| Year | Dates | Trip i.d. | Mapping[1] J | W | A | Small enclosure[2] | Dung survey[3] | Other |
|---|---|---|---|---|---|---|---|---|
| 1980 | May | A | - | - | - | - | - | veg'n maps |
| | Aug | B | c | - | c | - | - | - |
| | Nov-Dec | C | cf | c | c | - | - | - |
| 1981 | Jan-Feb | D | cf | c | c | - | Y[4] | - |
| | Apr-May | E | cf | c | c | Run 1 | - | s/flock tracking |
| | July | F | cf | c | c | - | Y | veg'n exclosures |
| | Nov-Dec | G | cf | c | c | Run 2 | - | - |
| 1982 | Jan-Feb | H | c | c | c | Run 3 | Y | heat balance |
| | Apr-May | I | cf | c | - | Run 4 | - | - |
| | Sep | J | - | - | - | - | Y | s/flock tracking |
| | Nov-Dec | K | f | - | - | Run 5 | Y | - |
| 1983 | Jan-Feb | L | f | - | - | - | - | water observ'ns |
| | Apr | M | - | - | - | Run 6 | Y | - |
| | Oct (10 d) | N | - | - | - | - | - | 24 h observ'ns |

[1] Paddock mapping (see this chapter): J=Jervoise, W=Wizzo North, A=Adam's West paddocks; c=coarse, f=fine (section c.ii)

[2] small enclosure observation Runs (Chapters VIII & IX)

[3] dung surveys (section d.iii): Y=survey carried out

[4] this dung survey was a dung pickup: remainder used the estimation technique.

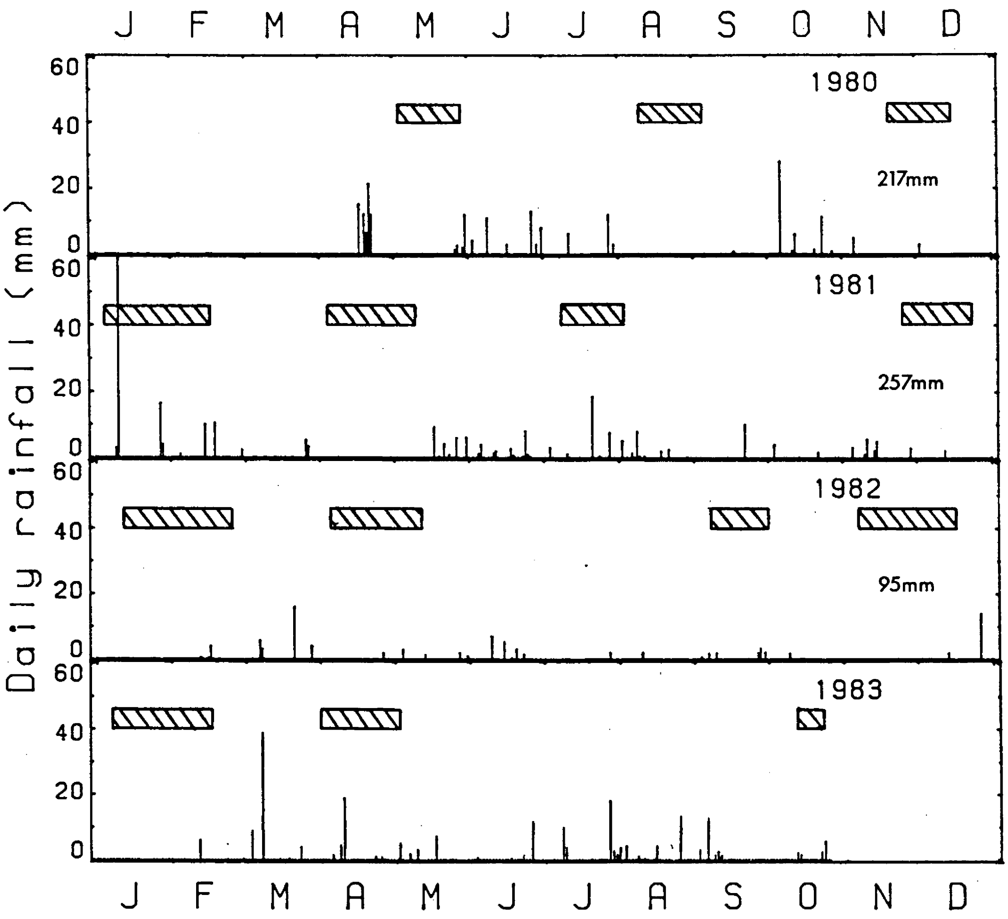


Figure IV.6: Rainfall over the years of this study, and the occurrence of fieldtrips (marked as hatched blocks).

Figure IV.6 shows the relation of these fieldtrips to rainfall. Most importantly, 1982 was considered to be one of the worst droughts in the memory of the local pastoralists (and for much of southeastern Australia). All dams dried up, and significant shrub mortality occurred independently of grazing. Rains in early 1983 alleviated the drought conditions, although soil moisture deep in the profile was very slow to recover.

## (b) Paddock-scale approaches.

In this section I review the approaches that were available for investigating behaviour large paddocks. I needed information on general spatial patterns of paddock usage under many conditions, with more detail about specific activities. There are three categories of approaches available in the large open paddock. These are a long-term 'cumulative' approach, a short-term intermittent sampling, and a dynamic, continuous tracking of individuals. I have used all three, and shall briefly discuss each in turn.

### (i) The long-term cumulative approach.

The long-term cumulative approach is based on information which integrates the lasting effects of animal activity over significant periods of time. These may range from months to years. At the longest term, there are the fenceline contrasts on aerial photos or Landsat imagery already mentioned. Such records are not referred to a particular climatic sequence, as it is not certain when the vegetation pattern may have developed; consequently, they cannot usually delineate critical periods, or the related behaviour patterns. The integration is over too long a period.

Over months to years, Lange & Willcocks (1978) have shown that dung accumulation may be used successfully to predict the relative amounts of time spent by sheep in different areas. It is not possible to be sure what activity was engaged in during this time, although the effects of shade, camp and water can be excluded by design. Seasonally-changing patterns of foraging and total ingestion on the part of the sheep necessitate a regular sampling program if data from different periods are to be compared. I have developed a dung estimation technique that is both quicker and covers a larger area than the method of Lange & Willcocks, and have used it to determine some general patterns of usage. This method has its own drawbacks, and is described in section (d.iii).

Vegetation sampling is another cumulative technique, which has special value for determining the impact of sheep on plants since it includes the effects of trampling and wastage. To get observable results in the open paddock, however, it usually has to be integrated over too long a period to highlight critical behaviour. I maintained some vegetation quadrats at various distances from a waterpoint which did show clear cumulative effects due to grazing during the drought.

### (ii) Intermittent, short-term sampling.

An intermittent, short-term sampling regime has often been used to study ranging behaviour of animals, as mentioned in Chapter II. Collection of data may be from the air, from ground vehicles or from stationary vantage points and towers. Regular aerial survey was not possible due to cost; it would be useful at times of grazing activity, especially early in the morning, but of little value when animals were in shade.

Data were collected from a stationary tower or Toyota roof rack near waterpoints, and hilltop vantage points were used on several occasions, especially for observing shade usage. In general, however, distances, topography and heat-haze were all too great for this system to be of use for observations over a whole paddock.

Mapping of paddocks from the ground, by vehicle or on foot, is cheaper, more flexible and provides similar information to other techniques. Its major drawback is that it is not always possible to keep track of individuals' movements in one part of the paddock whilst another area is being mapped. It was the technique I most commonly used, and details are described in the next section. The problem of keeping track of individual subflocks was partly addressed by marking a number of sheep in each paddock, and attempting to locate them in each survey. If maps are made frequently enough, and a reasonable number of subflocks can be re-identified each time, this method can be similar to individual subflock tracking.

### (iii) Individual subflock tracking.

The third approach provides the most detailed information, but is the most time-consuming for any given level of statistical significance. This method involves following the activities of one individual, or subflock, continuously. It is an approach commonly used in ethology, and has at times resulted in descriptive reports based on inadequate sample sizes. Since a full day can easily be used to obtain only one datum point for a final analysis, it can be very inefficient. At Middleback, these problems were compounded by the wild and wary state of the sheep which made close observations difficult without affecting their behaviour. There was insufficient time to train sheep at the paddock scale. This Heisenbergian risk of the observer confounding the observations, although possible in all the approaches mentioned, was certainly most significant here.

Despite these problems, the approach of tracking individuals has often been applied successfully, and statistically, in recent years.

Low et al's (1981a,b,c) observations of individual cattle in Central Australia are an example, and there are many others in the ethological literature. I did try to follow individual subflocks at times. I usually gained plenty of useful anecdotal information, but rarely any reliable data. Remote alternative methods were also tried, such as photographing a subflock's position regularly, and later using the photographs to relate vegetation quality to sheep activity. This was successful as far as avoiding disturbance was concerned, and failed to fulfill its purpose for different reasons (see Chapter VII).

### (c) Mapping procedures.

This section describes the paddocks in which ranging behaviour was studied, and the procedures used in the open paddock.

#### (i) Paddocks used.

Wertigo, the paddock that was used in the original model construction, was ideal for observing sheep flocks, because it was almost flat, and had low vegetation and good visibility. However, the homogeneity and particular layout of the paddock masked some details of sheep behaviour. Additionally, the management of Wertigo had changed since the previous study, so that it was no longer suitable for work.

I needed to use paddocks with some variety of vegetation pattern, but with reasonable visibility, and in close proximity to each other so that I could examine several in a day. Three paddocks were located on Roopena which satisfied these criteria adequately, and most of the data to be discussed was derived from these. They are 'Wizzo North', 'Jervoise', and 'Adam's West'. Another paddock, 'West End', would also have been suitable, but was too far away from any others; however, it was used for some other observations. Some mapping was also done in 'Two Mile' paddock, near Middleback homestead, since other people were doing work there simultaneously. These paddocks are outlined on Figure IV.2.

Some important characteristics of the three main paddocks are summarised in Table IV.2, and the schematics used for mapping sheep in them are illustrated in Figure IV.7(a-c). Jervoise was selected as the most amenable for detailed study, being smallest, least wooded, and

Table IV.2

Some characteristics of the main study paddocks. D is the approximate distance that would normally be travelled to map the paddock in a 'coarse' mapping run. The number of sheep is the typical stocking rate during mapping observations.

| | Approx. size | | No. waterpoints | | Sheep | | D |
|---|---|---|---|---|---|---|---|
| | Area (ha) | Dimensions[1] (km) | Permanent | Dams | No. | Type | (km) |
| Jervoise | 1250 | 5.7x2.5 | 1 | 2[2] | 250 | ewes | 12 |
| Wizzo North | 3600 | 6.0x6.0 | 2[3] | 2[3] | 400 | ewes | 18 |
| Adam's West | 2600 | 6.0x4.0 | 2 | 1[4] | 350 | wethers | 20 |

[1] as if rectangular
[2] very small: these never contained water during mappings
[3] variously available, see Chapter VI(c)
[4] this dam was only briefly dry, and then water was piped in

central: a campsite was established near to it (in Honeymoon paddock) to facilitate early morning observations. The waterpoint in Jervoise is unusual in being in the northeast corner of the paddock: this resulted in some interesting pattern developments in the vegetation, but also in some loss of generality.

(ii) Mapping and sheep activities.

Mapping of a paddock was carried out by driving around as much of the paddock's trackplan as was necessary to find the majority of the flock within the paddock, and marking their positions on the map. Either a Toyota Land Cruiser or a 200 c.c. bike was used for this, although Jervoise was sometimes surveyed on foot. To examine the whole paddock usually required between 40 and 60 minutes. Care was taken to avoid any duplication of groups over this time, and a minimal observation was always recorded. The sheep could be frightened by my

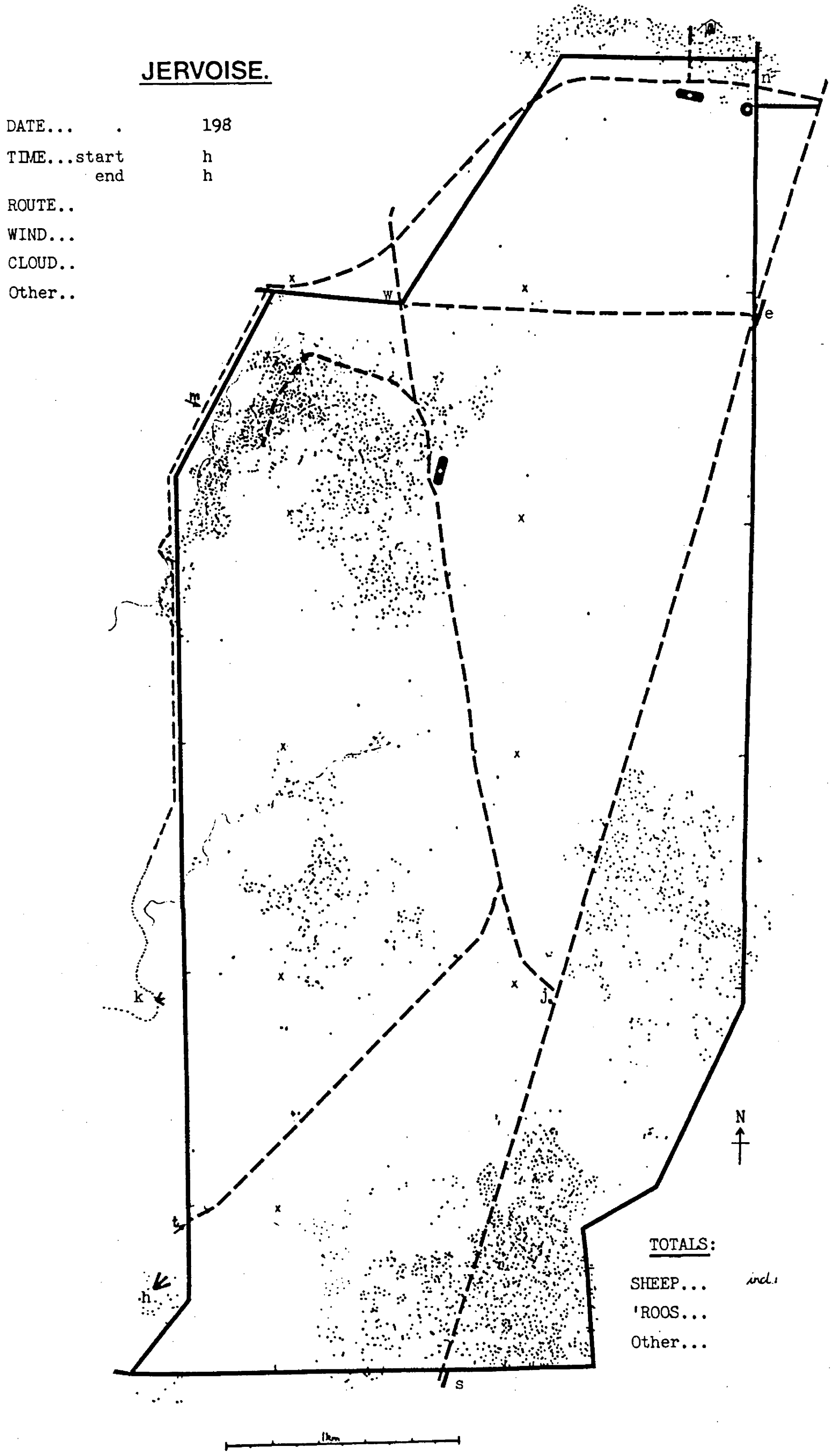


Figure IV.7: (a) schematic used for mapping Jervoise paddock. Dots are trees, solid lines are fences, dashed lines are tracks, letters are identification points for the route description, x's mark 1 km grid posts. The main waterpoint is the circle in the north east corner; oblong symbols are two small dams.

Wizzo North

DATE: . 198 .

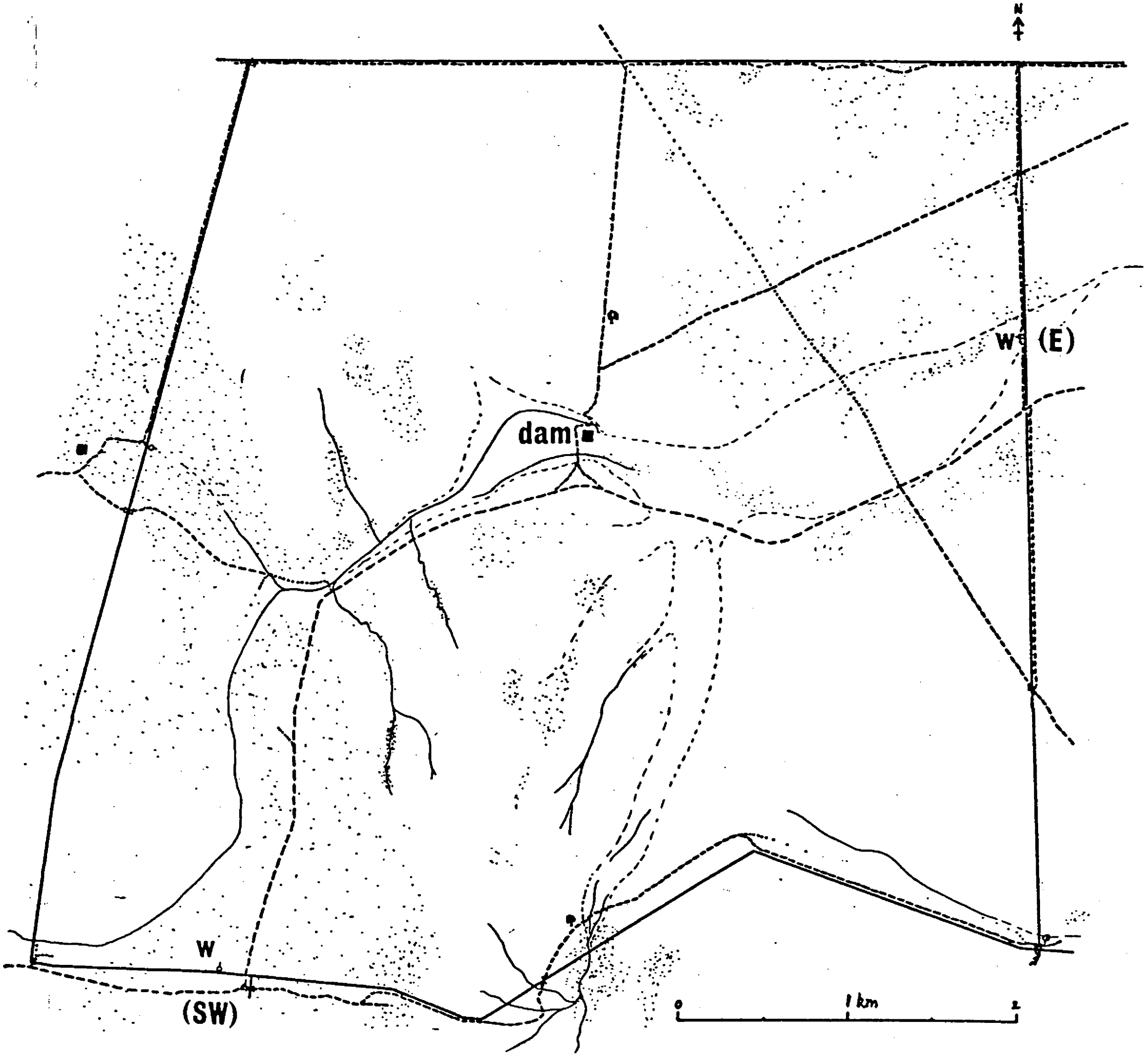
WIND...

CLOUD..

Other..

TIME: start.. h

end.. h



TOTALS: sheep incl.

other.

Figure IV.7: (b) schematic used for mapping Wizzo North. Symbols similar to (a), except solid squares are dams, w marks permanent water-points, and water-courses are outlined.

**ADAMS WEST**

WIND....

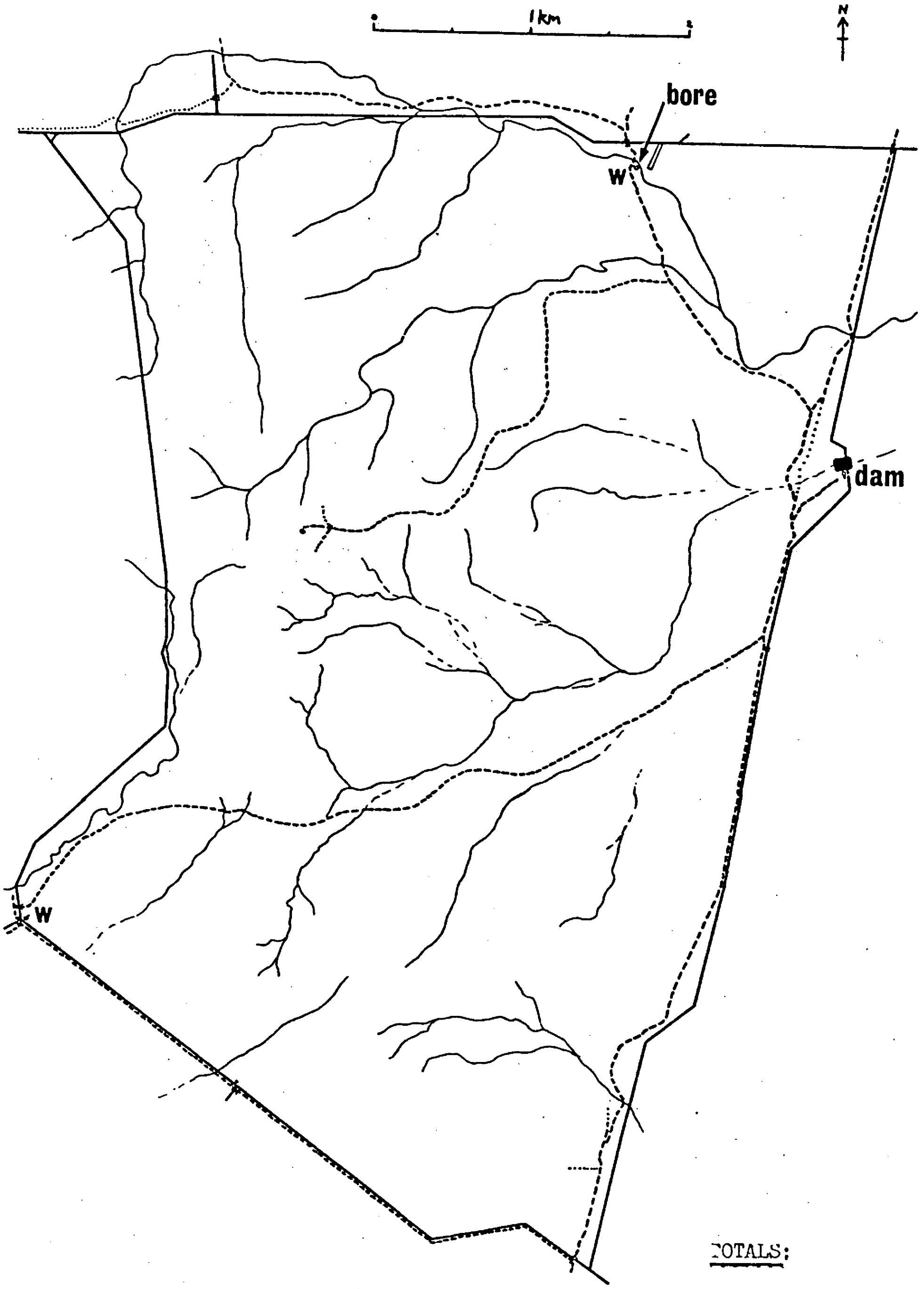
CLOUD...

Other...

DATE: . 198 .

TIME:start.. h

end.. h



TOTALS:

sheep incl.

other...

Figure IV.7: (c) schematic used for mapping Adam's West. Symbols similar to (a), except the solid square marks the dam, w marks permanent waterpoints, and no trees are shown. The water-courses rise in a range of hills down the west and south sides of the paddock.

presence: they did not usually move far, and I took great care to avoid disturbing them.

At the position of a group of sheep on the map, four characteristics were noted: the number of animals counted in the group, the general activity of the group, the direction of movement of the group (if any), and any marked sheep seen in the group. On most fieldtrips 15-20 sheep in each paddock were spray-painted in individually recognisable patterns with scourable dye. These 'marked sheep' could be identified at up to about 1 km if fully visible, but it was not often that I could locate many of them. However, they helped confirm flock movements.

Mapping sequences are categorised as either 'coarse' or 'fine'. Each sequence usually consisted of evening maps for day 1, maps all day for days 2 to 4, and morning maps for day 5. In coarse sequences, I mapped all three paddocks three times a day. Thus the coarse sequences consist of an early morning, middle of the day and late afternoon survey each day for each paddock. These were intended to characterise the general patterns of sheep activity and movement over each paddock, and extra effort was not expended in finding every individual sheep.

For the fine sequences, I mapped Jervoise only, usually 7 times each day. These maps were intended to include, as near as possible, all sheep, and to give a better idea of the sequence of activities of individual sub-flocks. Two maps would be made close to dawn, one mid-morning, one at midday, one mid-afternoon, and two around sunset; this corresponded to departure from campsites to graze, the end of morning grazing and movement to rest or shade, presence at rest or shade, departure from rest or shade to graze or to water, and evening watering or grazing.

The first survey of the day was begun at first visibility, usually about 40 minutes before dawn, and the last was finished after sunset. Grazing and movement certainly occurred in the dark but this could not be determined except by inference and occasional chance encounter. I rarely saw every sheep in the paddock: visible animals could not always be counted exactly, and only a few individuals were usually visible in shading groups. In Jervoise I usually found most groups, but could not always count exact numbers; in the coarse records, the reliability of group location is reduced too.

Table IV.3

Activity codes used in paddock mapping, and their descriptions.

| Code | Name and description |
|---|---|
| c | camping (night-time resting) |
| r[1] | resting (resting in the open during the day) |
| s[1] | 'shading' (resting in the shade during the day) |
| g | grazing (0-25% of the group moving at any time) |
| gm | grazing with movement (25-50% ditto) |
| mg | moving with grazing (50-75% ditto) |
| m | moving (75-100% of group actually moving) |
| w | watering (within water enclosure, or drinking at dam) |

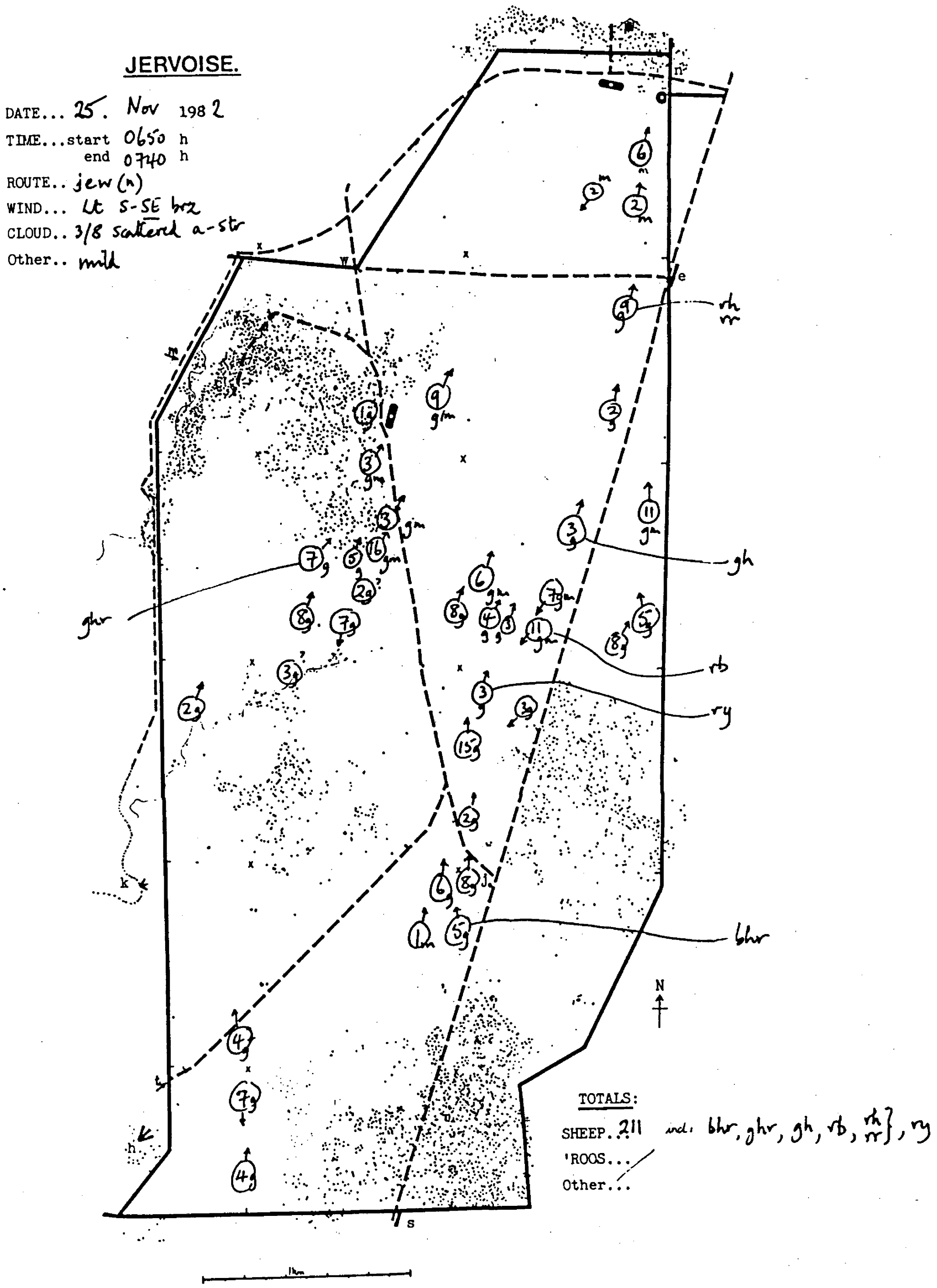
[1] sheep may be lying or standing, but majority are inactive

The activity codes used here are listed in Table IV.3. They apply to the majority of a group. 's' for shading implies the definite use of a shade site with some sheep in 'shade' even when the weather might be cloudy. 'g', 'g/m', 'm/g', 'm' make up a sequence with increasing movement during grazing until most of the sub-flock is walking. In most cases a definite direction of movement was evident, based on the direction in which the majority of the sheep were facing, although none could sometimes be determined for activity 'g'. 'c' for night-time camping is equivalent to resting ('r'), but before dawn, and usually at a specific site.

Weather conditions were recorded at all times of mapping, and a note was made of the route that was taken. A typical completed map for Jervoise on 25.11.82 is shown in Figure IV.8. The occasions of coarse and fine observations were summarised in Table IV.1. Observations were least regular in Adam's West, where management of stocking rates was most affected by the drought. At the height of the drought, patterns of movement were so rigid during the day that the frequency of mapping was generally reduced: more activity was occurring at night, but attempts to define it were unsuccessful.

### (iii) Analysis of mapped data.

About 400 maps, representing 81 days in Jervoise, 39 in Wizzo North and 41 in Adam's West, were made during the course of the study. Subflocks in Jervoise had been marked on maps to within 100m, and in Wizzo North and Adam's West to within about 300m. The approach taken to reduce this data for analysis was based on the structure of the model. A grid (500x500 $m^2$ for Jervoise, and 1x1 $km^2$ for the other paddocks) was superimposed on each map, and the location and activities of groups in each cell were recorded. Computer programs were written to analysis this data, taking account of marked sheep, activities and movement directions, as well as numbers and locations of sheep. The grids used for Jervoise and Wizzo North are shown superimposed on the paddock outline in Figure IV.9. Some forms of more detailed analysis, including tracing the movements of subflocks, were performed by



**JERVOISE.**

DATE... 25. Nov 1982
TIME...start 0650 h
end 0740 h
ROUTE.. jew (n)
WIND... Lt S-SE brz
CLOUD.. 3/8 scattered a-str
Other.. mild

TOTALS:
SHEEP. 211 incl. bhr, ghr, gh, rb, rh rr}, ry
'ROOS.../
Other...

Figure IV.8: A completed survey map of Jervoise for 25.11.82. Subflocks are indicated by circles containing the numbers of sheep counted in the group and the group activity; the arrow indicates the direction of movement, if any, and marked sheep are noted on the side of the map.

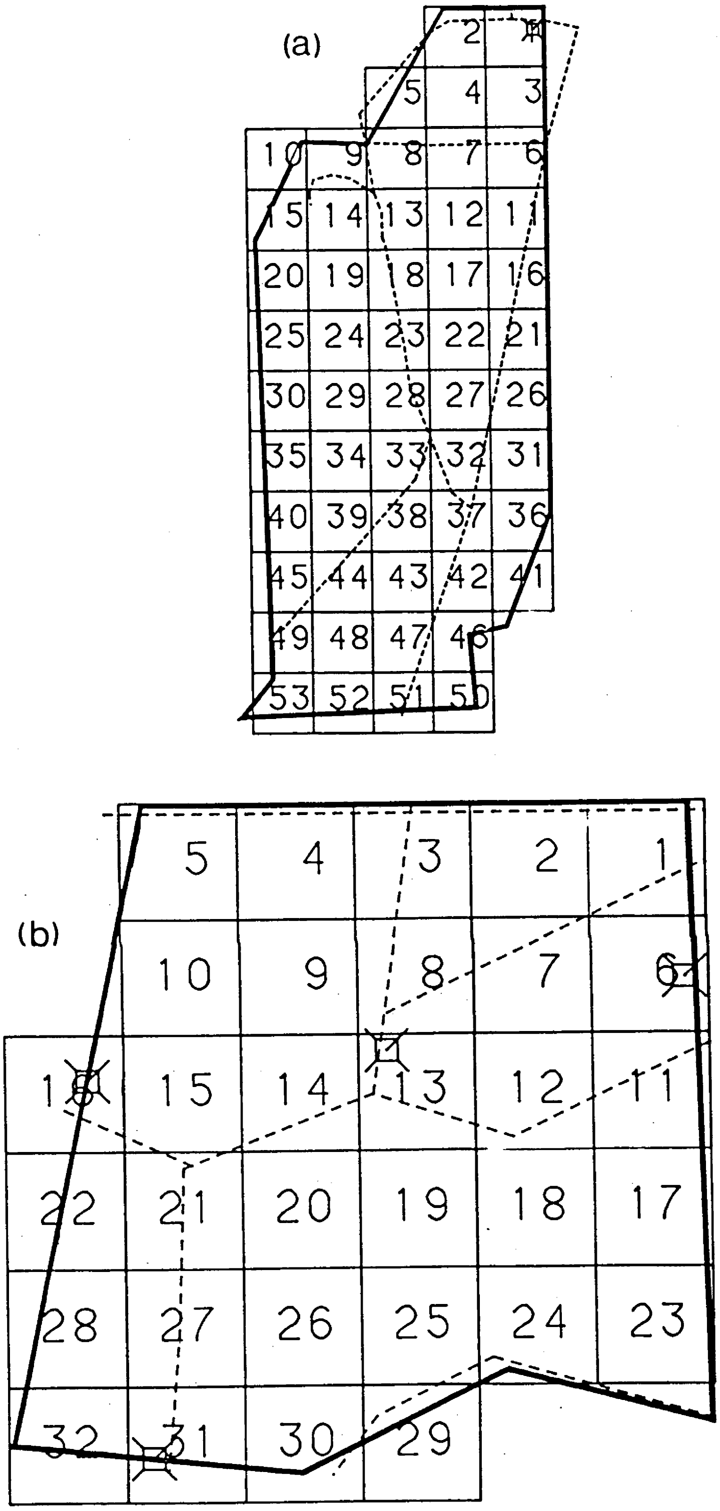


Figure IV.9: (a) the 500x500 $m^2$ grid used for Jervoise, and (b) the 1x1 $km^2$ grid used for Wizzo North, shown superimposed on the computer-generated paddock maps. The cell numbers are often referred to in other chapters, and alternate versions of these maps are bound inside the back cover for easier reference.

recourse to the raw map information.

A general problem in ethology is that of how to characterise the spatial distribution and intensity of the ranging behaviour of animals. In this study, most of the paddock can be reached by the sheep at some times, so that an outer absolute limit to their range at the fenceline is not meaningful. Furthermore, I need to be able to compare their activities under different conditions, but centred on the same supposed 'range'. It is possible to contour-map the numbers of animals (or groups) found in different cells. It is better, however, to use some form of moment to both define a centre of activity and to smooth outlying data into a probability function for usage density.

Anderson (1982) summarises a number of methods of describing home range, but the methods are generally too sophisticated and detailed for the data here. Many of them involve arithmetic means, which suffer from being singular; because of this, they can predict a peak of activity in an area that is really midway between two centres of activity.

An alternative method is described by Dixon & Chapman (1980), which I have generally adopted. This is the harmonic mean moment, which sums the harmonic means of the moments to every animal in the range from each cell on a grid of unspecified dimension, that is,

$$M_j = N / \Sigma_{i=1,N} (1/r_{i,j}),$$

where $M_j$ is the moment to the jth cell of all the distances $r_i$ to the ith of N animals (or groups) in the paddock. The result of this algorithm is to obtain a value for each cell considered; these values may be used as a smoothed function on which to draw isopleths of equal 'activity' (actually in units of distance), and minima may be located which correspond to centres of activity. Dixon & Chapman state that the measure is quite stable to grid dimension, the magnitude of which limits only the accuracy with which minima can be located.

This method is ideally suited to the format of my data, for which there is an obvious choice of grid cell size, and it has several other advantages. Amongst the most important of these is that it can define multiple centres of activity (after inspection), which is essential when, for example, two waterpoint are in use. I have used this measure on paddock maps of activity in Chapters V, VI and X. Note that it is possible to analyse by moments to individual sheep, or to subflocks. In different situations, each method is likely to have its biases as a result of observation techniques; I use numbers of groups usually, since the group is the primary unit of movement for the sheep.

Classification is a quite different approach which treats each grid cell in the paddock as an observational entity. I have attempted to use two techniques of this type on the gridded data. Firstly, it is possible to treat each cell of the paddock as an independent observation in characterising one map record, and perform a principle coordinates analysis on the data (Austin, pers.comm.). This is something of a hit and miss method, in that it is only possible to interpret the results usefully if the principle vectors correlate with any extrinsic variables considered to be of importance. I did not find the method successful.

Alternatively, each cell entry may be regarded as an independant observation, characterised by certain descriptive features of that cell. Discriminant analysis may then be used to examine which of the cell characteristics are important in predicting the presence of sheep in the cell. This method of analysis is used in Chapter V to examine which cell characteristics are important in the patterns of ranging.

### (iv) Dung survey.

The use of dung as an indicator of activity has been mentioned in Chapter II and section (b.i). Regular sampling of cleared quadrats, preferably at monthly intervals, is necessary for the technique of Lange & Willcocks (1978). I could only sample intermittently at much longer intervals, when the dung pick-up method becomes much more time consuming and much less reliable. I made one dung pick-up at 50 quadrat sites in Jervoise in February 1981, which took about seven full days to complete. In consequence I developed a rapid estimation technique that allowed me to cover a much larger sample area (about 1/250th of the paddock, compared with about 1/1250th in a thorough pick-up sample) in one day and about 30 km of walking.

This method involved what I have termed 'egestion event estimation', in which each pile of dung found in a 2 m wide transect walked across the paddock is counted as one egestion event (E.E.). Lesser amounts are counted in quarters of an event, and the total rounded and recorded every 250 m. I had previously positioned a steel post at the centre of every 500x500 $m^2$ grid cell in Jervoise (see Figure IV.9), so it was possible to pace between these, back and forth across the paddock. Two 250x2 $m^2$ transect estimates were then summed to give the cell mean, and the result expressed in thousandths of the total number of E.E's seen over the paddock. This data was collected on 5 occasions (see Table IV.1).

On one occasion, I compared my estimations using this method with the dung picked up shortly afterwards at fixed dung quadrats in Two Mile paddock at Middleback by Mr David Thompson; his collections were part of a regular monthly survey at Middleback, and I am grateful for access to this information. My estimates correlated well with his dry weights (Pearson's correlation, $r = .98$, $n=32$, $p<.0001$), even though the quadrats were smaller than those that I use in the open paddock, and fixed errors in the technique (such as rounding approximations) were therefore exaggerated. In Jervoise, four repeated transects, parallel to each other but differing in line, and containing about 30 E.E.'s, proved to be consistent to within 3 E.E.'s: similar consistency was found on other occasions. Additionally, the values for the two quadrats that were combined to define a cell in the actual data collections usually agreed well, except where there were good reasons for expecting a sudden gradient. Finally, the resulting patterns did reflect in the general spatial patterns of usage by the animals at the time.

The method has three drawbacks. Firstly, for walking at a steady pace, it was found very much less reliable in strong sunlight, when high contrast resulted in dung pellets easily being missed, or mistaken for pebbles. Sampling therefore had to be confined to overcast days, which meant that on some fieldtrips no survey occurred.

Secondly, the age of the dung that is being estimated is unknown, unless some samples are regularly marked from known dates. Ageing of dung is greatly accelerated by rain. I normally limited my estimation to 'fresh' dung, which I defined as retaining some black patina: this represented a significant error in the technique. The data therefore refers to an unknown time period previous to the survey date, but usually between 2 and 4 weeks. This is long enough to include a variety of weather conditions, so that sheep ranging activity should be reasonably averaged.

Finally, as with any dung technique, one cannot know what activity is being engaged in at the time the dung is deposited. I avoided known camp and shade sites, as well as the waterpoint itself, in my quadrat routes, but the activity sampled included both extensive grazing and movement, and resting in the open.

(v) Heat balance and shade usage.

Chapter VI(b) and the Appendix will refer to work which investigated when sheep move to shade: the conclusions are based partly on a model of sheep heat balance, which is derived from Noble (1975) and described in the Appendix, and partly on open paddock observations of time and degree of usage of shade. Observations of times of entry to, and departure from, shade, as well as preceding and subsequent activities, were derived from the maps discussed above, both by examining the mean patterns of activity of a paddock's flock, and by following individual groups that could be identified between maps. Proportions of sheep actually in shade were obtained by observing the flock in Adam's West paddock from a vantage point on a central hill. It was possible to track the activities of most of the paddock's flock throughout days when they were using shade in the mid-eastern area of the paddock. Records of activity followed those described above.

(vi) Waterpoint observations.

In summer 1982-1983, an attempt was made to relate patterns of movement of individual sheep into a waterpoint with their patterns of departure. With the help of Mr Paul Jupp, a student from the A.N.U., I obtained records of arrivals and departures of all sheep at the eastern trough in West End paddock and at the Jervoise waterpoint for 11 and 3 days respectively. Directions, speeds and times of movement were recorded, and the presence of any of 20 marked sheep was monitored. The observations in West End were carried out from a 6 m tower (to which the sheep had become acclimatised), and included two overnight watches. It was intended both to relate arrival and departure patterns, and to record individual watering frequencies for sheep in open paddock conditions. The former aim was not successfully met: the data is discussed in Chapter VI(c).

### (vii) Jervoise water meter.

The Jervoise trough is fed from the Morgan-Whyalla pipeline, which passes some 3 km away, rather than from the Roopena well. Its water is metered on entry to a tank which then feeds the trough. The inflow rate from the pipeline is slow relative to the rate at which the sheep can drink from the trough, and the tank is designed to buffer this difference. In consequence, the reading on the pipe meter can be lagged by several hours relative to the consumption by the sheep, depending on how recently drinking has occurred. Whilst I was mapping, I usually recorded the reading once a day, and Mr David Illman, the Roopena station hand, kindly took recordings at other times of the year. Because of the lag, the details of readings are not reliable, but do provide a general indication of water intake during 1980-1983. The readings do not distinguish which type of animal is watering, but the background rate of kangaroo watering (determined at shearing time when there were no sheep in the paddock for about 3 weeks) was low in comparison to the sheep. These data are discussed in Chapter VI(c).

(viii) Subflock tracking.

Some tracking of individual subflocks in the open paddock was attempted, in order to test certain of the small enclosure findings. Most important was the relation between movement speeds in grazing and vegetation quality. Two methods were tried, and these are discussed in chapter VI, since the methodology relates to their success.

## (d) Vegetation assessment and other data.

In this section, I briefly describe other sampling techniques used repeatedly, including biomass estimation, and the derivation of paddock vegetation maps. Sections on meteorological data and computing then complete this catalogue of methods within one chapter. The other major section on methodology - in small enclosures - is to be found in Chapter VIII.

### (i) Biomass estimation.

It was often necessary to make an assessment of the edible and available component of the vegetation; this was carried out using the method of Andrew et al.(1979) for shrub biomass estimation, based on a handheld comparison unit. This unit can be standardised in several ways both for between-days measurements, and to obtain absolute estimates of biomass. All methods were used at times, depending on the accuracy needed.

The most accurate method is an extension of that recommended in their paper. A standard run of about 20 shrubs, encompassing the range of condition and size of those to be estimated, is established somewhere convenient. Each shrub in this standard run is re-estimated with the hand-held comparison unit between measurement runs. At the end of the measurement period, these bushes are stripped of foliage by hand, and the resulting material is oven-dried at 80°C. The dry weights are regressed against the standard estimates for each trial to provide an estimator of the size of the unit for that run. Not all of the bushes in the standard run need be stripped - large numbers merely serve to reduce the chance of remembering previous counts.

A similar method was used for estimating the biomass of grasses on some occasions, in which a run of 1x1 $m^2$ quadrats was used for standardising a handheld clump; this unit was then used in the estimations, and the quadrats were later clipped. The method was less accurate for grasses than shrubs. A co-sampling method, also described by Andrew et al.(1979), was used for assessments that required less accuracy (e.g. open paddock measurements).

I performed some special trials, and regularly assessed my accuracy of estimation using these methods, but I do not present details here. In summary, I found that repeated sampling within a day (e.g. contemporaneous comparisons between adjoining enclosures) had a repeatability of better than 5%, whilst for between-day comparisons (e.g. enclosures on successive days), or absolute estimates (i.e. correcting from estimated units to absolute dry weight biomasses), the figure was better than 10%. The co-sampling technique had an accuracy of only 15-20%, but it was always used in conjunction with a normal standard run (which was not stripped), so that comparisons were 5-10% accurate even though absolute quantities were worse.

### (ii) Paddock vegetation classification.

Vegetation monitoring in the open paddock was done in two ways. In May 1980, an estimation was made of the biomasses in two 50x1 $m^2$ quadrats at each of 22 sample sites scattered across the main study paddock, Jervoise. Using other ground observations and aerial photographs, divisions between vegetation associations were established over the paddock, primarily on the basis of differences in the shrub layer. These major vegetation associations are described where they are used (Chapter V (a)); the absolute biomasses are used as baseline data in model runs (Chapter X).

Fixed quadrats were also established over Jervoise paddock and in the Chimney Yards (further south) in July 1981 to monitor general trends in the condition of the vegetation. In Jervoise, open quadrats were placed at distances of 125, 250, 500, 1000 and 2000 m from the waterpoint, with additional fenced quadrats at 250, 1000 and 4000 m. There were two fenced quadrats in the Chimney Yards.

Initially a major sampling programme for both ephemeral biomass and perennial shoot growth was established in all of these, but it was found too time-consuming to obtain useful samples. In consequence, only a sequence of photographs was maintained unbroken: an ordered index of vegetation condition was obtained from these using the method that Noble (1977) developed for the Koonamore Vegetation Reserve photos. This index adequately showed the trend in the condition of the perennial vegetation through the drought, as well as the presence or absence of an ephemeral layer. The sequence out from the waterpoint also clearly showed some grazing effects as the drought intensified: this series is used for validation of the model.

### (iii) Meteorological data.

Daily rainfall is recorded at both Middleback and Roopena homesteads. I maintained an additional rainguage in Jervoise, since storms can be locally very variable. In fact, the Jervoise readings parallelled those from Roopena, except for one 12 mm event at Jervoise which hardly registered at the homestead 10 km away. The readings at Middleback are often noticeably different to Roopena's, so I use the latter for most purposes.

Other meteorological data was collected intermittently at Middleback homestead by residents at the field station, in particular by Mr David Thompson, to whom I am indebted. Maximum and minimum daily temperatures, wind direction and daily run, some indication of cloud cover, and occasional relative humidity readings were recorded. Continuous records were kept during fieldtrips, but an average of one day in ten is missing at other times. Meteorological records are also available from Whyalla, but the town is more affected by sea breezes than is Middleback.

In late 1982, an automatic weather station was installed at Middleback by the A.N.U. This station is based on a Campbell Scientific Inc. CR21 Micrologger, and stores hourly temperatures (air, ground surface and at 10 cm depth), wind runs and directions, and solar radiations on magnetic tape. Soil moisture and rainfall are also monitored. This data was accessed for the later fieldtrips, and for some of the model validation referred to in the Appendix.

### (iv) Computing.

This section is not directly related to fieldwork practicalities, but is relevant to data analysis and figure production. On most field trips, an Horizon micro-computer with NorthStar BASIC software was used at Middleback for direct dumping of records collected in the field, and for a considerable amount of preliminary analysis. In Canberra, most of the major data analysis was done on the Univac 1100/80 at the Australian National University. I used many of my own FORTRAN programs, a data-handling package of I.R.Noble's called 'DAPR', and occasionally the systems packages 'GENSTAT' (Alvey et al.1982) and 'SPSS' (Nie et al.1975). Graph plotting was mostly done using H.N.Comin's package, 'GRAFX', and all the paddock figures on my own data handling and plotting package, 'PLOTPAK'.

# Chapter V.

## Factors affecting ranging behaviour in the open paddock.

In the previous chapters, I have described the importance of ranging in determining the pattern development of grazing impact in the open paddock. I have also outlined the approaches available for studying the subject, and those that I have used.

These approaches, and the model, assume that only a few variables will have an important influence on ranging behaviour at the open paddock scale. In this chapter I use my map data to test whether this assumption is justified. After discussing which variables may be important, I show that the area of the paddock in use is primarily influenced by distance to water and the other foci of non-grazing activities. I then examine flock structure, and the impact on it of universal variables such as climate and time of year.

This chapter is a post hoc look at observational data, although there are a priori reasons for expecting certain relationships. This approach is inevitable in examining the general influence of many variables on a few descriptors of a whole system, when, in reality, the variables are interacting in a very complex and detailed fashion. The approach to more detailed process is to be found in later chapters.

## (a) Factors likely to be important.

Factors which might influence the ranging behaviour of sheep in a large arid zone paddock may be divided into three categories: those that are intrinsic to the sheep themselves, those extrinsic to the sheep and varying in space in the paddock, and universal variables that vary in time.

### (i) Factors intrinsic to the sheep.

This chapter's analysis does not, on the whole, consider sheep individually. Most factors intrinsic to the sheep are likely to vary synchronously within the flock. The most universal of these is wool-length, which, due to management procedures, is about 7 mm in early March, growing to about 75 mm by the middle of the following February, when shearing again occurs. Clearly this will be confounded with season.

It is possible that all sheep show some physiological adjustments to the extremes of temperatures during the year (i.e. night-time cold in winter and afternoon heat in summer): by definition this will be confounded with season, or such variables as monthly mean temperatures. Other physiological effects, which may be almost universal, are those associated with lambing. In general, I tried to avoid the lambing period, but lambs were suckling during the winter observation periods. There was an increase in numbers of subflocks that was partly related to this, since the increase was less evident in Adam's West, the wether paddock. Rams were in the paddocks during late summer observations, at about 3 per 100 ewes. They appeared to have no effect on most groups: when in oestrous, the ewes seem to individually search out the rams. The sparser records from Adam's West paralleled those of the ewe paddocks at this time of year, and it is assumed here that there was no effect of the rams.

It is possible that there are some interactions between factors intrinsic to the sheep and spatial factors. For example, the need of some sheep to water could be affected by the area of the paddock that they habitually use. Cattle on the Barkly Tablelands are known to include cows that will stay relatively close to water, and others that will walk out before starting to graze under the same conditions (Yeates & Schmidt 1975), and I examined whether any similar effects might be important in Jervoise.

A few sheep that are usually obviously ill or lame do not move far from water, but these represent a very small minority of the flock. Amongst the bulk of the flock, the marked sheep data does not support a division between 'walkers' and 'non-walkers'. Figure V.1 shows the number of times that four particular marked sheep were seen in the different cells of Jervoise during the Nov-Dec 1980 fieldtrip. I have selected two showing the widest ranging seen, and two showing the least, for similar numbers of sightings. Although some differences can be seen, they are not significant in comparison to potential sampling errors; no records show any clearer differences. The harmonic mean centres of activity for all four are in or next to cell 4 (see Figure IV.9).

Different sheep certainly show different ranging distances within a given day, but there is no evidence at the moment that this relates to consistent differences between healthy individuals between days. I may have failed to have marked or observed an animal in the non-walking

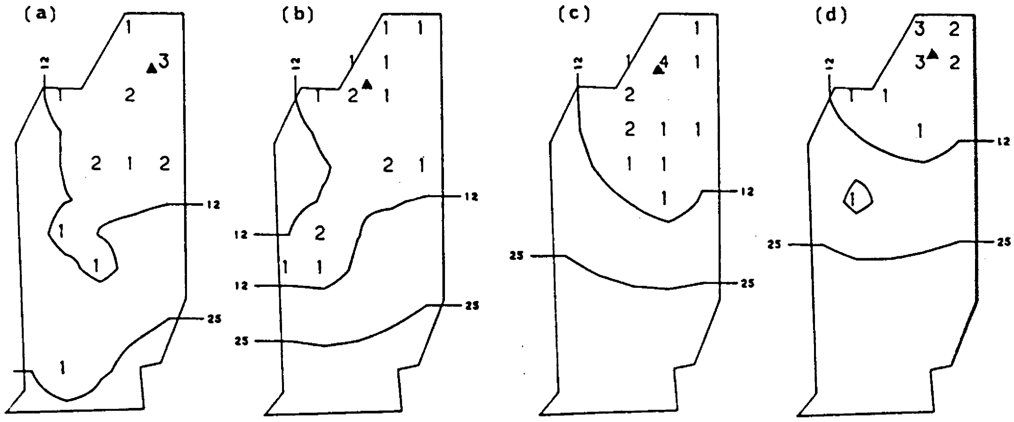


Figure V.1: Some 'extremes' of marked sheep ranging during Nov-Dec 1980. Maps of all sightings of four marked sheep, two showing maximal movement (a,b), and two showing minimal movement (c,d) for similar numbers of sightings. Numbers are numbers of sightings per cell, contours are isopleths of equal activity (by harmonic mean moments). The solid triangles mark the centres of activity (the cell with minimum harmonic mean moment).

class, but the sample size is reasonable (viz. 20 marked sheep in ca. 250, re-chosen on 6 out of the 10 mapping runs). I therefore assume subsequently no special propensity by individuals to overuse particular areas of the paddock.

### (ii) Spatial factors.

There are many spatial characteristics of each cell that might affect the probability of sheep being found in that particular cell. Vegetation type, and distance to the various foci of non-grazing activities are obvious ones. The vegetation in Jervoise had been mapped in May 1980 (Chapter IV(d.ii)), and Figure V.2 shows the resulting vegetation map of the paddock. On the basis of this, all the cells were classified into one of six vegetation types, which fell into the three broad categories of bluebush plain, stunted saltbush hill vegetation, and run-on areas (including washes) usually characterised by some blackbush. Table V.1 shows the details of these categories, and the names I use for them in this chapter. Additionally, the presence of heavy timber was noted as a separate character to the presence of shade; the heavily wooded areas often have a lower density of shrubs of the local vegetation type, as well as different plant species under the canopies, and the possibility of significant browse.

Table V.1

Major vegetation types in Jervoise, and my abbreviations. Codes are those used in Figure V.2: 2 and 3 are both hillside types, whilst 4, 5 and 6 are run-on areas.

| Name | Code | Description |
|---|---|---|
| BB/SB | 1 | Tall Bluebush/Saltbush plains |
| SB/BB | 2 | Hillsides dominated by low saltbush, but with substantial bluebush (including M. astrotricha), stony shallow soils. |
| SB(BB) | 3 | As SB/BB, but scattered bluebush only. |
| SB/PYR | 4 | Tall blackbush/saltbush run-on and watercourse areas, often sandy soils, significant for ephemeral growth. |
| SB(PYR) | 5 | Saltbush-dominated run-on and watercourse areas, with scattered blackbush only. |
| 'SWAMP' | 6 | Low-lying swampy area in cell 22, with few shrubs except scattered Muehlenbeckia cunninghamii. |

The three important foci I have mentioned are the waterpoint, shade and campsites. Distances to the nearest of each were used as additional cell characteristics. Note that shade availability does not correlate highly with heavy wood, since many cells with a small

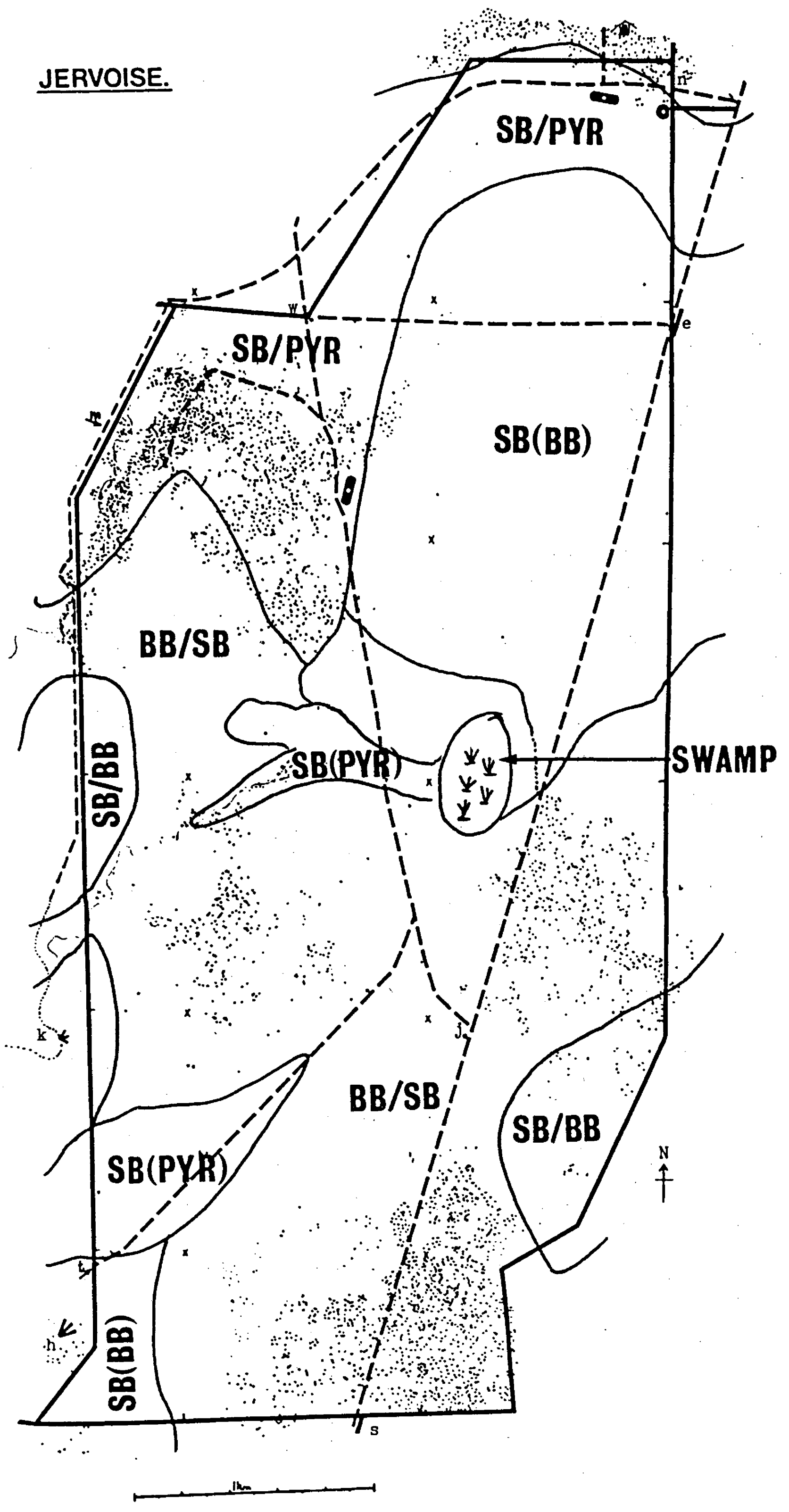


Figure V.2: Vegetation map of Jervoise paddock: abbreviations for vegetation categories are given in Table V.1.

number of trees still provide shade sites. Only the major campsites were considered (see Chapter VI(d) and Figure VI.9). If ranging is severely curtailed by fencelines, these may also have an influence, so the presence of an E-W or a N-S fence line is included.

There are other characteristics that might be important, but which are confounded with those already mentioned. Some cells carry more ephemerals after rain: these correlate highly with the run-on vegetation types. Topography might be important: hill cells correlate completely with the hill vegetation type, and highly with campsite presence. Presence or high densities of potential animal competitors might be important (e.g. Lange and Willcocks found some negative correlation between kangaroo and sheep dung in Wertigo, as quoted in Noble 1975). The limited data that I have on other herbivores suggest that rabbits are universal, with a possible tendency to use the wash vegetation types, and that kangaroo presence tends to be associated with wooded areas and the hills. I do not add any of these factors to the following analysis, therefore, although the possible correlates should be borne in mind.

### (iii) Universal factors.

Universal factors are those that affect the whole paddock simultaneously. These include a number of climatic factors which may influence sheep behaviour, such as temperature, wind, rain and cloud density. Only wind is hypothesised to have a directly spatial influence, and for the discriminant analyses mentioned in the next section it was coded as a 'pseudo-spatial' characteristic of each cell. For this, it was given a value of +1 for a cell if the cell lay in the end of the paddock from which the wind was coming for that map record,

-1 if it was at the other end, and 0 if conditions were calm. Wind is discussed in more detail in later chapters, since it clearly is significant in the open paddock.

Cloud might be expected to affect the need to use shade: on clear days, up to 90% of the thermal load on a sheep outside shade comes from the direct component of shortwave radiation. Rain can reduce dependence on water as well as changing vegetation characteristics in the short-term (in the longer term it may affect vegetation condition too, of course). Temperature may affect behaviour in a great number of direct and indirect ways, including the need to go to shade, to water, and, possibly, the amount of time spent in night-time campsites. Indirectly, it affects vegetation growth. Long-term mean values are correlated with season, and, in the short-term, both maxima and minima may be important. Other climatic features are probably irrelevant (e.g. lightning), or inextricably correlated with those already mentioned (e.g. relative humidity, atmospheric pressure).

Other universal factors mostly relate to the march of the seasons. Many proximate variables 'correlate' with season, including mean temperatures, daylength, many perennials' vegetative growth flushes and flowering cycles, and management regime.

Longer term climatic trends such as drought years are important to overall vegetation condition. The general state of vegetation in the paddock was classified as a cumulated score from all exclosed Jervoise photopoints for 1981-1983 (Chapter IV(d.ii)), and augmented for the earlier trips from some unstandardised photographs: 1980 was a wet year, and the vegetation was generally better than any of the following years. The presence or absence of ephemerals, green or dry, was also noted from these photographs. The resulting values, used in the following analyses, are shown in Table V.2. The general state of the vegetation correlated well with total rainfall in the previous three months. All these universal factors may act on those intrinsic to the sheep by affecting sociality and dispersion: this is taken up in section V(c).

Table V.2

Vegetation indices obtained from the Jervoise and Chimney Yards photopoints, 1981-83, supplemented from other photographs for 1980.

| Fieldtrip | | Ground material[1] green (0-3) | dry (0-3) | Shrubs[2] (0-10) | Rainfall (mm)[2] in prior 3 months |
|---|---|---|---|---|---|
| Aug 80 | B | 2 | 3 | 10 | 81. |
| Nov/Dec 80 | C | 1 | 3 | 9 | 58. |
| Jan/Feb 81 | D | 0 | 2 | 9 | 91. |
| Apr 81 | E | 1 | 2 | 10 | 116. |
| Jul 81 | F | 3 | 3 | 10 | 49. |
| Nov/Dec 81 | G | 1 | 3 | 6 | 36. |
| Jan/Feb 82 | H | 0 | 3 | 6 | 22. |
| Apr/May 82 | I | 0 | 1 | 7 | 36. |
| Sep 82 | J | 0 | 0 | 4 | 22. |
| Nov/Dec 82 | K | 0 | 0 | 2 | 14. |
| Jan/Feb 83 | L | 0 | 0 | 1 | 16. |
| Apr 83 | M | 1 | 0 | 8 | 83. |
| Oct 83 | N | 1 | 2 | 8 | 89. |

[1] ground material indices: 0 = none, 1 = barely visible in photo, but available to searching sheep, 2 = noticeable in photo, 3 = heavy.
[2] shrub index correlates with rainfall in the previous 3 months, r=.79, n=13, p=.001

Finally, time of day is an important determinant in both the sheep's current activity, and its immediate past history. The general patterns of activity at Middleback corresponded well with those previously reported in the literature (see Chapter II). The distribution of animals between activities under different conditions is discussed briefly at the end of this chapter.

There are a total of 291 map records of sheep in Jervoise to be discussed in the remainder of this chapter and the next. All of these were assigned to one of the categories of 'dawn' (within an hour of dawn), 'midday' (within an hour of solar noon, but best representing the flock's distribution if there was any choice), 'dusk' (within an hour of sunset) or none of these. Thus one record per day could be drawn on for each time category to reduce bias from having mappings close to each other in time. The resulting number of days represented is listed in Tables as the sample size.

## (b) Influence of cell characteristics, and wind.

This section considers the influence of the cell characteristics, and of wind, on the use of different cells under different conditions, using discriminant analysis. The method was mentioned in Chapter IV(c), using the discriminant analysis routines of the statistics package SPSS. The quoted 'standardised canonical function coefficients' (which I call SCF coefficients) are the weightings given to different cell characters in a stepwise inclusion procedure, using the method of minimising Wilks' lambda to distinguish the significance of discrimination by a character. All the cell characteristics and wind were allowed to contribute to the analysis, and the SCF coefficients are quoted for those that were sufficiently significant to be entered into the analysis at a partial F-ratio value of 1.0 (p=.50): this is very low, so that any variable which has any discriminating power at all is included.

The groupings to be discriminated here are simply the presence or absence of sheep in a given cell (coded as 2 and 1 respectively). Since the SCF coefficients are standardised, their relative magnitudes within a single analysis correspond to the relative importances of the associated characteristics. Quantitative comparisons between analyses are doubtful due to different sample sizes and different success in discrimination (as indicated by the difference between the group centroid values). In some instances where these factors are similar, trends are assessed.

All the results are standardised so that 'presence' in a cell has a positive group centroid, and 'absence' a negative one. The sign on the SCF coefficient for a character then indicates in which direction

## Table V.3

Name in subsequent Tables, description and meaning of positive SCF coefficient sign for discriminant analysis factors.

| Name | Description | Meaning of +SCF coeff. |
|---|---|---|
| WDIS[1] | ( water | ( water |
| SDIS[1] | distance to ( nearest shade | use cells away from ( shade |
| CDIS[1] | ( nearest camp | ( camps |
| FENCE E/W[2] | cell has east-west fence | use cells with E/W fence |
| FENCE N/S[2] | cell has north-south fence | use cells with N/S fence |
| WOOD[2] | cell contains heavy timber | use cells with timber |
| BB/SB[2] ) | | |
| SB/BB[2] ) | | |
| SB(BB)[2] ) | cell contains this veg'n | use cells with this veg'n |
| SB/PYR[2] ) | (see Table V.1) | |
| SB(PYR)[2]) | | |
| WIND | cell position relative to wind (see text) | wind direction matches cell position |

[1] coded as distance (100's m)
[2] coded as 1=present, 2=absent for each cell

that character is contributing to the discrimination. It is important to be clear what the sign implies, and this is listed for each character in Table V.3; for example, a positive sign on 'WDIS' implies that the sheep are avoiding the cells close to the waterpoint. The other quoted statistic is the percentage group members classified correctly by the discriminant function: with two groups possible, a random classification would result in 50%. All the percentages are significant overall, but because of the larger number of cells with animals absent, the classification of this group often biases the total percentage. I therefore quote the percentage successfully classified for each group separately: not infrequently this is smaller for the present group.

### (i) The data set at different times of day.

I first analyse the data set of 176 records that were classified as dawn, midday or dusk. This serves no subtle end, but clearly shows (Table V.4) the expected influence of distance from the waterpoint, with the likelihood of sheep being present in a cell increasing towards the waterpoint. The importance of distance to water is general to most of these analyses, and will only be referred to again where exceptions occur.

Table V.4

SCF coefficients for discriminant analysis of presence/absence of sheep in cells of all records, and breakdown for dawn, midday and dusk records. Discriminating factors described in Table V.3.

| | All data | Dawn | Midday | Dusk |
|---|---|---|---|---|
| n (records) | 176 | 61 | 56 | 59 |
| Factors | | | | |
| WDIS | -.57 | -.50 | -.40 | -.62 |
| SDIS | -.18 | | -.65 | .08 |
| CDIS | .22 | | .32 | .31 |
| FENCE E/W | -.08 | -.11 | -.21 | |
| FENCE N/S | | | | |
| WOOD | -.26 | -.21 | -.28 | -.26 |
| BB/SB | -.34 | | -.86 | -.18 |
| SB/BB | -.22 | | -.41 | -.21 |
| SB(BB) | .21 | .46 | | .17 |
| SB/PYR | | .32 | -.20 | |
| SB(PYR) | | .11 | -.18 | |
| WIND | .21 | .28 | .24 | .22 |
| Statistics: % correct classifications | | | | |
| total | 70 | 69 | 69 | 74 |
| presences | 66 | 60 | 63 | 70 |
| absences | 71 | 71 | 70 | 75 |

(missing values are factors with partial F-ratio < 1.0, see text)

I also point here to a tendency to avoid the heavy timber, which occurs frequently in the analysis. Some of this timber was in the southeast corner of the paddock, the under-utilisation of which is corroborated by other data (e.g. dung pattern data, which is not dependant on finding sheep). However, there is also the possibility that this indicates some failings in the observations, as sheep were more likely to missed in the well-wooded areas.

Table V.4 also presents the breakdown of records by time of day. About 60 days are represented in each category. Throughout, there is the dependence on the waterpoint, slightly lessened in the middle of the day. Also throughout, there is a consistent but not strong influence of wind: as expected, sheep are more likely to be present in cells at the end of the paddock from which the wind is blowing.

Other spatial factors show most significance in the middle of the day, that is, when the sheep are most likely to be resting or in shade. There is a strong tendency to be close to shade, not surprisingly, and a tendency to be away from campsites. The latter is interpretable as a tendency to keep away from hills on which there is no shade. This effect persists into evening, when shade has become a trivial discriminator; at this time many sheep may be headed into water, and they rarely move to camp before at least an hour after sunset. The positive value suggests that they are not seeking camp at this stage.

It is surprising that there is no effect of campsite distance in the early morning. Sheep tend to move off campsites around first light, so this may merely indicate that I did not often catch them all still camping. Most of the campsites are also on hills of the stunted SB(BB) vegetation type, so it may be that the discriminative power of campsite distance is overshadowed by that of this vegetation type as the sheep move off from camp. Fencelines seem to be minor in effect, despite the frequent presence of campsites close to them.

As regards vegetation, I have already noted the possible avoidance of heavy wood. Negative indices on the vegetation category parameters imply avoidance, and can be difficult to interpret. The potential interdependence of variables in this type of analysis is illustrated by the significant avoidance of BB/SB in the middle of the day. The presence of this vegetation type in fact shows a chance negative correlation with shade distance for Jervoise ($r=-.40$, $n=53$, $p=.003$, Pearson's correlation coefficient), that is, it tends to occur in cells with a short distance from shade. The combined closeness to shade and avoidance of this vegetation type therefore suggests the preferential usage of shade in cells of other vegetation type. However, this in turn is likely to be a result of a positive correlation of BB/SB with distance from water ($r=.48$, $n=53$, $p<.001$), so that in reality the whole effect is one of using shade relatively close to water. Conversely, SB(BB) has a positive correlation with distance to shade ($r=.70$, $n=53$, $p<.001$) which may explain why it has no effect on the midday distribution at all. Such interactions mean that only strong trends are useful.

Positive SCF coefficients are easier to interpret, and the SB(BB) vegetation type is important in the morning. This may be a result of campsite positioning, as already discussed, but local pastoralists describe this stunted saltbush form as being especially 'sweet', and it may be a preferred shrub fodder when ground material is in short supply. SB/PYR also seems preferred in the early morning grazing period: at times of ephemeral presence, these run-on areas are likely to contain good feed.

(ii) Variation with wind and season.

I next examine the significance of these cell characteristics for some different weather and seasonal conditions. Two factors are particularly important: wind, and overall vegetation trend between 1980 and 1983. Firstly, in south winds in Jervoise, the sheep use a larger area of the paddock: influences other than water should therefore become more apparent in records from these wind conditions. Secondly, summer vegetation condition generally declined from 1980 to 1983 (see Table V.2). This should affect many parameters, amongst them water use, heterogeneity of vegetation and daily behaviour patterns.

Records were first divided on the basis of the wind directions experienced: 'N winds' refers to winds only from NW, N and NE, whilst 'S winds' were only SW, S and SE. The few E, W and calm records were omitted from the analysis. The cell criterion of 'WIND' now becomes only an index indicating cell position for a given wind direction.

For northerly winds (see Table V.5), waterpoint distance remains important, and the north end of the paddock is in use, as is indicated by the positive WIND coefficient. For south winds, waterpoint distance becomes unimportant, and other physical and vegetative factors become significant as spread over the paddock is increased. The WIND coefficient actually becomes negative, which merely reflects the fact that sheep are still to be found in the north end of the paddock as well as the south. This is no great surprise, and is equally evident from Figure V.3.

North winds are generally correlated with higher temperatures, as

Table V.5

SCF coefficients for discriminant analysis of presence/absence of sheep in cells for northerly and southerly winds, and for summers from 1980 to 1983, midday records only. Discriminating factors described in Table V.3.

| | N winds | S winds | 1980-81 | 1981-82 | 1982-83 |
|---|---|---|---|---|---|
| n (records) | 19 | 28 | 20 | 12 | 5 |
| Factors | | | | | |
| WDIS | -.26 | | | -.51 | -.98 |
| SDIS | -.21 | -.99 | -.71 | -.31 | -.34 |
| CDIS | .56 | .34 | .27 | .61 | |
| FENCE E/W | .13 | -.41 | -.35 | .21 | |
| FENCE N/S | .09 | -.12 | | | -.45 |
| WOOD | -.17 | -.43 | -.36 | -.14 | |
| BB/SB | | -1.28 | -1.04 | -.22 | |
| SB/BB | | -.60 | -.53 | | |
| SB(BB) | .28 | | | .47 | |
| SB/PYR | .37 | -.78 | -.15 | | |
| SB(PYR) | | -.23 | | -.12 | |
| WIND | .24 | -.26 | .37 | -.24 | -.31 |
| Statistics: % correct classifications | | | | | |
| total | 81 | 67 | 72 | 89 | 71 |
| presences | 76 | 66 | 76 | 71 | 74 |
| absences | 82 | 67 | 71 | 91 | 70 |

(missing values are factors with partial F-ratio < 1.0, see text)

discussed earlier with respect to the cyclonic cycles. The important result from this analysis, then, is that physical factors other than distance to water become much more important in south winds, when the sheep are spread over more of the paddock. Because of the shape of Jervoise, it is not possible to determine in this analysis whether this is because of a genuinely greater dependence on the waterpoint in warmer weather, or whether it is simply a wind effect on movement direction from the waterpoint; both may be implicated. Similar comments apply to the vegetation characteristics.

The results of the dawn and dusk analyses (not presented)

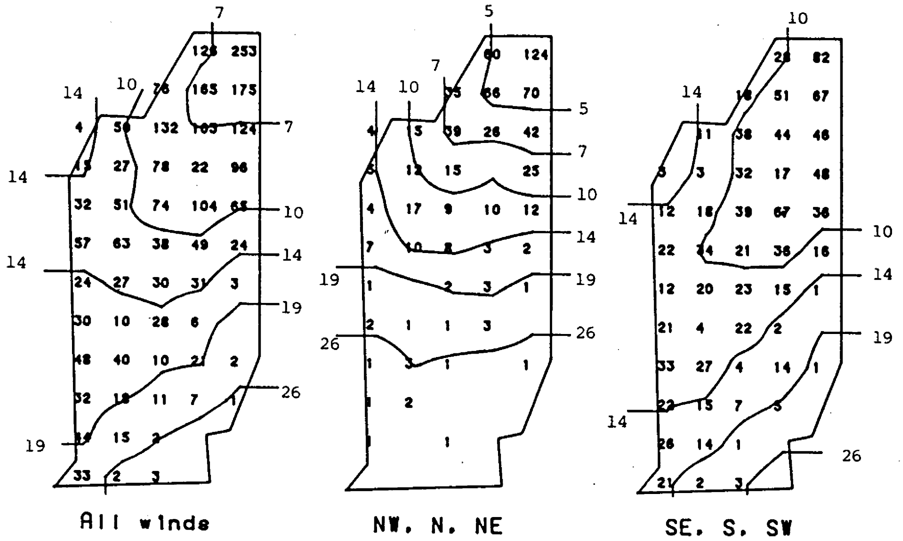


Figure V.3: Distribution of all groups of sheep seen in Jervoise during mapping records, in all records, and in those from northerly or southerly winds only. Numbers are groups seen in each cell; contours are isopleths of equal activity (harmonic mean moments to each group), where higher numbers indicate less activity (see Chapter IV(c)).

generally parallel those of Table V.5, with the differences to midday being similar to those described in section (i). Notably, distance to the waterpoint remains important at dusk even in south winds, reflecting the likelihood of sheep to be watering at this time.

The second half of Table V.5 presents the breakdown for summers (Nov-Feb) 1980-81, 1981-82, 1982-83. This series corresponds to a steadily declining general vegetation condition as the drought became more severe (see Table V.2). The sample size for summer 1982-83 is doubtful, but there is a clear trend to increasing importance of the waterpoint in the middle of the day through the series. In 1980-81, few sheep would stay near the water except when actually watering in the morning or the evening. In 1981-82, more water was being drunk (see Chapter VI(c)), despite similar temperatures, and more sheep were resting near the water in the middle of the day. By 1982-83, the change in behaviour was more pronounced. Correspondingly, the importance of distance to shade declines, and does the influence of vegetation type and wind.

A similar trend is apparent in the dawn data (not presented). Additionally, near dawn, the vegetation category SB(BB), which was influential in the overall data (Table V.4) for reasons I suggested were associated with proximity to camps, declines in significance through the years. This may reflect earlier departures from campsites areas, and more night-time grazing, although plants on the shallow hillside soils also seemed most affected by the drought. At dusk, the waterpoint is still significant throughout, in line with the evening waterings which occurred even in 1980-81.

I had wished also to examine the differences between summer and winter, to demonstrate a lesser attachment to water in winter than summer, and a correspondingly greater influence of wind. The winter sample sizes are, however, too small to be reliable and the analysis is not presented. It suggests that wind is indeed more significant in determining which end of the paddock is used in winter than in summer; unexpectedly, however, the waterpoint remains important in both.

### (iii) Summary.

Plainly this analysis is very general in its approach, and often delphic in its interpretability. Nonetheless, I draw from it the following points:

1. Distance to the waterpoint, as expected, is almost always important in sheep distribution. For Jervoise, this is less so in

south winds when the sheep tend to spread out further down the paddock. This factor was much less important in a summer of good vegetation condition than during drought.

2. Wind is generally, but weakly, significant in that sheep are more likely to be at the end of the paddock from the wind is coming. This matches widely-held beliefs and long-term aerial photograph evidence.

3. Position of shade is important during the middle of the day (although the sample is biased towards summer).

4. Fencelines seem of minor importance in a paddock of these dimensions, although they must be constraining movement northwards (in these analyses, this is likely to be over-ridden by the effect of the waterpoint).

5. Campsite location seems of minor importance by an hour or so after departure from it, although,

6. vegetation types near campsites are likely to be over-utilised early in the day. This is a justification for regarding campsites as significant foci.

7. Few vegetation preference effects were seen that were not likely to have been due to correlation with other variables: many of the effects were negative. This may be a reflection of how relatively uniform chenopod shrublands are.

8. The downwards trend in general vegetation quality from year to year has an effect on ranging behaviour, most apparent in the increasing significance of the waterpoint.

Most of these results were expected, but the analyses support commonsense. Most importantly, they show that vegetation type and fence lines are less significant than the centres of non-grazing activity, and vegetation condition.

### (c) Flock structure, dispersion and activities.

I now turn to consider the effects of the universal variables on some general descriptors of the flock in the open paddock. To make discussion of dispersion meaningful, I first remark on flock structure in these merinos. I then relate dispersion to climate and physiological state, and finally briefly outline how the breakdown of the flock's activities varies with these factors.

#### (i) Flock structure.

Feral sheep on Soay (Grubb & Jewell 1974) and wild Bighorn sheep (Geist 1971) seem to have very rigid group structure, for females at least. The groups are often of related animals, and in numbers are comparable to the 'subflocks' that I describe in the paddocks. Although merinos are renowned as being amongst the most social of domestic sheep, maintaining close inter-individual distances and being particularly frantic when isolated, I found little evidence for any consistent structure to the subflocks in the open paddock.

Anecdotally, during the tracking of individual subflocks, I have often observed groups diverge into two sections in areas with high shrubs. Sheep may transfer between two groups as they move past each other in opposite directions, even in conditions of open visibility and when moving at considerable speeds (e.g. relative speeds of up to 3 km $h^{-1}$). Very occasionally, on the other hand, frightened sheep were observed to run counter-intuitively to another animal before both set off to join the nearest larger group; this included a few times when the first sheep frightened actually ran towards me to join a companion.

I tested how stable the groupings are more objectively from the marked sheep observations, using cases of sheep seen in pairs. Firstly, as context, over all Jervoise map records, the mean probability of a marked sheep being seen in a given mapping session was about .25: this probability was higher in the morning and evening active periods (usually about .5) and lowest during the middle of the day when animals were likely to be lying down (e.g. 0.05). If, however, one marked animal could be seen in a group, any others in that group were usually visible too.

From all the mapping in Jervoise, I have over 500 records of pairs of marked sheep being seen in the same subflock. In 310 cases, both sheep were seen again simultaneously more than 24 h later. Of these 310, only 29 (9%) were still together at the second sighting. Of the remainder, 197 (64%) were confirmed in separate groups within 36 h, and the other 84 (27%) before the end of that trip (Figure V.4).

Remelding of the groups was certainly occurring. For the 281 which split, in 168 (60%) cases, at least one of the two animals originally seen paired was seen at the second sighting in the company of a third marked individual which had been seen in a different group on the first occasion. Furthermore, 55 (20%) of these split pairs were seen again in their original pairing before the end of the trip.

Suppose a group of sheep splits at random, so that the chance of a pair of marked animals being separated by the split is 0.5. Then if only 29 of 226, or 0.128, pairs remain unsplit after about 24 h, the mean number of splits that must have occurred since the first sighting is n, where $(0.5)^n=0.128$. 'n' is approximately three, and group sizes should be reduced to about one eighth during the day. By an

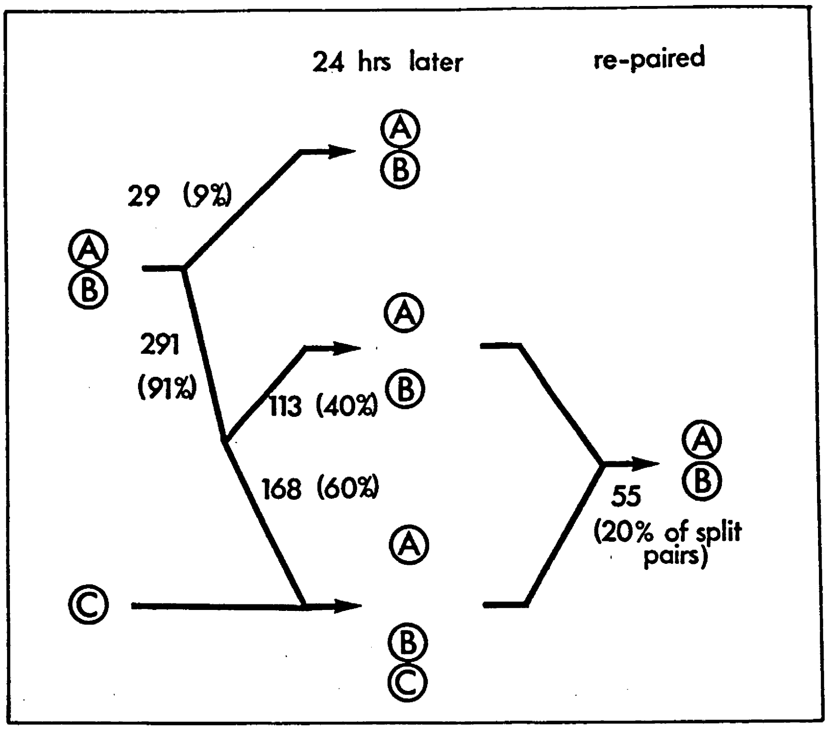


Figure V.4: Schematic illustrating the frequency of break-ups of pairs of marked sheep seen at Middleback.

alternative approach, if splitting may occur during any of h hours, then the probability of not splitting in a given hour is p where $p^h$=0.128; for, say, eight hours of extensive movement in a day, which is when splitting is likely to occur, p is about 0.77. These calculations will be used in Chapter X.

It is now possible to estimate how big any 'core group size' might be at Middleback. The analysis is complicated by the fact that marked sheep were not located reliably, and because re-pairing may have been occurring in the open paddock. However, most close contact between groups occurs at the waterpoint and campsites, little more than once a day; these may act as re-grouping centres around the night-time. This suggestion is supported by the fact that group sizes tend to fall during the day, although the great variability means that no differences are significant; over all dawn records, the mean group size away from water was 19.4 sheep (57 days), in midday records it was 15.3 (57 days), and at dusk it was 14.3 (60 days).

Even if all 250 sheep met up at once, group breakdown should result in subflocks of about 30 sheep. In fact the animals rarely all meet up, and the mean group size over all observations was 18.8 sheep (n=174 records, 2520 groups). If this is a mean size during splitting, the maximum stable group size in merinos at Middleback under these conditions cannot exceed about 10 sheep, and may be less.

### (ii) Dispersion and group sizes.

If only the smallest groupings of sheep are directed by social behaviour as the previous section suggests, subflock sizes and dispersion may be affected by external factors. I have reviewed (Chapter II) evidence suggesting that sheep do subgroup more when grazing in conditions of scarcer feed. The resultant impact on the vegetation is determined by two factors: what portion of the paddock is ever used during some period, and how much dispersion there is within this area on a particular occasion. These two aspects can vary independently, and may determine whether a narrow swathe of total destruction is grazed through the vegetation, or whether the impact is evenly spread over a larger area.

Figures V.3 and V.5 illustrate the first point. Figure V.3 shows the average usage of Jervoise for all mapping occasions (dawn, midday and dusk as defined previously). The adjoining maps are derived from records for northerly or southerly winds only. Clearly the patterns of usage can be changed in the short-term, and wind directions may correlate with the changes.

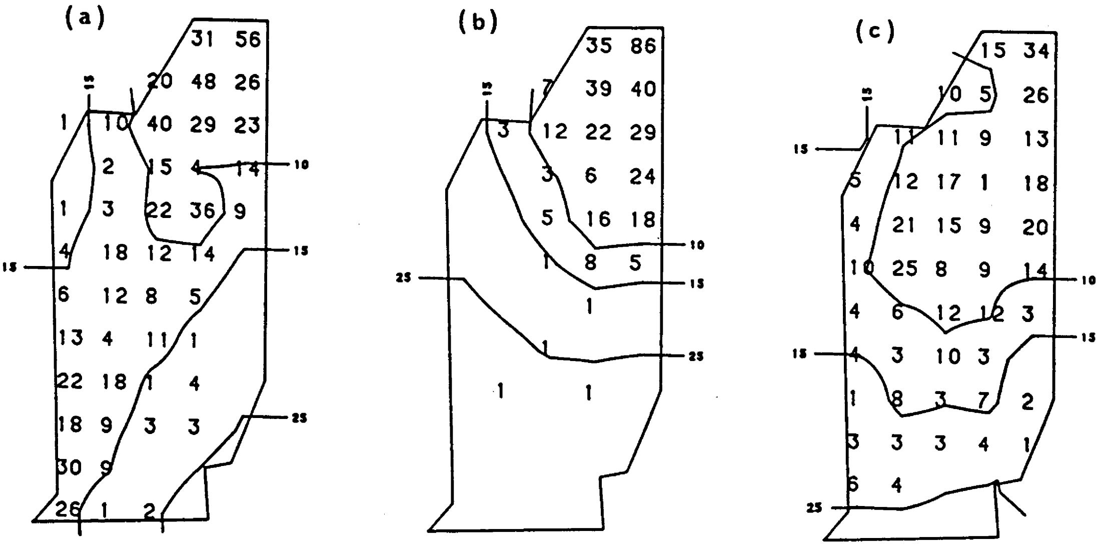


Figure V.5: distribution of all mapped sheep groups in Jervoise during fieldtrips of summers (a) 1980-81, (b) 1981-82 and (c) 1982-83. Numbers and contours as Figure V.3.

Patterns also change in the longer term, however. Figure V.5 shows the paddock usage for summers 1980-81 (pre-drought), 1981-82 (early drought) and 1982-83 (height of drought). Although the waterpoint was important in all three cases, it assumed a greater importance with the drought. Usage was constrained northwards in 1981-82, but, despite increasing use of water, it expanded southwards again in 1982-82. This pattern was corroborated by the dung survey data. It was not a consequence of different winds, but was due to the over-utilisation of vegetation in the north end of the paddock, and a consequent need to forage further south later in the drought. The vegetation pattern development is detailed in Chapter X(b.iii). Whilst these changes overall paddock usage were occurring, however, there were partially independent trends in group dispersion, to which I now turn.

In the remainder of this section I test whether subgrouping is increased in adverse conditions. Such conditions can occur seasonally, and with declining vegetation condition. I exclude animals that were within the waterpoint cell from the analysis, so that the numbers and mean sizes of groups in the rest of the paddock are considered. I use a seasonal index that varies sinusoidally from -1 in mid-July to +1 in mid-January (i.e. treating Dec-Feb as summer and Jun-Aug as winter); this correlates highly with mean temperatures ($r=.74$, $n=174$, $p<.0001$ for daily temperatures at Middleback during the fieldtrips).

Table V.6 presents the results of this analysis. In the data as a whole, there is a significant seasonal effect on numbers of groups and group size: this is, however, contra hypothesis, such that numbers of groups increase during winter, when temperatures are less extreme, and forage is usually in better condition. This is partly a result of lambing, since many of the groups were one or two ewes with their offspring (the lambs are not included in the numbers). Nonetheless, there was a smaller increase in numbers of groups in the wether paddock, Adam's West, so that the change in behaviour is seasonally-influenced as well as physiologially-mediated.

There is a weak negative correlation between numbers of groups and vegetation indices, in support of reports in the literature already

Table V.6

Correlations between numbers of groups and group sizes away from water against season and vegetation condition indices (see Table V.2).

| Correlate | N | Mean group size | r<br>Number of groups | r<br>Group size |
|---|---|---|---|---|
| All records | 174 | 16.3 | | |
| season | | | -.41*** | .19* |
| shrub index | | | -.17* | .14 |
| ephem. index | | | .01 | .19* |
| All summers | 111 | 18.9 | | |
| shrub index | | | -.57*** | .29*** |
| ephem. index | | | -.63*** | .36*** |

* p<.05 ** p<.01 *** p<.005

referred to (Chapter II). This effect is much stronger within the summer seasons from 1980/81 to 1982/83. I have additionally examined any correlates with wool-length, temperatures and other climatic variables, both within and between season, and none shows any comparable predictive value.

The previous section suggested that the waterpoint operates as a re-grouping centre, and that group size in the open paddock is a function of the rate of group break-up, and of the time since last re-grouping. The results of this section are consistent with this view if the rate of splitting is affected by vegetation condition and, perhaps, the physiology of lambing. Group size then decreases in winter partly due to less frequent watering, and partly because of lambing. It also decreases in poorer vegetation conditions because of increased rates of group splitting, perhaps a result of more grazing search movement.

(iii) Activities.

Many studies of animals present detailed charts of daily activity patterns for the animals concerned. This descriptive exercise may be of little use to a detailed modelling approach, except for validation. However, I briefly present here some histograms of mean proportions of animals in different activities at different times of day, and show some changes with season. The histograms present the mean percentage numbers of groups seen in different activities, where the percentages are derived for each map record and averaged; a small background of uncertain activities (about 3% of numbers of groups for each histogram) is omitted.

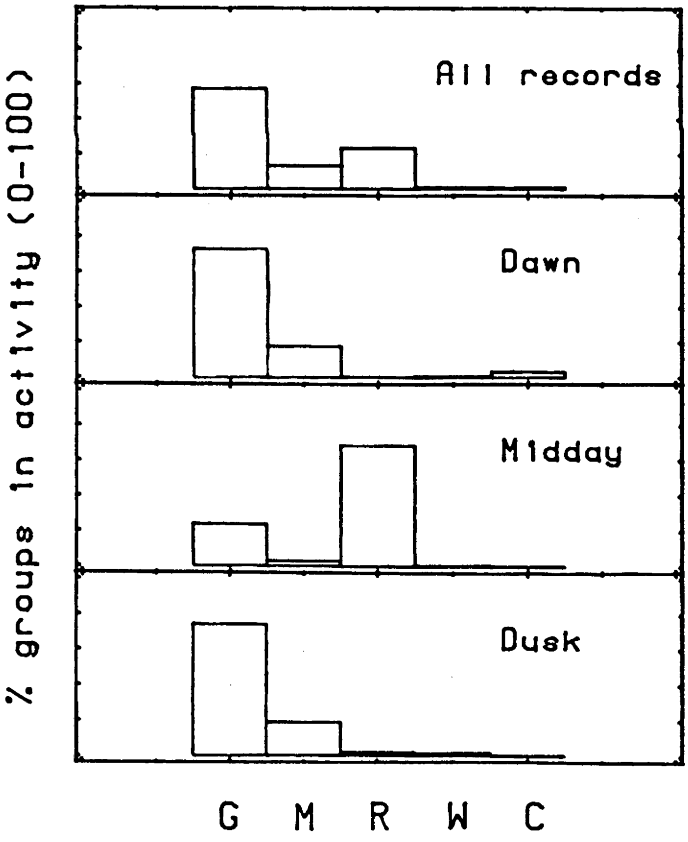


Figure V.6: Percentage of all groups seen in different activities for all data, and for dawn, midday or dusk records. Activities are as in Table IV.3, except that g=g+gm, m=mg+m, and r=r+s.

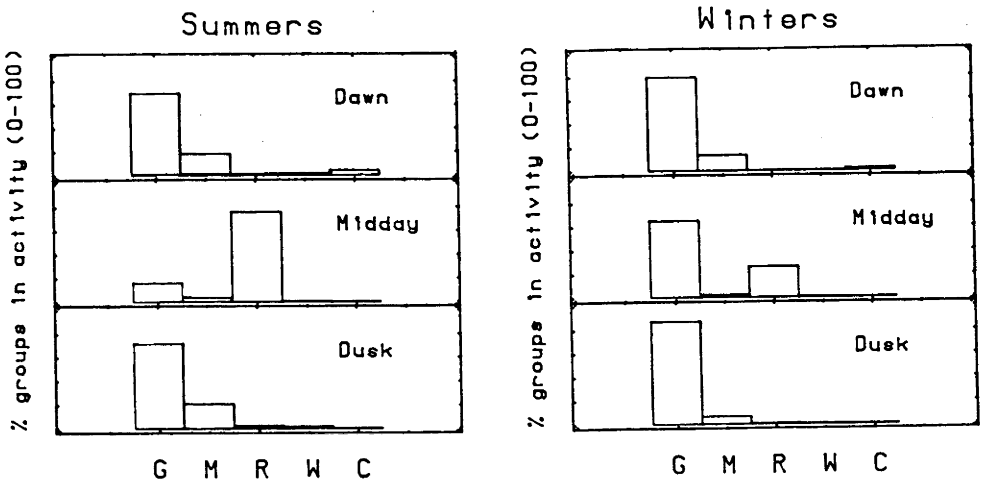


Figure V.7: Percentage of groups seen in different activities at different times of day in summer and winter records. Activities as Figure V.6. Note the reduction in midday resting in winter compared with summer, and the increased movement in summer compared to winter.

Figure V.6 shows the pattern for all the data, and breaks it down into the dawn, midday and dusk categories. There is the expected increase in resting during the middle of the day. There is a major change in pattern between summer and winter, as Figure V.7 shows, with much more activity throughout the cooler, shorter days. Note that there is rarely a total consistency of activity type, so that subflocks are not usually wholly synchronised. Such synchronicity may does occur on the hottest afternoons (see Chapter VI(b.i)) and at campsites, but a complete model must allow different subflocks to pursue their own ends under most conditions. In general, however, the patterns correspond well with those described in the literature (Chapter II).

### (iv) Summary.

Observations of marked sheep show that the groupings of merino sheep are volatile and transitory. The maximum size of a stable core group (if any) is about 10 sheep. Under the range of vegetation conditions observed, groups split about three times a day on average, with the waterpoint and campsites acting as re-grouping areas. Group size is affected by season, probably because of changes in the frequency and synchronicity of the use of water and camp sites. Group size also declines with declining vegetation condition and during lambing. Activity patterns in the open paddock at Middleback are shown to be similar to those reported elsewhere. Grazing is usually bimodal in the day, but there is a marked increase in midday activity in the cooler months. Subflocks are rarely fully synchronised in their activities.

# Chapter VI.

## Non-grazing activities in the open paddock.

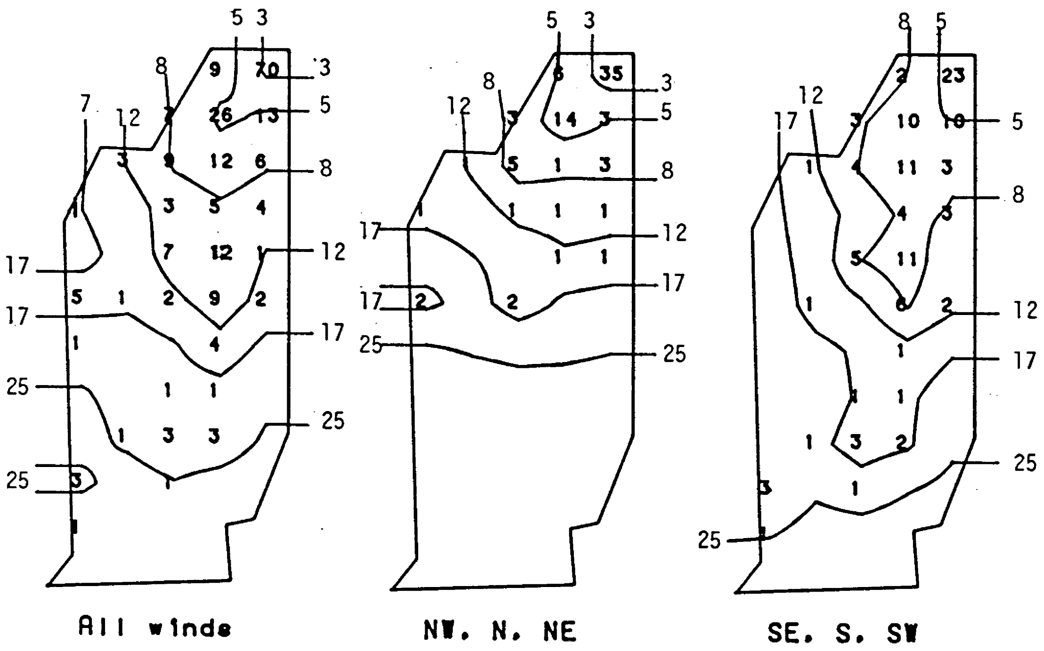
The previous chapter has delineated certain variables that are important to the ranging behaviour of sheep in the open paddock. These include the long-term condition of the vegetation, season, wind, and temperature inasmuch as it influences the use of shade and water. Spatially, the positions of water, shade and campsites seem to be more important than vegetation type or fencelines. In this chapter, I examine the sites used for non-grazing activities in more detail, considering both when they are used, and where this usage may take place.

## (a) Resting.

Resting is hypothesised to occur wherever a sheep is when it has no impulse causing it to move. Normally this will be at the end of a grazing period, although it may also occur after a move to water if the sheep is not hungry. Except in the latter case, the location of rest sites should be strongly dependent on movement in grazing, a topic which is considered in more detail in the next chapter. Here I examine location of, and movement to and from, rest sites, so that they may be compared with shade sites in the next section, and I briefly discuss how long sheep should stay in rest sites.

### (i) Location and movement.

Figure VI.1 shows the locations of all resting groups taken from observation records in Jervoise, with the division into records from northerly and southerly wind directions. An extension of use into the southern end of the paddock is evident in southerly winds. There is also a negative correspondence between cells containing shade and cells used as rest sites (correlation of distance to shade with number of uses as a rest site: $r=.36$, $n=52$, $p=.009$). This may either be due to sheep avoiding shade sites when they are not needed, or because they use a shade site for resting when they are in a shade area on a stressful day. Observation supports the latter explanation, since shade sites would often be used under total cloud cover, for example, and consequently be recorded as shade use rather than as resting behaviour. This phenomenon increases the focusing effect of shade sites at a fine scale, although it is not relevant at the cell size of 500x500 $m^2$.



All winds NW, N, NE SE, S, SW

Figure VI.1: Locations of all groups of sheep seen resting in Jervoise; all data, and records from conditions of northerly and southerly winds only. Numbers are the numbers of groups seen in each cell; contours represent isopleths of equal activity (as measured by harmonic mean moments to each group from each cell, see Chapter IV(c.iii)), where higher values indicate less activity.

To test whether movement to and from rest sites was determined by wind direction or by previous and subsequent activities, I re-examined the raw data maps of Jervoise. Where I could be sure of correct identification, I followed individual subflocks through the course of the day, recording the area of the paddock in which they were resting, their directions of arrival and departure for that location, and their previous and subsequent sites of inactivity (i.e. before and after the associated grazing periods). Groups resting near to one another in the same set of records were considered as a single unit if they had similar histories and futures. Cases of resting near the waterpoint were ignored, since they may be confounded with watering behaviour.

This analysis produced only 38 separate recordings of resting behaviour during 1980-83. Of 32 cases for which the previous activity was certain, 15 derived from the waterpoint and 17 from campsites. After departure from resting, and after at least some grazing, the next site of non-grazing activity was the waterpoint in 16 cases, a camp in six, and shade in one; 15 cases were indeterminate.

Table VI.1

Arrivals and departures by sheep subflocks at rest sites in Jervoise, 1980-83. Numbers of records of movement in different wind conditions and for different previous or subsequent activities are shown. Where relevant, $\chi^2$ tests are given.

| | | Arrival or departure directions | | | | n |
|---|---|---|---|---|---|---|
| | | NW,N,NE | | SE,S,SW | E/W | (total) |
| ARRIVAL (from) | | | | | | |
| in winds: | northerly | 4 | | 4 | 1 | 9 |
| | southerly | 16 | [1] | 8 | 0 | 24 |
| last site: | water | 13 | | 2 | 0 | 15 |
| | camp | 6 | | 10 | 1 | 17 |
| from camp in: | N'ly winds | 2 | | 2 | 1 | 4 |
| | S'ly winds | 4 | [2] | 8 | 0 | 12 |
| DEPARTURE (to) | | | | | | |
| in winds: | northerly | 6 | | 0 | 0 | 6 |
| | southerly | 13 | | 4 | 0 | 17 |
| next site: | water | 16 | | 0 | 0 | 16 |
| | camp[3] | 1 | | 4 | 0 | 5 |
| | shade | 1 | | 0 | 0 | 1 |

[1] $\chi^2_1=2.67$, $p>.10$, arrival directions not significantly related to wind directions.

[2] $\chi^2_1=1.33$, $p>.10$, arrival directions from camp not significantly related to wind directionn.

[3] all 5 records of departure to camp were in south winds.

Table VI.1 shows the distribution of arrival and departure directions in northerly and southerly winds, and in relation to previous activity. Mismatching sample sizes between departures and arrivals reflect cases where some characteristics could not be determined. The records correspond to 23 cases of resting in the northern third of the paddock, 12 in the central third, and three in the southern third.

Arrival directions were not significantly related to wind directions over all the records. Because the waterpoint is located in the north of the paddock, animals usually arrived at rest sites from the north after watering; in the two cases where this was not so, the sheep had grazed southwest of the waterpoint, and then returned northwards before resting. Arrival directions to rest sites from campsites are also not significantly related to wind direction. There was a tendency to arrive from the south in south winds; this implies that the animals graze northwards from campsites used in south winds, which is necessary if, as was often the case, the campsite was near a southern fenceline.

Despite the majority of the records being from southerly winds, departures were strongly biased towards the north, because they usually involved movement to water. Even though over half (11 of 16) of the departures to water were in southerly winds, the sheep always left the rest site in the direction of water. Direction in grazing movement can thus be affected by the location of the next activity. There were insufficient records to separate the effect of winds on departures, although most departures to campsites were into the direction of the wind.

There is a slight correlation between the arrival direction and the day's maximum temperature ($r=.41$, $n=35$, $p=.011$), indicating a greater likelihood of arrival from the south as temperatures rise. Since arrivals from the south must always be from campsites, and most departures were to water, this suggests a tendency to rest en route to water on days of higher temperatures; movements of sheep may be oriented towards watering later in the day even from the early morning.

### (ii) Timing of resting.

An animal which rests when its hunger is satiated, and when it is neither thirsty nor hot, should cease resting when one of these criteria is no longer satisfied. Although the time involved may be affected by the digestibility of feed, it should be useful for validating the hunger thresholds used in the model, and their interactions with thirst thresholds. Unfortunately there were too few reliable records to attempt this analysis (partly because of under-representation in the winter records, when greater numbers of groups made their identification less easy).

### (iii) Summary: resting.

Resting is presumed to occur when no other impulse predominates. Sheep which are resting in areas where shade sites are available often use those shade sites. The location of rest sites is dependent on grazing movements that have occurred since leaving a previous site of non-grazing activity. Rest sites in the south end of the paddock are used only in south winds, but those in the north end are used in both south and north winds. Directions of departure from rest sites are determined by the subsequent non-grazing activity. Time spent resting should be related to hunger and thirst, but insufficient evidence was obtained in the open paddock to verify this.

water on days of higher temperatures; movements of sheep may be oriented towards watering later in the day even from the early morning.

### (ii) Timing of resting.

An animal which rests when its hunger is satiated, and when it is neither thirsty nor hot, should cease resting when one of these criteria is no longer satisfied. Although the time involved may be affected by the digestibility of feed, it should be useful for validating the hunger thresholds used in the model, and their interactions with thirst thresholds. Unfortunately there were too few reliable records to attempt this analysis (partly because of under-representation in the winter records, when greater numbers of groups made their identification less easy).

### (iii) Summary: resting.

Resting is presumed to occur when no other impulse predominates. Sheep which are resting in areas where shade sites are available often use those shade sites. The location of rest sites is dependent on grazing movements that have occurred since leaving a previous site of non-grazing activity. Rest sites in the south end of the paddock are used only in south winds, but those in the north end are used in both south and north winds. Directions of departure from rest sites are determined by the subsequent non-grazing activity. Time spent resting should be related to hunger and thirst, but insufficient evidence was obtained in the open paddock to verify this.

The Appendix describes in detail the prediction of the wooltip temperature of a sheep under given environmental conditions of wind, air temperature and cloud at any time on any day of the year and at any location (fixed by latitude and local solar noon). From this prediction, which is very good, conduction of energy into the body is calculated and a 'respiration index', R, is derived; this correlates well with the observed respiration rate of sheep under various conditions. The index exceeds real respiration rates numerically because it subsumes all evaporative cooling, not just that involved in respiration.

A similar index derived by Noble (1975) was assumed to represent the heat loading felt by the sheep, and consequently was used to predict their behaviour. I justify this assumption here by showing, firstly, that the index, derived from a physical model, is related to open paddock behaviour, and, secondly, that the index can predict the specific decision to move to shade.

Firstly, I collected data on sheep in shade in Adam's West paddock from a hilltop vantage point. Figure VI.2 shows the relation between the proportion of sheep at a shade site that are actually in the shade and the predicted respiration index, R, for the then-prevailing conditions, over eight days. The correlation is good ($r=.81$, $n=35$, $p<.0001$). This is taken as justification that R is relevant to the behaviour of sheep in open paddocks under environmental conditions of increasing severity. In this instance, the animals are already near shade, and have only to decide whether or not to move into it.

Figure VI.3 shows the response of this behavioural measure of heat

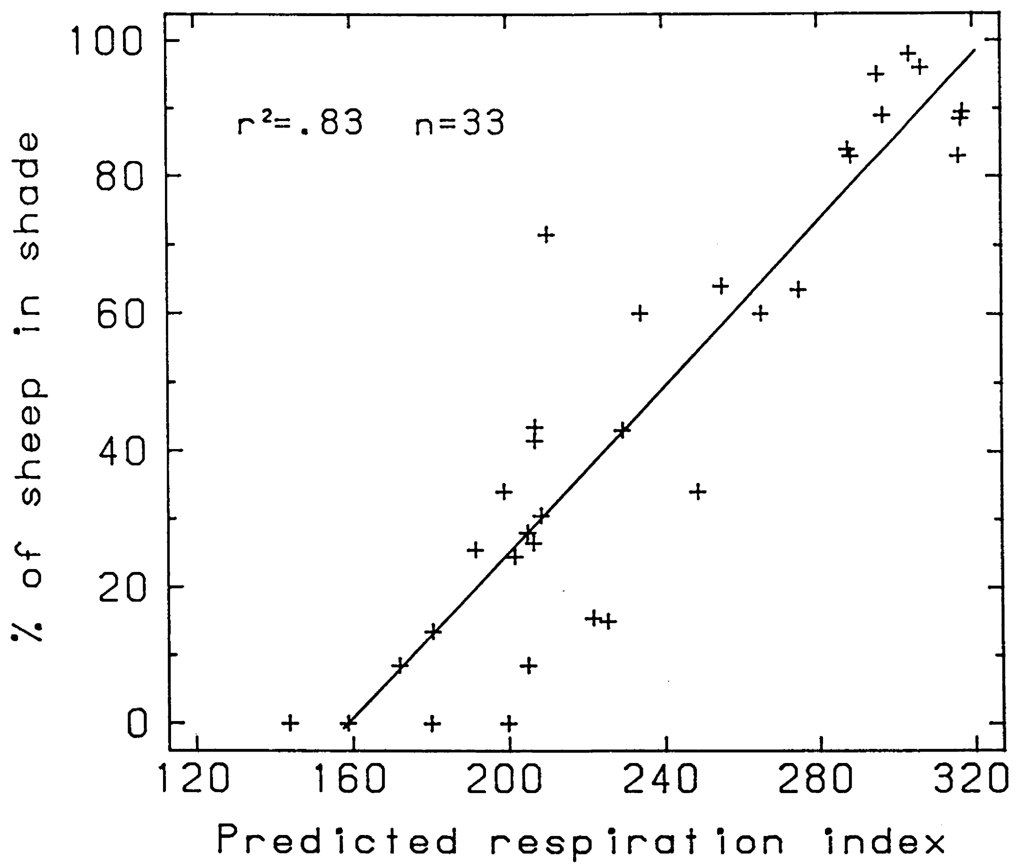


Figure VI.2: Plot of percentage of sheep actually in shade at a shade site in the open paddock against predicted respiration rate for various environmental conditions on 8 days in Jan-Feb 1982. Regression line is, $y = -95 + .60 * x$.

loading during one day (23rd January 1982), plotted alongside R for sheep in the shade or the open. The conditions on that day were extreme - a maximum temperature of 46°C, with 0/8 cloud until midday, which increased to 3/8 in the afternoon. The wool length of these sheep was long (about .07 m), and effect of this insulation is shown by the relatively small reduction in R that the sheep obtain by moving to shade. The respiration index closely tracks the percentage of sheep in the shade (which reaches a plateau when all sheep are in the shade) until late in the afternoon, when sheep leave shade earlier than might be expected from the index on the basis of their morning behaviour.

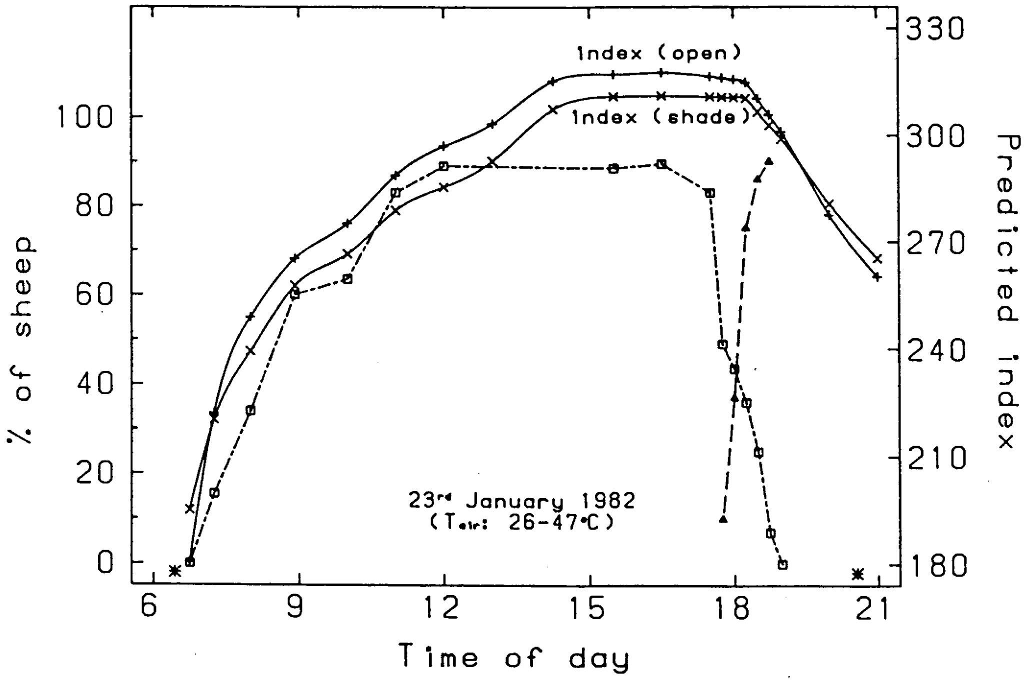


Figure VI.3: Traces of predicted respiration index (in the open and in shade) for sheep on 23rd Jan 1982, compared with percentage of sheep actually in the shade (□); ▲ show percentage of sheep leaving water to graze rather than move directly to water. All sheep were inactive from 1100-1730 h. * mark sunrise and sunset.

(ii) Prediction of entry to shade.

Given that the index is related to heat-avoidance behaviour, I now test whether it may be used to predict the decision to move to shade. Time of arrival at shade in the morning might be related to heat loadings alone, since hunger and thirst are often satisfied early in the day. However, there are three possible complications. Firstly, some sheep may rest in the open before moving to shade, whilst others may go to shade immediately after grazing. In the latter case, hunger may delay movement to shade by temporarily over-ruling the heat response. 'Directed' grazing (towards a shade site) might be expected under these circumstances.

Secondly, for a sheep that is resting in the open, there will be a trade-off between the saving gained by being in shade and the effort involved in getting there. Thus distance to the nearest shade will normally be important (as well as possibly affecting the recorded time of arrival of an animal at shade).

Thirdly, the difference between respiration indices in the open and in the shade (and consequently the energy and water savings of being in shade) decreases with increasing wool length, for any given set of conditions. Although sheep with any length wool may reach a critical threshold of the respiration index, other influences, such as distance to shade, are likely to increase the variability of behaviour shown by woolly sheep over their shorn counterparts. It is also important to know whether the absolute value of the respiration index, or the difference between its value in the open and in the shade, is likely to be the better predictor of behaviour.

The following predictions may therefore be made:

(1) sheep which have been grazing immediately beforehand should enter shade at a higher value of R than those entering after resting.

(2) with increased distance to shade, sheep should only move there at higher values of R.

(3) variability in the use of shade should decrease when sheep have shorter wool, since they then have more to gain by going to shade in hot conditions.

Using the mapped data from the various paddocks for days on which sheep used shade sites, I have determined the approximate time when the main movement to and from shade occurred for known conditions. I have also recorded whether animals went directly to shade from grazing, or after a period of resting in the open. As usual, there is a confounding effect of season (and consequent temperature) and wool length. I have categorised by long and short wool length (dividing in winter and at shearing time), and calculated the predicted indices for the prevailing conditions (Table VI.2).

Table VI.2

Threshold levels of the respiration index for entry to and exit from shade by shorn (wool length about .02m) and woolly (wool lengths .055-.07m) sheep, with and without the possible effects of hunger or thirst. $\Delta R$ = open index - shade index, one factor in the relative cost of not being in shade.

| | index threshold level | | | $\Delta R$ | |
|---|---|---|---|---|---|
| | mean | s.e. | n | mean | s.e. |
| Entry to shade. | | | | | |
| SHORN | | | | | |
| - | 201.9 | 13.8 | 5 | 64.7 | 15.5 |
| WOOLLY | | | | | |
| after resting | 226.7 | 11.2 | 6 | 11.4 | 4.4 |
| direct from grazing | 245.0 | 12.5 | 8 | 19.8 | 4.8 |
| Exit from shade. | | | | | |
| SHORN | | | | | |
| direct to water | 209.6 | 16.5 | 3 | 47.0 | 14.7 |
| to graze first | 189.6 | 30.9 | 3 | 35.2 | 17.8 |
| WOOLLY | | | | | |
| direct to water | 249.6 | 13.9 | 10 | 8.1 | 1.3 |
| to graze first | 249.0 | 12.0 | 11 | 4.2 | .8 |

Although I do not have suitable data for the testing of prediction (2), both it and prediction (3) imply considerable variability in behaviour in the open paddock, and this is certainly shown. Firstly, shorn animals enter (and leave) shade at lower levels of the index than do woolly sheep (t-test, p=.08). Because wool length is confounded with time of year, this may result from physiological adjustments to cooler nights. As required by prediction (3), the shorn animals have much more to gain ($\Delta R$ values) by going to shade at a given index level than do woolly sheep (t-test, $p<.0001$). However, the sample size for shorn sheep is too small to be categorised by previous activity, which may be why this difference is not reflected in reduced variability as also predicted.

Woolly sheep tolerated a higher index value when going to shade direct from grazing than if they had been resting in the open. This is reflected also in an increased difference between shade and open indices ($\Delta R$), representing an increased cost incurred by not going to shade. The differences are not significant (t-test, $p>.10$), but support prediction (1) as well as the suggestion that some other index - here hunger - may delay entry to shade. There were not enough cases for this effect to be examined in the shorn sheep.

### (iii) Prediction of exit from shade.

Departure from shade may be affected by other factors. The respiration index in the open falls below that in the shade towards sunset. Once in shade, however, there is little reason for an undisturbed sheep to leave, if neither hunger nor thirst become significant. On hot days, sheep first leave shade with remarkable synchrony from points so widely scattered, in and between paddocks, that it is unlikely that they could have influenced one another. For example, on the day referred to in Figure VI.3, after at least 6 h in the shade, the first sheep to depart from eight of the ten shade trees under observation did so within 12 minutes of each other. These trees were scattered over more than 2 km. This initial synchrony of behaviour is common on hot days, but breaks down in cooler weather.

On hot days, most early departures from shade are animals that proceed rapidly to water. Only later do departing animals graze more and more en route to water, until the last departures may not even go to drink. In Figure VI.3, for example, sheep leaving shade about 1800 h all moved to the waterpoint (.5 to 2 km from the shade trees) with little grazing, whilst those leaving shade around 1900 h were predominantly grazing, as the triangular symbols show. Those sheep remaining at shade trees shade until 1900 h maintained the same high proportions actually in the shade. In a similar fashion, sheep that have been in shade near a waterpoint (and often watering during the hot afternoon) usually become active about one hour after the first departures from shade trees at a distance from the waterpoint.

These observations suggests that the first departures from shade occur when the significance of thirst over-rides that of the heat loading incurred by leaving shade, whilst the later departures are influenced by hunger. Thus, at about 1800 h on 23rd January 1983, the thirst of some animals had out-weighed the advantage of staying in shade. Other animals, whose water status was better (e.g. they had drunk that morning instead of the previous night), stayed in shade until close to the time at which there was no advantage in doing so (i.e. respiration index in shade equal to that in open). Since some animals voluntarily spent as much as 10 h without grazing on this day, the effect of hunger may be less important relative to heat loading than that of thirst.

The prediction that, in the open paddock, thirst should hasten the departure from shade is supported in Table VI.2 by the data for shorn sheep. There is no difference in the threshold level for woolly sheep that depart shade to different activities. However, for sheep of both wool lengths there is a reduced cost ($\Delta R$) in leaving shade by the time animals depart to graze. Again, none of these differences is statistically significant (t-test, $p>.05$).

Finally, can a threshold level of the index be set for movement to and from shade ? It is clear that the absolute value of R is a better predictor than the cost ($\Delta R$) of not being in shade. The threshold levels of R for entry to and exit from shade are consistent for sheep within each class of wool lengths, but a correction factor is apparently needed for wool length. The predicted threshold levels of Table VI.2 correlate significantly with wool length over all the data ($r=.41$, $n=52$, $p=.003$). The energy balance model is accurate in predicting wooltip temperatures (see the Appendix), so that this represents variation in the response to energy loading, rather than an error in calculating the energy flux into the sheep's body. Because wool length is confounded with season at Middleback, I cannot tell whether the variation in response is a result of physiological adjustment to seasonal temperatures, or because the relative use of different cooling pathways changes with wool length (see Appendix Figure 5 and related discussion).

In either case, a correction factor for wool length can be inserted in the threshold value, and consistent threshold levels can then be determined to predict movement to shade for a given breed. This physical model is therefore successful at predicting an aspect of ranging behaviour in the large open paddock.

(iv) Location and use of shade sites.

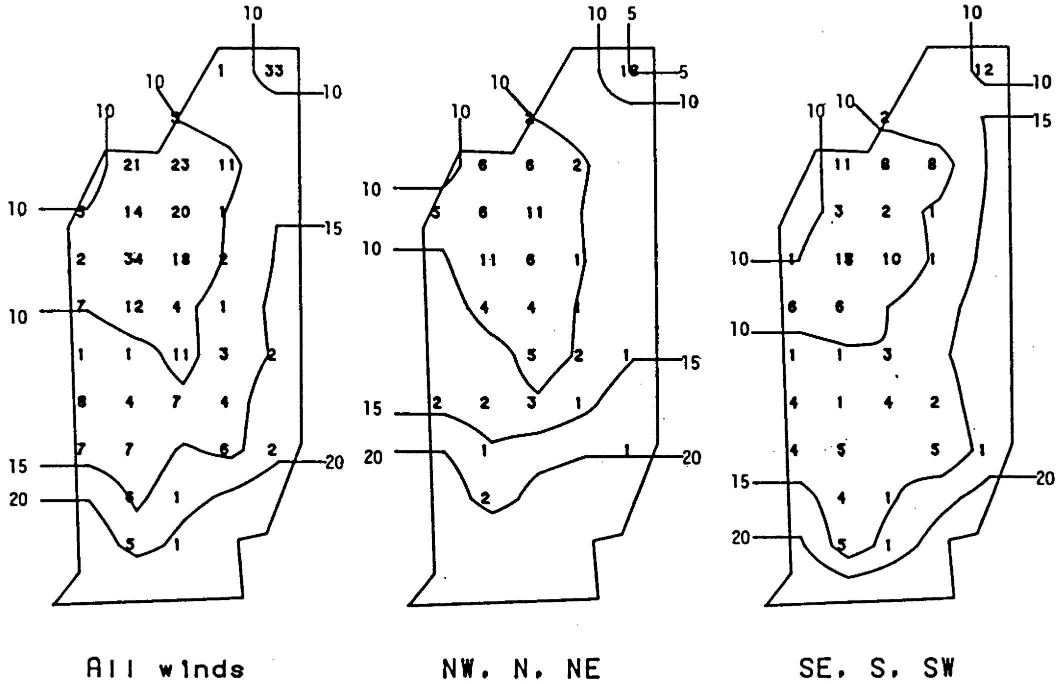
Once it is possible to predict when a sheep will move to shade, the next question concerns which shade site will be used. Not all trees in Jervoise are used by sheep. Most isolated trees will harbour sheep at times, but where there are many to choose from, only a limited number will ever be used, and fewer still will be used regularly in any given year. Trees which are used frequently for shade have less undergrowth and are surrounded by more bare ground than others. This is likely to be a result of their use as shade sites, as well as a cause of their continued use. Their original selection is historic, perhaps entirely due to chance, but is now self-perpetuating.

Some learning by sheep seems to occur from year to year: I mention this observation briefly, but have no good data to support it. With respect to shade, learning effects were most evident in the use of the trees in cells 29, 30, 44 and 45 (see Figure IV.9(a)). In summer 1980-81, about 20 trees in this area were used for shade by sheep; two trees in particular would always have sheep under them when there were sheep in the area. In 1981-82, these two trees were never seen to be used, and had very little fresh dung under them in comparison to others. In summer 1982-83, one was again in heavy use, but the other continued not to be used. In all these summers, sheep were using other shade located less than 100 m from each of these two trees. There are no obvious correlates to this behaviour, and it may be simply a function of chance learning about local shade sites from year to year.

On a small number of occasions when I frightened sheep from under a shade tree, I observed that the fleeing group moved rapidly away from me for about 100 m, and then one of the leading sheep turned abruptly and headed towards another tree. On some occasions, this was not the nearest tree, but was the nearest tree used regularly as a shade site. These two types of casual observations strongly suggest that at least some individuals learn the location of specific shade sites over the whole area of the open paddock during the year. It would be interesting to investigate the nature of this learning by moving all or part of a paddock's flock elsewhere; however, on this scale, and with any controls, the necessary trials would be monumental. More importantly for modelling, these observations suggest that sheep do know where the nearest shade site is, but that selection between individual trees takes place on a scale which is sufficiently local to be irrelevant at a cell size of 500x500 $m^2$.

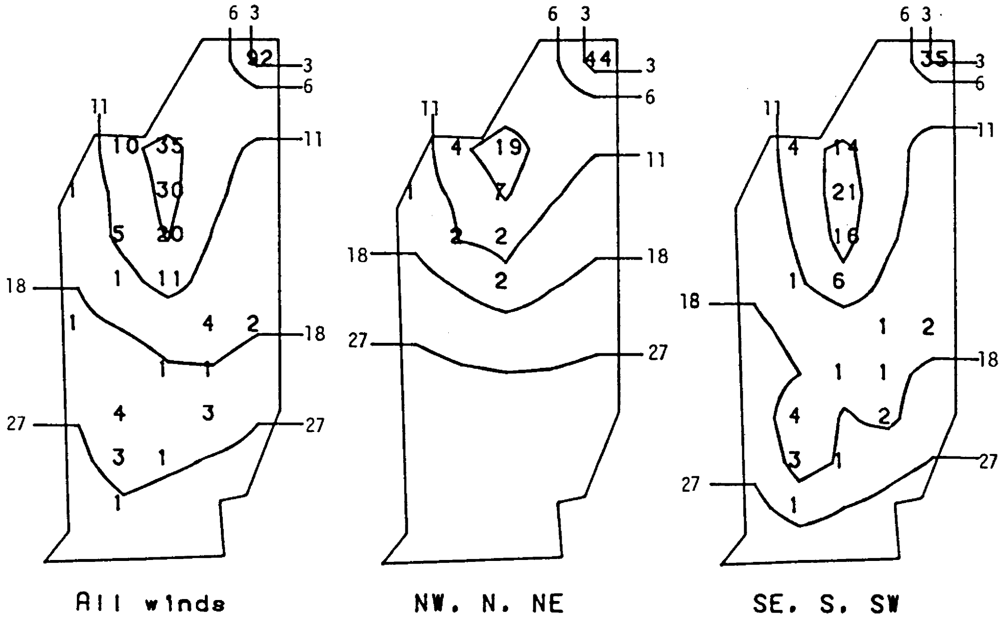
The general location of shade sites which is used under given conditions might be 'chosen' as that area nearest to the position of the animals when the respiration index exceeds critical values. Alternatively, the sheep might foresee that shade will be needed later in the day and graze towards a specific shade location. In the first case, shade location would be determined predominantly by grazing movement, and in the second, the grazing movement would be biased or 'directed' towards the shade location.

It is difficult to test between these possibilities at the scale of my mapping. However, Figure VI.4 shows the distribution of all shade site usage over the paddock, divided into records from southerly and northerly winds. As usual, there is a considerable extension of activity into the south of the paddock in southerly winds. The activities r and s were not separated in the map records until April 1981, so this data does not include my first three fieldtrips.



All winds NW, N, NE SE, S, SW

Figure VI.4: Maps of shade use by groups of sheep for all records from Jervoise, 1981-83; all data, and records from northerly and southerly winds only. Numbers and contours as in Figure VI.1.



All winds NW, N, NE SE, S, SW

Figure VI.5: Maps of all the resting groups from Figure VI.1 translated to the nearest shade site. Numbers and contours as in Figure VI.1. Note the similarity in disposition to Figure VI.4.

Figure VI.5 shows the data for rest sites shown in Figure VI.1 translated directly to the nearest cells with shade. The records in the two figures are not matched exactly for environmental conditions, since shade is used predominantly in conditions different to those in which the sheep rest. There is a reduced use predicted for cells 14 and 19 (see Figure IV.9(a)), because the surrounding shade cells were closer to the rest sites in the translation. However, there is a marked similarity in the distribution of the translated rest data to the shade data, which suggests, apropos of the first hypothesis above, that the locations for both these activities depend on similar factors; in other words, on movement in grazing and the position of the previous site of inactivity (camp or water), biased only by the location of the nearest shade.

As a further test of the first hypothesis, I examine the amount of directed grazing that precedes the occupation of shade sites. The potential occurrence of directed grazing is important because it can alter the location of grazing impact both by increasing movement speeds in grazing, and by adjusting movement directions. The first alternative above does not predict directed grazing towards shade, whilst the second does. I have already shown that hunger can delay entry to shade, and this might be expected to cause directed grazing.

Figure IV.6(a,b) shows how the extensive activities of g, gm, mg and m (see Table IV.3) vary during the course of the day. It is clear that most directed grazing (gm and mg) occurs near dawn and dusk, and is therefore related to watering (as is the increased absolute numbers of groups moving - m - at these times). In the mid-morning, when sheep are moving to shade, there is very little directed grazing, which again supports the first hypothesis. Figure VI.6(c) shows the

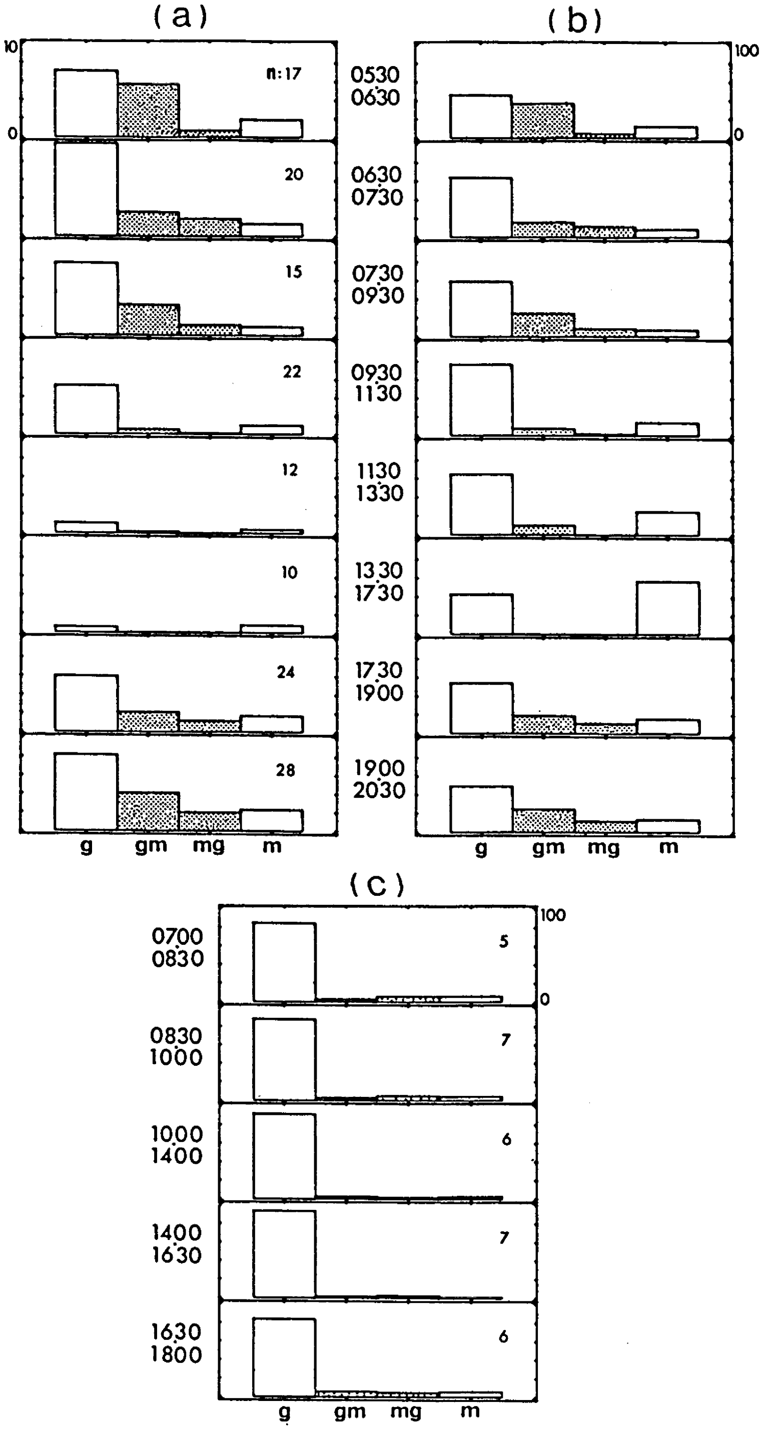


Figure VI.6: Distribution of groups between grazing activities with different amounts of movement during the day. (a) numbers and (b) percentages of groups for all summer days on which shade was used, and (c) percentages for winter records. 'Directed' grazing activities are shaded. The time periods and sample sizes are indicated.

equivalent winter records which include negligible directed grazing. The small amount of gm in late morning in summer may therefore be movement to shade, but it is of minor proportions.

### (v) Movement directions.

Finally I test whether movement directions before and after the use of shade were influenced by wind or other foci of activities. I collected data on shade site usage from the maps using similar methods to those described for the rest sites (section (a.i)). I found a total of 91 records, excluding shade use by the waterpoint. The details of these records are shown in Table VI.3, to which similar comments apply as for Table VI.1.

The location of the waterpoint again constrained arrivals to be from the north when the previous non-grazing activity was watering. However, there are sufficient records where campsites were the previous focus to analyse these by wind direction. In northerly winds, sheep were always moving north from camp, whereas for southerly winds, the division between directions is not significantly biased to the south. This reflects the use of campsites close to the south fence in south winds, from which it is necessary to move north. Here paddock geometry over-rides any effect of wind. However, it is notable that in many cases when the sheep were grazing north from the southwest campsite (see Figure VI.9), they moved up to shade in cells 39 and 40 (see Figure IV.9(a)) despite the presence of less-used shade further south. These animals would usually continue north to water in the late afternoon, and this may be an example of movement directed by the need to water later in the day.

## Table VI.3

Arrivals and departures of sheep subflocks to and from shade sites in Jervoise, 1980-83. Numbers of records of movement in different wind conditions and for different previous or subsequent activities are shown. Where relevant, $\chi^2$ tests are given.

| | | Arrival or departure direction | | | n |
|---|---|---|---|---|---|
| | | NW,N,NE | SE,S,SW | E/W | (total) |
| ARRIVAL (from) | | | | | |
| in winds: | northerly | 14 | 17 | 2 | 33 |
| | southerly | 25 | 20 | 2 | 47 |
| last site: | water | 26 | 1 | 2 | 29 |
| | camp | 11 | 35 | 2 | 48 |
| from camp in: | N'ly winds | 0 | 16 | | 16 |
| | S'ly winds | 11 ——[1]—— | 19 | | 30 |
| DEPARTURE (to) | | | | | |
| in winds: | northerly | 29 | 3 | 1 | 33 |
| | southerly | 37 | 10 | 1 | 48 |
| next site: | water | 52 | 0 | 0 | 52 |
| | camp | 2 | 11 | 1 | 14 |
| to camp in: | N'ly winds | 0 | 1 | | 1 |
| | S'ly winds | 2 ——[2]—— | 10 | | 12 |

[1] $\chi^2_1=1.63$, $p>.10$, arrival directions from camp in S winds not significantly related to wind direction (Yates' correction applied).

[2] $\chi^2_1=4.08$, $p=.04$, distribution of departure directions to camp in south winds significantly related to wind direction.

In these records, most animals leave shade for water and therefore move north. For such sheep as do go to a campsite, there is a significant southerly movement in south winds, which may be related either to grazing movement or to the choice of a southerly campsite. In summary, results are very similar to the more sparse records for rest sites (section (a.i)).

### (vi) Summary: shade use.

Use of shade is related to heat loading of the sheep. A physical model of the energy balance of a sheep provides a good prediction of respiration rate with a respiration index that is related to the evaporation needed for cooling. This index is shown to be relevant to shade-seeking behaviour in the open paddock, and to be a good predictor of when shade will be used. There are interactions with hunger which delay entry to shade, and with thirst which advance exit from shade. The specific trees used for shade sites may be influenced by learning, but the area of shade sites occupied under given conditions is closely related to the usage of rest sites, corrected by movement to nearest shade. The location depends largely on movement during grazing since the last non-grazing activity, but may involve some directed grazing towards shade.

### (c) Water.

It is well-known that the waterpoint is a significant focus of activity in a paddock. In many paddocks, there is only one source of water, so that when animals need to drink regularly their activity patterns are bound to be centred on this waterpoint. The water requirements of an animal are a function of the amount of water that it can take in a single drink, and its net rate of water use. A model of water balance may be used to predict when drinking should occur. In some paddocks, animals do have a choice between waterpoints, and this selection must also be modelled.

#### (i) Water balance and requirements.

Following Noble (1975), the water balance of a sheep may be written as,

drinking intake + water in food + metabolic water = evaporative
losses + urinary losses + faecal losses.

Metabolic production of water is taken as being approximately constant, whilst the water obtained from food depends both on the condition of the vegetation and diet selection. Evaporative losses may be determined from the heat balance model described in the previous section and in the Appendix. These will be slightly over-estimated, since the model does not allow for other heat loss mechanisms (see Appendix), but this may be allowed for in the setting of threshold levels. Urinary and faecal losses of water have an approximately constant component, but must also allow for the disposal of dietary salt, a factor which is also dependent on vegetation condition and diet selection. The equation will normally be balanced as a result of the sheep adjusting its drinking intake. If this becomes impossible, it could also maintain the balance by reducing feed intake where water content is low, and by using shade to minimise evaporative losses.

Figure VI.7 shows the water usage by sheep in Jervoise for 1980-83, obtained from the waterpoint meter records (see Chapter IV(d.iv)). Each point represents the mean intake of water per head per day, averaged over the number of days since the previous reading (this interval varied from 1 to 82 days, mean 5.5, mode 2, n=147).

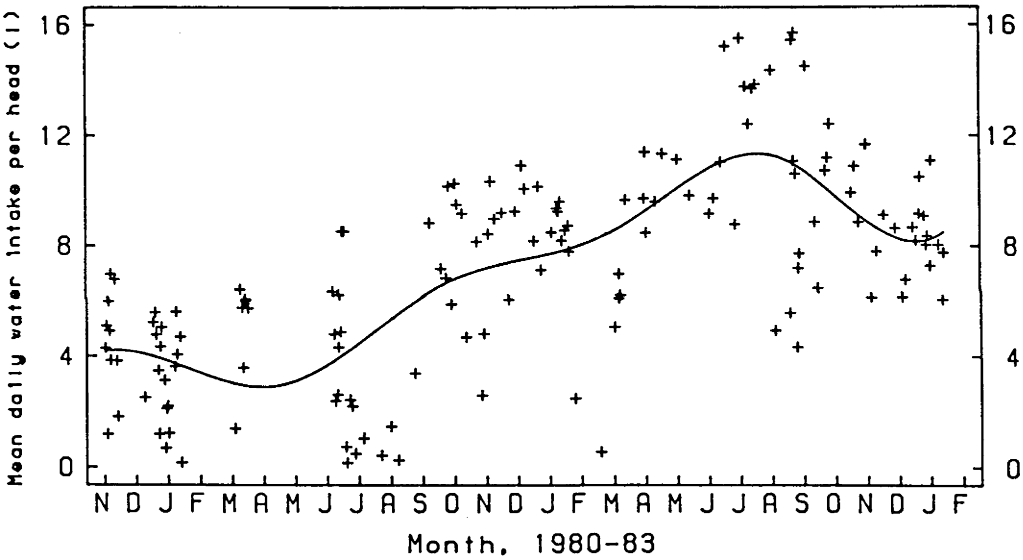


Figure VI.7: Mean daily intake of water intake per sheep from late 1980 to early 1983, estimated from intermittent readings at the Jervoise water meter. The curve is a spline fit.

The water-balance equation above predicts that the intake of water should be affected by the variables of the heat balance model, and by vegetation condition. For saltbush, and some other chenopod shrubs, salt and water contents are approximately inversely related (e.g.

Sharma et al.1972). My indices of vegetation condition (Table V.2) are likely to correlate with both. I performed a multiple regression between the intake per head per day and year, maximum and minimum temperatures, index of season (as described in Chapter V(c.ii)), wool length, and the vegetation indices (shrub and ephemeral). The temperatures used were the mean maximums and minimums for the interval concerned, except that periods of longer than seven days were excluded from this analysis. Whilst temperature maxima should affect the heat loading on the sheep, low overnight minima correlate both with low humidities and clear weather.

Table VI.4

Multiple regression of water intake per head per day in Jervoise against various environmental parameters. The linear regression equation is: intake = constant + Σ b*V, where V are the independent variables listed below, and b their respective coefficients.

| Independent variables | % reduction in S.S. | Predicted equation coefficient | significance[1] |
|---|---|---|---|
| Constant | - | 5.59 | - |
| Shrub index (1-11) | 44.3 | -.675 | <.001 |
| Wool length (.01-.07m) | 4.5 | 52.1 | .005 |
| Mean max. temp. (°C) | 3.6 | .185 | .002 |
| Mean min. temp. (°C) | 2.0 | -.137 | .058 |

[1] from t-test on predicted coefficient, d.f.= 88

Shrub condition, wool length and temperature contributed to more than 1% reduction in the sum of squares. Their contributions and the resulting coefficients are shown in Table VI.4. A total of 54% of the variation is explained by these parameters (F-ratio = 25.0, d.f.=4,84, p<.0001), corresponding to a multiple correlation coefficient of 0.74 (n=89, p<.0001). The effect of shrub condition is unexpectedly strong, but is due to the major changes that occurred during the major drought year (1982). It has over-ridden the effect of season, and of the presence of ephemerals (which correlates with drinking in a separate Pearson's test, r=-.41, n=89, p<.001). None of the other three independent variables contribute greatly to the regression (in separate Pearson's correlations with volume drunk, the coefficients are: wool length, r=.16, p=.126; temperature maxima, r=.20, p=.054; minima, r=-.04, p=.708; n=89 for each), but each has the expected effect. There is no remaining trend in the residuals after this analysis: much of the remaining variance may be associated with errors in reading the meter (see Chapter IV(d.iv)).

Since the important factors influencing watering were those that were expected, data were collected to test the actual values of the water index in the model, and its possible threshold levels. The eastern waterpoint of West End paddock was observed from a tower on 20-21 and 27-28 January 1983, from 0530h on the first day of each pair to 2100h on the second. This was the only waterpoint available to the animals in the paddock. Temperature ranges were 12-43°C (20-21st) and 10-36°C (27-28th), and the nights were moonlit. There were 32 marked sheep in the paddock, and the presence of any of them at the waterpoint during these periods was recorded. I am grateful to Paul Jupp for collecting much of this data.

Figure VI.8(a) shows the distribution of watering by the marked sheep over the 24-hour periods. Sometimes a sheep would move into shade near the waterpoint after drinking, and return to water within a few hours. Such repeated watering was defined as a single event when the sheep did not depart more than 200 m from water (the distance was marked with flags). There were strong peaks of watering in the morning and evening, as has been recorded elsewhere (e.g. Squires 1976, Arnold & Dudzinski 1978 p47), but some watering events were scattered throughout the day and night.

During these 39-hour observation periods, many sheep returned to water. Figure VI.8(b) shows the frequencies of different return times. Again there is a bimodal distribution, which seems to reflect the preference to water at one of the modal watering times.

For each individual, I have calculated the water deficit it would have experienced by the time it returned to water according to the water balance equation described above. Values for metabolic water production (.3 l $d^{-1}$), urine losses ignoring salt disposal (1 l $d^{-1}$) and faecal losses (1.5 l $d^{-1}$), distributed evenly through the day, are taken from Noble (1975), who quoted Brown & Lynch (1972) and Macfarlane et al. (1956, 1966). Brown & Lynch (1972) did find a lower value of urinary losses (.25-.42 l $d^{-1}$) for sheep on low salt diets and under water stress.

In January 1983, there was no ephemeral vegetation present, and the water content of saltbush and bluebush ranged from .45-.75 l per kg of dry weight for non-woody plant material. Assuming some forage selection by the sheep, I used .70 l $(kg\ d.w.)^{-1}$ as an intermediate figure, and 140 g $(kg\ d.w.)^{-1}$ for salt content (after Wilson 1966). I assume a slightly low intake of 1 kg d.w. $d^{-1}$, distributed evenly through the day. Noble (1975), after Wilson (1966) and Macfarlane et al. (1966), assumed that an additional 30 ml of water were required to excrete 1 g of salt. Finally, evaporative losses associated with cooling were calculated directly from the respiratory index, which was derived from hourly weather records for the days in question.

Figure VI.8(c) shows the distribution of the calculated water

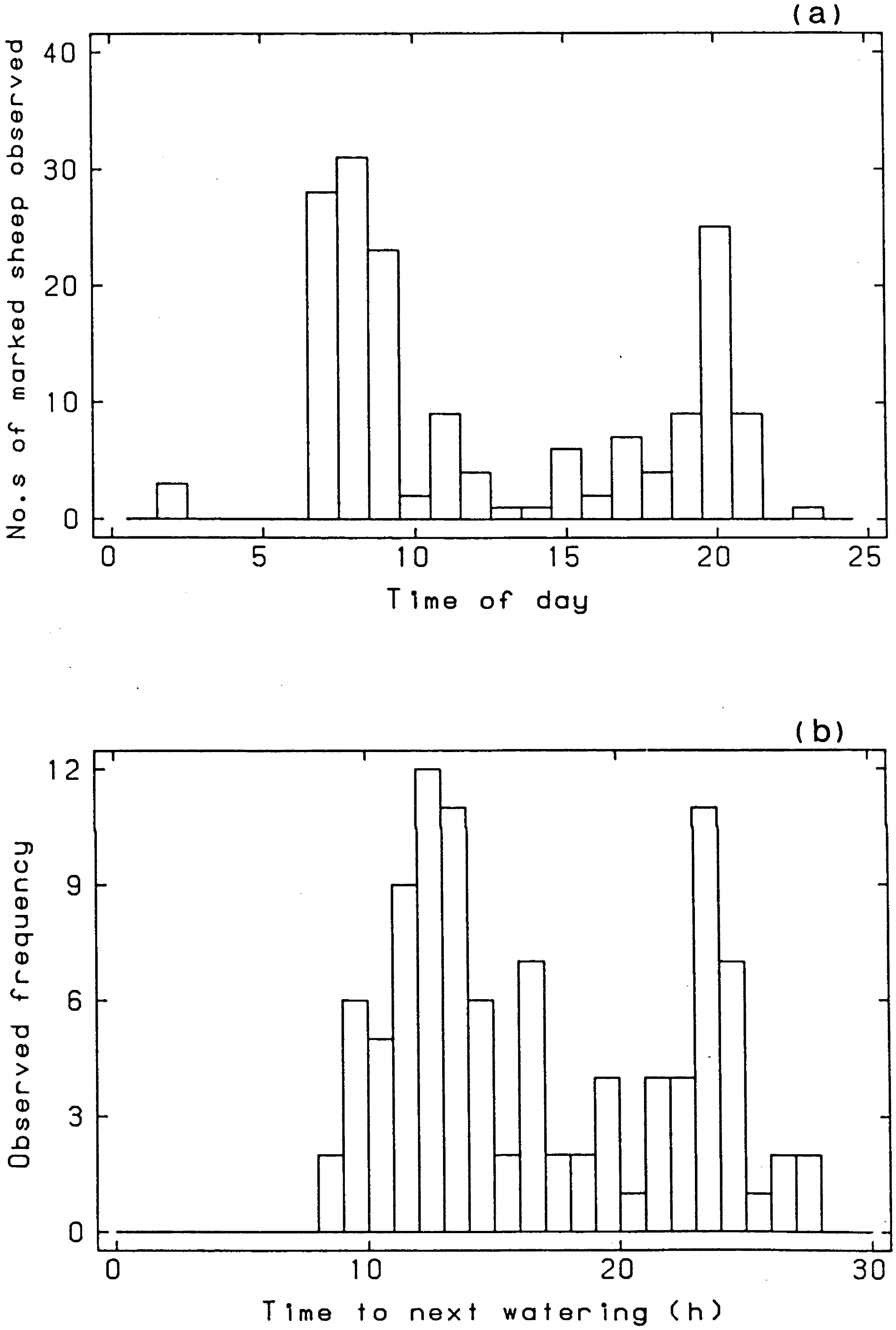


Figure VI.8: Watering behaviour by marked sheep at the West End trough, January 1983. (a) Distribution of watering through the day (* marks sunrise, 0640 h, and sunset, 2020 h). (b) Distribution of return times for re-watering. (Continued on next page).

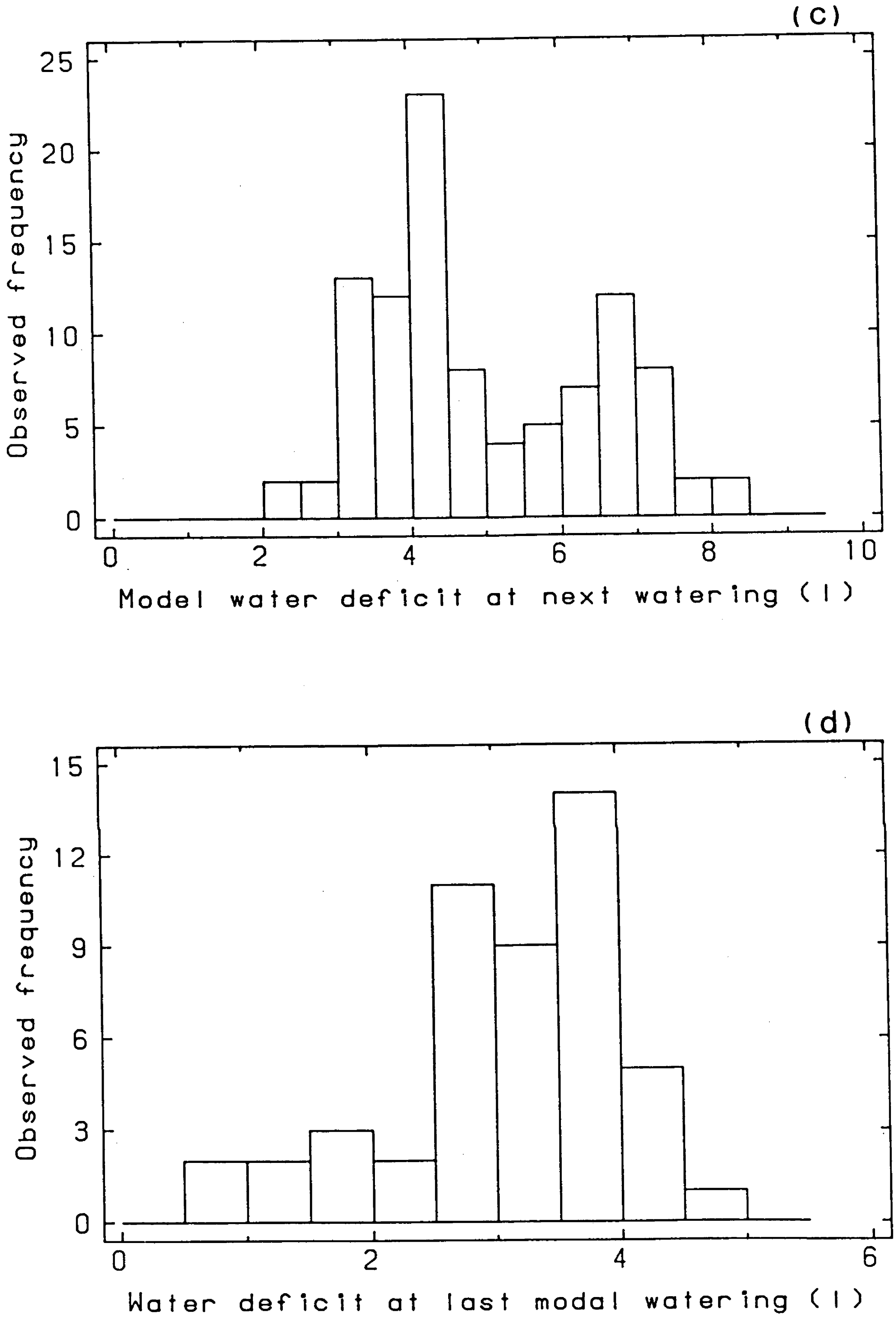


Figure VI.8(ctd): Watering behaviour of marked sheep at the West End trough, January 1983. (c) Modelled water deficit at the time of re-watering. (d) Modelled water deficit at the modal watering time (0800 h or 2000 h) nearest preceeding the time of re-watering.

deficit at the time when individual sheep watered again. There is again a bimodality. This is likely to have occurred because heat loadings tend to restrict animals to shade in the afternoon, and other factors (perhaps genetic) encourage them to remain camping at night.

According to the original model, sheep became thirsty at a pure water deficit of 3 l, and severely dehydrated at 5 l. On the basis of Figure VI.8(c), a 3 l deficit seems a reasonable approximation for the first level of thirst, but the sheep can evidently tolerate much greater deficits than 5 l. To what extent is this tolerance related to the factors which constrain most watering to the two modal peaks ?

Many sheep delayed at least one possible modal time before watering again. Figure VI.8(d) shows the frequency distribution of modelled water deficits that these sheep would have experienced at the last modal watering time (taken as 0800 h or 2000 h) at which they did not drink; there is a sharp cutoff at about 4.5 l pure water. This may be taken as the maximum deficit that a sheep will tolerate at a time when conditions do not suppress watering. A deficit of about 8 l is the maximum that can be tolerated regardless of restraints placed by heat loads or camping behaviour. The relation of these figures to respiration index thresholds will be discussed in Chapter X.

An accepted tenet is that sheep take no more than 5 l in one drink (e.g. Wilson & Hindley 1968). As Figure VI.7(a) shows, individuals were drinking over 15 l per day at the peak of the 1982-83 drought. The maximum intake actually coincided with both winter and lambing, and may have been more extreme than otherwise because of lactation requirements. However, even in the following summer, over 11 l per head was being drunk in a day. Whilst this high water intake may be partly explained by multiple waterings - some sheep visited the trough morning and night, and others drank several times in the afternoon while resting near the waterpoint - it strongly suggests that larger amounts may have been taken during one visit. At times, a distinct sloshing noise could be heard as the sheep walked away from water.

Figure VI.8(b) also supports the latter suggestion, since the water deficit by the time of return may be as high as 8 l of pure water. The West End waterpoint supplies well water, with salt concentration of about 3500 ppm, so that 1 l of water drunk is equivalent to only .895 l of pure water. To obtain 8 l of pure water, it is then necessary to drink nearly 9 l of well water. Although a sheep need not entirely refill its water store, these figures support a higher maximal intake under extreme conditions.

### (ii) Selection of watering point.

In Jervoise, there is no choice of waterpoints available to the sheep. In Wizzo North, there are four waterpoints (see Figure IV.6(b)): the Central Dam, a trough fed from the Morgan-Whyalla pipeline (the E 'McGouishs' trough), a trough fed from the well at Roopena (the SW trough), and a trough windmill-pumped from a smaller dam in the neighbouring Ram Paddock (W trough). The western trough was only observed in use once, and is not discussed further.

I had intended to obtain data on the differential use of these waters, but two problems developed. Firstly, the drying of the dam in early 1982, and the failure of the eastern trough in February 1982, gave rise to an inconsistent availability of waterpoints. Secondly, although the sheep seem to prefer dam water to either the salty well-water or the chlorinated Murray water, the extent of any preference is unknown. Most of the brief discussion that follows is therefore based on anecdote.

Sheep are renowned to be slow to learn a new water site when shifted, and may return repeatedly to their original waterpoint. Sometimes this imputation is unfair, if, for example, they can sense the continued presence of water in a dam but are denied access. In Wizzo North, marked sheep were rarely observed to move from one waterpoint to another during a four day mapping period. In 1980-81, water was available at all waterpoints, but all observed watering occurred on the Central Dam and the E trough, which are separated only by about 2.5 km. Some transfer was seen between these two waters; two marked sheep were sighted at both waterpoints, out of 20 occasions where a marked sheep could be relocated on successive days. One marked sheep was seen by the east fence and then the west fence (6 km apart) on successive days, indicating that considerable movement was occurring, although this does not prove multiple water use.

In 1982, only the E and SW troughs were available and in April 1982, sheep were split more-or-less evenly between these. The groups associated with each waterpoint were separated almost entirely in range, usually coming into contact only in cells 25 and 19 (Figure IV.9(b)). Despite 13 resightings of marked sheep during that trip, no transfers between areas were observed. On one occasion, a group containing two marked sheep was frightened from cell 29 to 23 in the southeast corner of the paddock. Despite the close proximity of several groups from the E trough which were moving north to water, this group was observed to stolidly retrace its steps along the southern fence. It was seen by the SW trough the next morning, having travelled at least 5km across a range of hills.

Thus there appears to be an inertia in any change of waterpoint use, although changes do occur naturally, especially in the long-term. Presumably this inertia is related to the learning ability of sheep and the latency of their memories. Sheep in Wizzo North certainly knew the layout of the Central Dam when they were using it: if they were blocked at one exit, they would immediately depart by the alternative route, which is out of sight of the first. When two waterpoints are close together, they may be encountered often enough to remain in the sheep's memory: this appeared to be the case with the Dam and the E trough in 1980-81. With greater distances and consequently longer time periods between encounters, locations seem to be forgotten, as appeared to be the case between the SW and E tanks in 1982.

### (iii) Movement to and from water.

Because the waterpoint is such an important focus of sheep activity in the paddock, it can be seen as a pivot point for successive periods of non-watering activity. The direction of departure from the waterpoint then assumes importance in determining which area of the paddock will be used between waterings, especially if those waterings occur at frequent intervals.

To examine the influence of weather on the directions of departure from water, and with the help of Mr Paul Jupp, I collected data on movements to and from waterpoints in Jervoise and West End paddocks in January 1983, at the same time as recording watering frequencies as described above. All dams on the property were dry, and it was impossible to find a permanent trough located in the middle of a paddock. The eastern trough of West End subtends about 180° from the fencelines, and Jervoise waterpoint only about 90° (though movement patterns were better understood here, and there was better visibility). Arrival and departure directions were recorded for all sheep from first to last light on a total of 14 days (Chapter IV(c.vi)). However, I was unable to relate arrival and departure directions to prevailing wind directions and time of day, primarily because of the lack of a 360° approach (which compounded the complexity of movement patterns), and the need to track the subflocks further out into the paddock than could be seen from the West End waterpoint.

I also examined map records for watering in Wizzo North in the same manner as described above for rest and shade sites in Jervoise. The resulting data is confounded by varying waterpoint availability, and is too restricted to be useful. The most important question concerns whether and how movement out from water is affected by wind. Although limited, these data tend to support the hypothesis that the direction of movement out from water is preferentially into the wind.

The waterpoint is important in causing directed grazing, to a degree that shade sites are not. Analyses of the shade and rest site data for Jervoise have indicated that the sheep's need to drink in the evening may already be influencing their behaviour in the early morning (see section b.v). Figure VI.6 clearly demonstrates the increase in directed grazing at times when watering is occurring.

### (iv) Summary: watering.

The water balance of sheep may be modelled by balancing water loss from evaporation and excretion (including water necessary to dispose of dietary salt intake) with gains from drinking and from food intake. Drinking is shown to be related primarily to the condition of the vegetation in a series of dry years, as well as to the requirements of respiratory cooling. Time of watering may be related to a water deficit derived from the water balance equation, with allowances for the effect of other influences which constrain watering to modal morning and evening periods (in summer at least). For sheep in open paddocks, quantities of water consumed in a single drinking session are likely to exceed those quoted in the literature for closely penned animals. Switching between multiple waterpoints seems to be constrained by frequency of use and by consequent memory of waterpoint location; switching between distant waterpoints was rare. Although attempts to study movement in and out of waterpoints were unsuccessful, partly due to drought conditions, the need for water is the major influence in directed grazing.

## (d) Camping.

### (i) Location and movement.

It was difficult to obtain any reliable information on camping, since it was impossible to locate a significant proportion of the flock at night. Some spot-lighting was tried unsuccessfully and with considerable disturbance. However, from early morning records of animals leaving camp, and from frequent finds of fresh dung, it was certain that most camping in Jervoise was confined to a few localised areas (Figure VI.9). There were four regularly-used main areas (sites 1-4), all associated with hillsides; three were also by fencelines (2-4). A site was located on each of the main hills in the paddock. Sites 1 and 3 comprised a loose agglomeration of several smaller areas, each typically 50-100 m in diameter. Another area in the northwest corner (site 5) was used significantly only in 1980-81, and the use of site 4 varied greatly between years. Comments made in section (b.iv) about learning with regard to shade sites may also be applicable to campsites.

It is notable that the energy balance model described in the Appendix shows that sheep would be warmer under a tree on a clear winter's night (providing it was not located in a frost hollow), but in fact they invariably occupy the tops of hills. It is often argued that this occurs because temperature inversions result in warmer air temperatures at the top of hills, which is true on calm nights. However, the cover of a tree would significantly reduce radiant heat losses to the night sky. This suggests that inherited factors may influence sheep to camp on hilltops, so that the camping phenomenon cannot be modelled by an approach akin to that used for shade-seeking.

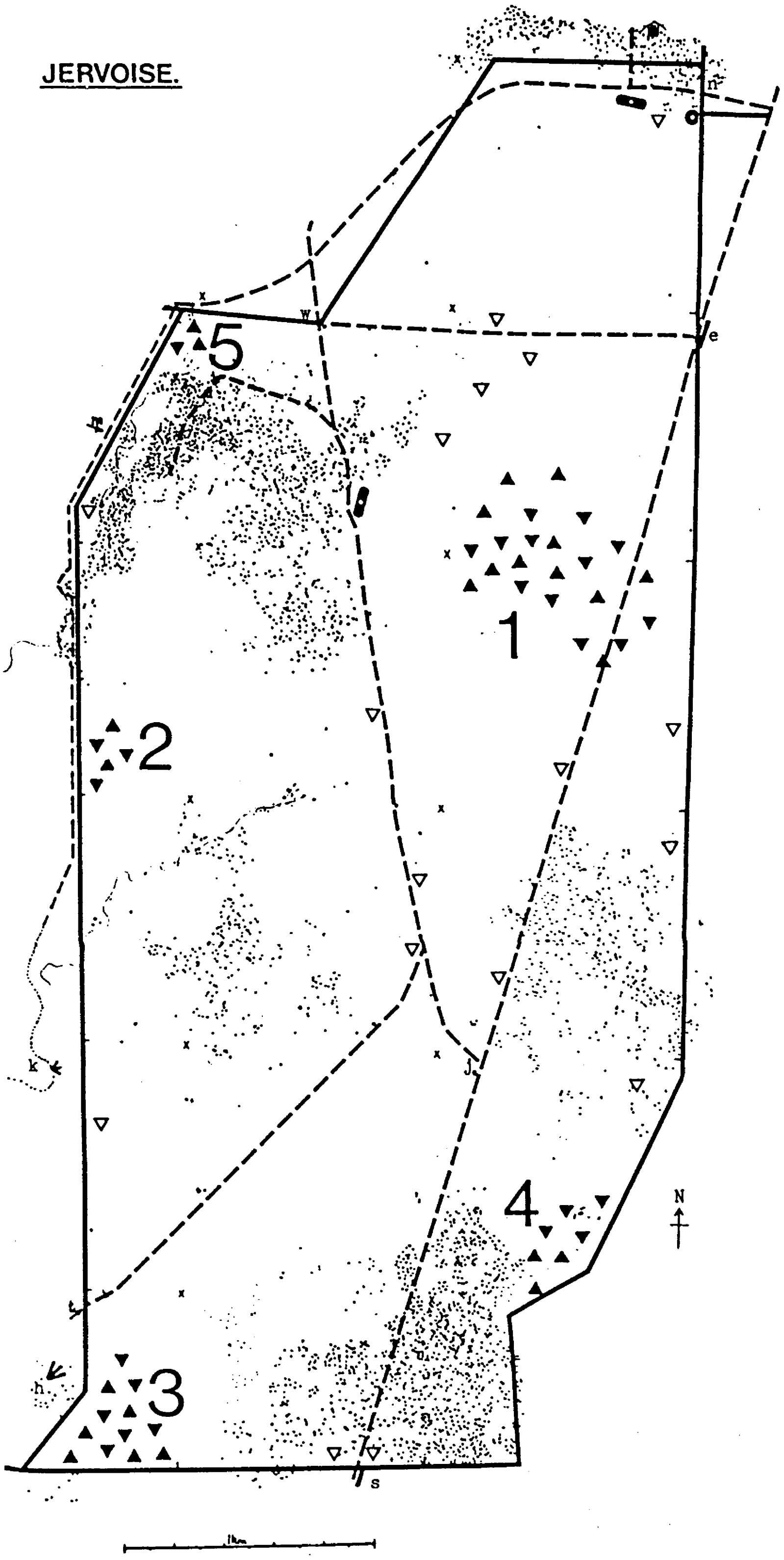


Figure VI.9: Areas used regularly as campsites in Jervoise (solid triangles). Open triangles mark other sites known to have been used, usually by few sheep only for one night.

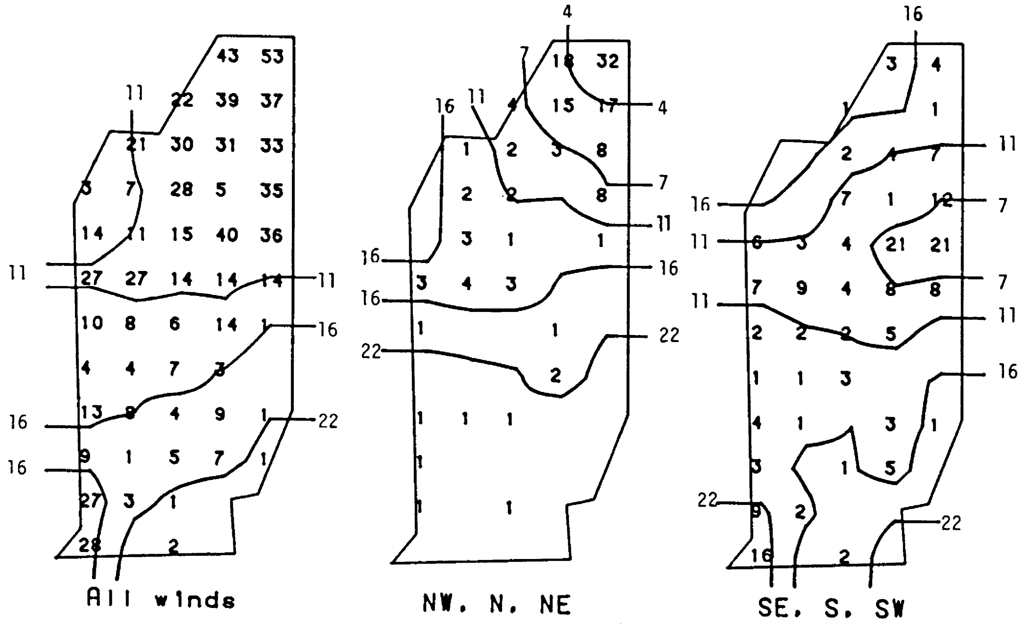


Figure VI.10: Distribution of all sheep groups in Jervoise in 'dawn' records; all records, and records from northerly and southerly wind conditions. Numbers and contours as for Figure VI.1.

Figure VI.10 shows the location of sheep in Jervoise for all early morning ('dawn') records, 1980-83 (many dawn records occur in calm conditions, which accounts for the disparity between the summed values of the righthand maps, and those of the lefthand map). Sheep activity is focused on the major campsites, especially sites 1 and 3. High densities also occur on the west fence where sheep were often moving north from site 3. The restriction of the use of sites 3 and 4 to southerly wind conditions is evident. The loss of discernable pattern in northerly winds reflects warmer mornings and consequent earlier starts by the sheep, especially in 1982-83.

There was some use of areas in cells 1 and 2 for camping during summer 1982-83. Other locations where camping is known to have occurred on at least one occasion are marked on Figure VI.9; these are not always associated with hills. Defining a night's campsite as the location at which sheep last rested before dawn, I estimate that 90-95% of all camping activity occurred on campsites 1-5 during the period of observations.

On the basis of late evening and early morning records for Jervoise, I analysed the maps for campsite usage in a similar manner to that described for rest and shade sites. The records are tentative, and biased towards campsites 1 and 3; these were more easily observed, although they were undoubtedly used more than the others. Site 3, being positioned on the southern fence, was invariably approached from the north, and departed from in the same direction. Site 1, centrally located in the paddock, should have been the most useful for the analysis of movement patterns, but was dominated by animals arriving from and departing to the waterpoint. No useful information was obtained from this analysis.

### (ii) Summary: camping.

Over 90% of camping activity occurs at very few sites (5 in the 1500ha area of Jervoise). These sites are associated with both hills and fencelines, and may be a diffuse association of smaller sites. Night time activity was difficult to study in the open paddock. Sites in the south of the paddock were only used in south winds.

# Chapter VII

## Grazing movement in the open paddock.

The previous chapter has examined each of the foci of non-grazing activities. It is possible to predict when these foci are used, and it is from them that grazing periods begin. The two chapters following this consider some aspects of diet selection once the sheep are in a given area of the paddock. In this short entr'acte, I examine movement in grazing, which determines the areas in which diet selection will occur after the sheep have left a rest, shade, camp or watering site.

I have already remarked on the possibility of 'directed grazing'. There are, then, two circumstances in which it is necessary to consider movement in grazing - when the animal is grazing towards a definite goal, and when it is simply grazing (which I shall term 'undirected grazing' hereafter). The two important questions are what conditions induce directed grazing, and how speed and direction is determined in undirected grazing.

### (a) Directed grazing.

If the occurrence of directed grazing is dependent on urges other than hunger reacting with the hunger trigger, as discussed in Chapter VI and as indicated in data such as that presented in Figure VI.6, then it should occur at times of year and of day when the animal is likely to be driven by these other urges. These times should normally be near the dawn and dusk watering periods, and towards the time of entry to shade. A similar effect may occur at night before camping, but I have only anecdotal information on this.

Table VII.1 presents the correlations between various environmental factors and the proportion of grazing groups that are moving significantly (i.e. [gm+mg]/[g+gm+mg]). Time of day has been included in the analysis as a binary index for records made near dawn, towards the end of morning grazing, midday, as grazing begins again in the afternoon, or near dusk.

Over all the data (1980-83), there is a clear between-season effect, shown also by maximum temperatures and vegetation indices. Increasing numbers of subflocks show directed grazing as ephemeral presence declines between summers, although the seasonal effect is stronger. Time of day is most significant in predicting directed grazing, however, with increased amounts at dawn and dusk, and a consistent lack of directed grazing in the middle of the day. Movement increases on clear days and on days on which shade was used, but the correlations with time of day suggest that this may be related to the need to water on days when shade is used, rather than to the use of shade itself.

## Table VII.1

The effects of various environmental variables on directed grazing under different conditions in Jervoise. Pearsons correlation coefficients between the arcsine transform of the proportion of all grazing groups (g+gm+mg) that are showing significant movement (gm+mg) and environmental variables. Records with less than 2 grazing groups are omitted.

| | All data | | Summers | | Winters | |
|---|---|---|---|---|---|---|
| Variable & range | r | p | r | p | r | p |
| Season (-1,1) | .19 | .004 | n.a. | | n.a. | |
| Max temp. ($^{o}$C) | .19 | .004 | .11 | - | .02 | - |
| Cloud (0-8) | -.14 | .031 | -.21 | .007 | -.12 | - |
| Wool length (m) | .02 | - | -.02 | - | -.20 | - |
| Shade use (0,1)[1] | .26 | <.001 | .21 | .008 | -.27 | - |
| Shrub condit (1-11) | -.13 | .043 | -.06 | - | n.a. | |
| Ephem. condit (0-6) | -.28 | <.001 | -.17 | .029 | .20 | - |
| Near dawn (0,1) | .27 | <.001 | .27 | .008 | .15 | - |
| Mid morning (0,1) | -.16 | .012 | -.26 | .001 | .22 | - |
| Near midday (0,1) | -.25 | <.001 | -.31 | <.001 | -.02 | - |
| Mid afternoon (0,1) | -.15 | .020 | -.09 | - | -.39 | .034 |
| Near dusk (0,1) | .09 | - | .14 | .067 | .03 | - |
| No. of map records: | 248 | | 179 | | 28 | |

- = p>.10; n.a.= not applicable (e.g. all data identical)

[1] days on which >1 group used shade coded as 1

Thus directed grazing is most likely to occur at watering times on days when water is needed, and perhaps on days when shade is used; this corresponds with the predictions of Chapter VI(b.iv). Directions and rates of movement may then be determined. Direction of movement will be related to the goal of the directed movement. Speeds in 'gm', 'mg' and 'm' range from about .5 to over 2.0 k $h^{-1}$ (and sheep may run into water at up to 5 k $h^{-1}$ from up to 500 m away).

### (b) Undirected grazing.

Undirected grazing is not confined to the 'unstressful' days of winter: it may also occur throughout cooler summer days, and at restricted times on other days. Movement in undirected grazing may partially determine which shade and rest sites are likely to be used. The two components to movement are direction and speed. If popular beliefs are to be confirmed, direction of movement in grazing sheep should be strongly influenced by wind direction. I examine this, and the influence of vegetation quality on movement speeds.

#### (i) Direction of movement.

I have described good evidence to show that wind direction influences which part of a paddock is used. This influence is often presumed to be due to the effect of wind on movement during grazing. Alternatives could be that sheep move without grazing to an area of the paddock, and then proceed with their activities there, or that intermittent directed grazing movements are the dominant determinators of grazing location. In fact dramatic 'trekking' movements out from the waterpoint (cf. Squires 1974b), which were not immediately followed by the use of shade or a camp, were occasionally observed, not caused by any human agent. These were rare, so I hold to the precept of movement being congruent with grazing if a move to a non-grazing site is not involved. I assume that such treks were caused by some stochastic frightening event in the environment (kangaroos and emus, amongst other less-obvious agents, certainly caused movement by subflocks at times).

Direction of movement in grazing was the least deterministic section of Noble's model of sheep behaviour. It was selected randomly, with an unvalidated bias towards movement into the windwhich is increased at higher wind speeds, or biased in the current movement direction if there is no wind. Local effects of other factors such as slope have been hypothesised, but were not noted in Jervoise. Grazing along a contour on the steeper slopes in Adam's West and Wizzo North paddocks (locally up to $20^{o}$) was sometimes observed, but on most occasions slope seemed to be ignored. The presence of incised sheep tracks might have an effect on preferred directions of movement: this is certainly important in directed grazing. Sheep tracks are themselves dependent on paddock geometry and previous usage, so their effect could only be distinguished where a major re-arrangement of a paddock had occurred (e.g. movement of a waterpoint).

The question as to why sheep should respond to wind has received little attention in the literature. If an animal has no reason to move in any particular direction, one might expect that some default factor such as the sun or wind should be adopted to orient its otherwise random movements. Any other factors, such as steep slopes, or the frightening presence of a predator, will override the default. For a herbivore strongly dependent on smell, an obvious possibility would be to graze in the direction from which the next odour is coming. Because winds shift, different areas will be used on different days, which could be a practical advantage for an animal that is centring its activities on a single waterhole. In any case, one should not expect dependence on any default factor to be complete; agents that may seem trivial to humans, such as crowing birds or moving kangaroos, are bound to introduce a stochastic element. This inevitably requires a non-deterministic element in a model which cannot attempt to describe the sheep's environment and reactions with perfect knowledge.

I have tested the hypothesis that grazing occurs into the wind by examining all records of the activity 'g' for movement direction in relation to wind direction and speed. Figure VII.1 shows wind and grazing directions for all the records in Jervoise and Wizzo North when there was a definite wind direction; all distributions are different to random ($\chi^2_7$, p<.001 always). The distribution of recorded wind directions was not even, as is shown by Figure VII.1(a) and (d), so the total number of subflocks seen grazing in each wind direction is also shown in (b) and (e) for comparison with directions of movement. The number of groups actually grazing in each direction, shown in (c) and (f), does not relate closely to the other distributions. There is a clear dominance of north-south movement, especially in the narrower Jervoise with its single waterpoint; this implies that paddock geometry may be a dominant factor in influencing grazing movement.

Table VII.2 contains the correlations between numbers of groups seen in a given wind direction and the numbers moving in that direction. The correlations are never significant, and actually negative in Jervoise, due to the strong predominance of north-south movement. Because of this, the data from Wizzo North, which is more-or-less square, should be more reliable for looking at the effect of wind; here the correlations are always positive, but still never significant. The influence of wind direction may be enhanced in higher wind speeds, although there is no parallel sign of this in Jervoise.

The apparent importance of factors other than wind is indicated by Figure VII.2, which shows the movement directions in the two paddocks in calm conditions (i.e. I could not determine a wind direction).

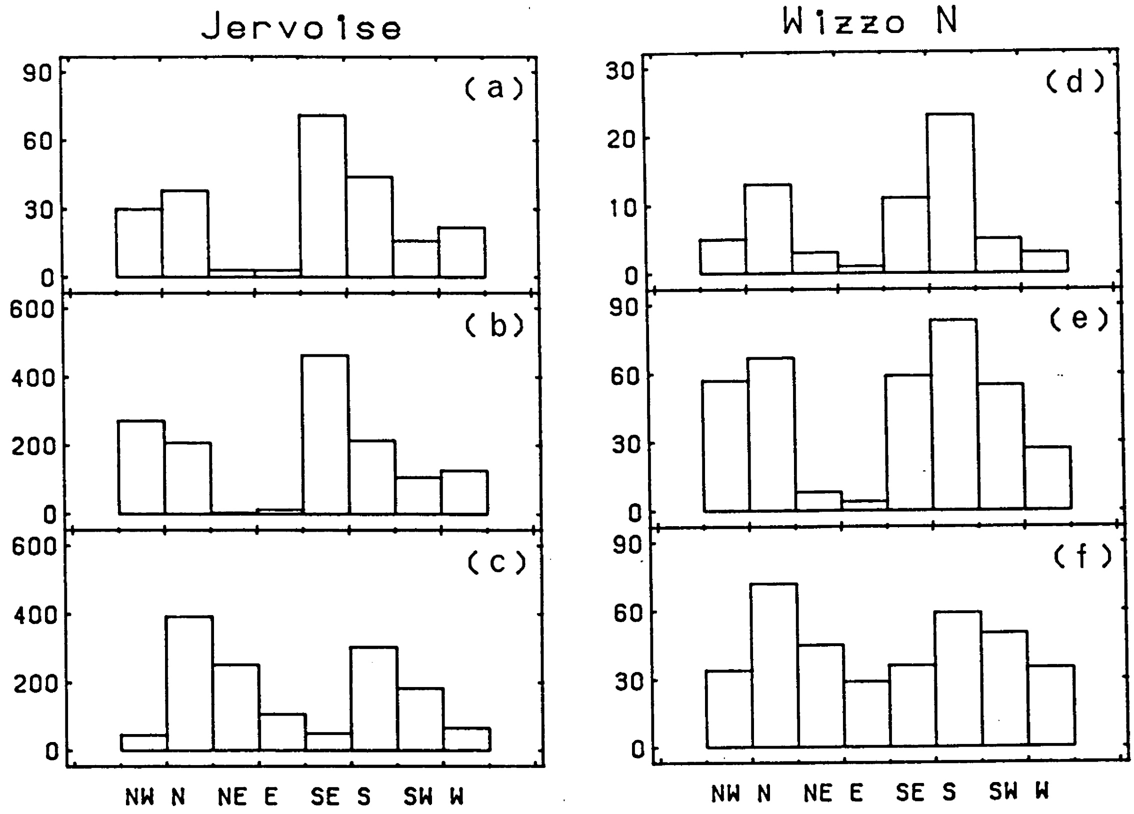


Figure VII.1: Recorded wind directions and grazing movement directions in Jervoise (a-c) and Wizzo North (d-f). (a) and (d), numbers of records for each wind direction; (b) and (e), numbers of sub-flocks seen in records from each wind direction; and (c) and (f), numbers of subflocks seen grazing in each direction.

Table VII.2

Correlations between the numbers of subflocks seen in records from a given wind direction and the numbers of subflocks seen grazing in that direction, for Jervoise and Wizzo North, under various environmental conditions. Statistic is Spearman's non-parametric correlation coefficient, all n=8, missing p-value indicates p>.10.

| | Jervoise | | Wizzo North | |
|---|---|---|---|---|
| | r | p | r | p |
| All data | -.38 | - | .67 | .068 |
| Summers | -.24 | - | .51 | - |
| Winters | -.30 | - | .11 | - |
| Wind speeds 1-9 k $h^{-1}$ | -.21 | - | .42 | - |
| Wind speeds 10-25 k $h^{-1}$ | -.41 | - | .60 | - |

All movement directions in Jervoise vs. all in Wizzo: r=.81, p=.015

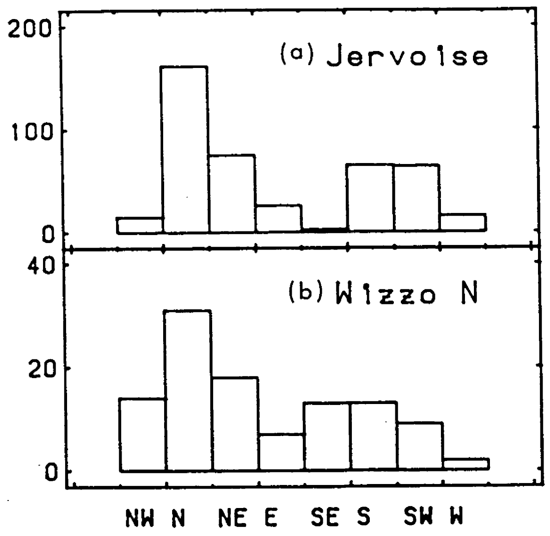


Figure VII.2: Numbers of subflocks seen grazing in different directions in calm wind conditions; (a) Jervoise, (b) Wizzo North.

These are similar to the windy data movements, especially in Jervoise (in Jervoise, Spearman's r=.95, p<.001; in Wizzo, r=.52, p>.10; for calm conditions in Jervoise versus Wizzo, r=.49, p>.10; all n=8).

The above results show that there are biases in grazing directions, but that north-south movements dominate any effect of wind. Finally, I test whether movement directions when transformed with respect to wind direction are different to random. Figure VII.3 shows grazing directions relative to the prevailing wind direction for Jervoise and Wizzo North. All these distributions are significantly different to random ($\chi^2_7$, p<.001). However, if grazing occurred consistently into the wind, there should be a peak at 'Same'. Such a pattern is never clearly seen, although there is some sign of it in stronger winds in Wizzo North.

As has been discussed previously, wind is known to have some

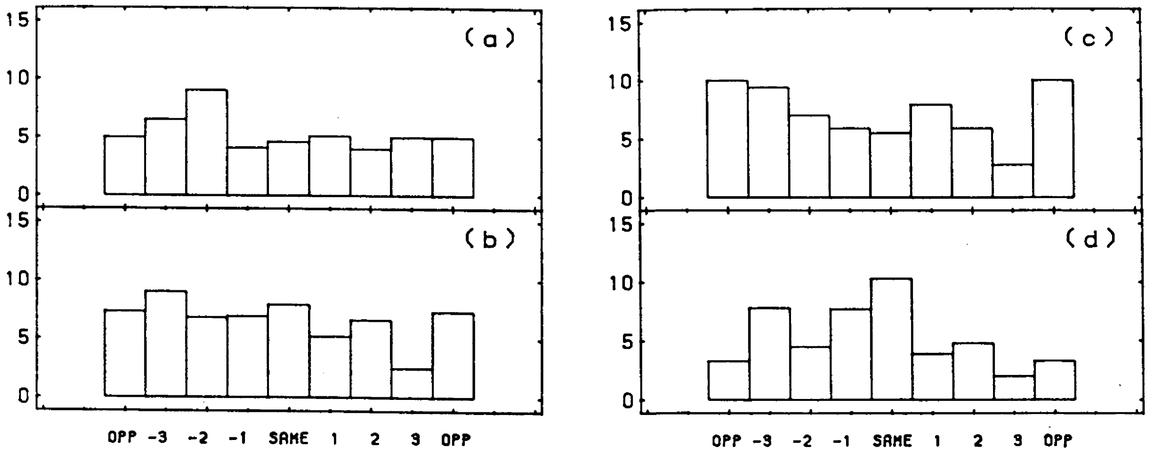


Figure VII.3: Grazing directions transformed for each records so that 'SAME' is numbers of subflocks grazing into the wind, 'OPP' is those grazing with the wind, and positive values are clockwise points in between. (a) all data from Jervoise; (b-d) Wizzo North, (b) all data, (c) records in wind speeds 1-9 k $h^{-1}$, (d) wind speeds >10 k $h^{-1}$.

effect on the area of the paddock in use. Since it has little influence on directions in grazing, this analysis therefore suggests that the effect of wind may be more important in determining which shade or camp site is used under given conditions. In other words, the choice of a southerly campsite in south winds may be far more important to location the next morning than some small amount of movement south during the previous grazing period. I shall return to this point in Chapter X.

## (ii) Speeds of movement in grazing.

Movement speed in grazing is important in determining how grazing impact is distributed as animals move out from foci such as water, camp or shade sites. Noble (1975) found it necessary to include an ad hoc effect in his model whereby movement speed was increased if the sheep had ingested less than a threshold amount of food in a cell during the previous time step. My small enclosure work showed that speed is affected by vegetation quality or density (Chapter VIII(c.i)). I therefore tried to find a similar dependence in the open paddock. When a non-disruptive and reliable technique was finally devised, it was unsuccessful for reasons probably associated with universal poor vegetation condition.

I was trying to find a relationship between movement speed in undirected grazing and local vegetation condition - in particular the biomass and numbers of palatable shrubs, and biomass of ephemerals. On the scale of tens of metres there is considerable variability in these parameters in the open paddock. It was therefore necessary to be able to determine a subflock's position accurately at frequent (e.g. 5 minute) intervals without disturbing their behaviour. The subflock had to have recently started its grazing period, to allow time for enough records, and had to be grazing without apparent intent to move to water.

Initially I tried following a subflock on foot, remembering their position every five minutes and marking it with a peg as soon as I could catch up. I then returned later to measure the distance between the pegs and to characterise the vegetation on a 30x3 $m^2$ quadrat between each pair of pegs. It was difficult to be sure of not affecting the animals' movement, and to remember the positions accurately when they were moving slowly or in open vegetation. Alternative triangulating methods would have been cumbersome, and required at least three people.

Finally a photographic method was developed. From a stationary vantage point (e.g. the top of a Toyota), with 400ASA colour print film and a 500mm lens, I took a photograph of a subflock every five minutes. The animals could be up to 1 km away, and the best accuracy was obtained if they were moving across the field of view. The film was then processed and printed cheaply. From the same vantage point, I would then direct a helper with a walkie-talkie to the centroid of the subflock in each photo; detail was usually adequate to position pegs to within 2m using the shrubs observable in the photo. This part was very quick, and I could then return alone later to measure distances and vegetation. The method had the advantages of being remote, of using two people only briefly and at leisure, of using already available equipment, and of being cheaply aborted if a watch was unsuccessful. It required reasonably calm weather, and had to be used during the morning grazing period to avoid heat haze. As with previous methods, it still involved many wasted early mornings when no suitable subflocks could be found, or they changed behaviour pattern during the watch.

This technique was used in summer 1982-83. Out of about 15 early mornings, I obtained four records of reasonable length. One showed no significant variation in movement speeds. The others certainly contained variation in speeds, but this could not be related consistently to vegetation parameters. The vegetation in any single location was in such uniformly poor condition that a much more detailed study of the remaining plant biomass would have been necessary to find the parameters, if any, that the sheep were selecting by (e.g. perhaps water content).

I believe that this technique would be useful in future studies, lthough radiotracking would be an alternative. Results would probably be clearest if there was spatial variation in the quantity of ephemeral material when it is at a low level, as often occurs in late spring.

### (iii) Summary: grazing movement.

Directed grazing occurs at times of year and times of day that are compatible with the hypothesis that it is a response to need for water and shade. Undirected grazing is more strongly influenced by paddock design than by wind direction, since the location of shade and camp sites seems more important than movements during undirected grazing in determining which area of a paddock is in use under given conditions. An attempt to link movement speeds in the open paddock with vegetation quality was unsuccessful, primarily due to the poor condition of the vegetation.

# Chapter VIII

## The grazing period in small enclosures: activities and movement.

In the previous three chapters, I have tried to establish where grazing will occur in the open paddock, and especially where grazing periods will begin. In this chapter and the next, I turn to small enclosure work to examine the process of grazing in more detail.

An animal's intake of a plant food type in a given area is determined by the following factors:

1. the instantaneous intake rates by the animal for that food type,
2. the animal's preference for that food in that area,
3. the proportion of time actually spent eating by the animal, and
4. the rate of movement of the animal through that area.

From the point of view of the plants rather than the animal, trampling and wastage are also important, as are other factors which operate at a finer scale.

In this study I have tried to examine the principles involved in the variation of some of these factors under different forage conditions, rather than simply describing values applicable to a single vegetation type. The latter are needed for a model of a given area, but an understanding of the principles is necessary to effect transfer of the model to other areas, and to delineate the parameters which need to be measured for the new site.

The next chapter concerns itself with the finer details of intake rates, and how selection changes with satiation. It also briefly examines switching rates between plant individuals and species. On trampling and wastage I have little data, and I do not mention them further. This chapter describes the small enclosure design and techniques used in this part of the study. I then discuss the changes in major activities during the grazing period, and examine movement speeds.

## (a) Small enclosure work: methods and analysis.

The small enclosure work was based on detailed observations of the grazing behaviour of groups of three sheep in 0.1 ha enclosures containing variously-treated vegetation types. In this section I briefly outline the experimental designs and data handling techniques.

### (i) Observation Runs and designs.

Between April 1981 and May 1983, small enclosure observations were carried out in six sets of trials: I refer to these as Runs 1 to 6. Each Run consisted of a number of acclimatisation trials, during which a new group of sheep became used to my presence, and then usually nine trials from which the data was actually analysed. The dates and general characteristics of the Runs are given in Table VIII.1.

Run 1 was mostly exploratory, and will not be greatly referred to. Each of the other Runs involved observations in three different vegetation treatments. Figure VIII.1 shows a typical fencing layout. Three 0.1 ha enclosures were located in uniform vegetation, with a 2 ha holding yard beside them in the same vegetation. Observations were made from the roofrack on a Toyota, so observation points were placed along an existing track where possible. There was a pen around the waterpoint into which the sheep could be mustered from the holding yard, and from which they could be released with minimal handling into any of the enclosures. In Run 4, I examined the effect of experience in the holding yard, so I built three separate enclosures with their own holding yards in different vegetation types (in West End, Depot and Chimney Yards paddocks); the design was otherwise similar to that described below, except that all trials in one vegetation type were

## Table VIII.1

Summary of Runs: dates, numbers of trials (N), shrub vegetation treatments in enclosures and holding yards, locations, duration of overnight penning (H, in h) and numbers of animals used in all.

| Run no. | Date | N | Treatments[1] (shrubs) | Holding[1] yard | Paddock location | H | Total sheep |
|---|---|---|---|---|---|---|---|
| 1 | Apr 81 | 5 | Mix | Mix | Chyds[2] | 13-14 | 4 |
| 2 | Nov-Dec 81 | 9 | Bb<br>Sb[3]<br>Mix | Mix | Chyds | 10 | 9 |
| 3 | Jan-Feb 82 | 9 | Bb<br>Sb<br>Mix | Mix | Chyds | 10.5 | 9 |
| 4 | Apr-May 82 | 9 | Bb<br>Sb[3]<br>Mix[3] | Bb<br>Sb[3]<br>Mix[3] | West End<br>Depot<br>Chyds | 12.5 | 3 |
| 5 | Nov 82 | 12 | 40:60[4]<br>55:45<br>20:80 | Mix | Barbers | 10 | 9 |
| 6 | Apr 83 | 9 | 50:50[4,5]<br>60:40<br>20:80 | Mix | Barbers | 12.3 | 3 |

[1] Treatments: Sb = saltbush only, Bb = bluebush only, Mix = mixture
[2] 'Chyds' = Chimney Yards paddock
[3] significant amounts of ground material present (usually dry)
[4] Bb:Sb shrub biomass ratios, by dry weight (approx).
[5] newly germinated ephemeral material in early trials.

consecutive, and four days acclimatisation to the holding yard were permitted.

Vegetation treatment was achieved by removing the above ground biomass of unwanted shrubs and herbs by chopping, hoeing and sweeping. One enclosure usually required at least a full day's work. Table VIII.2 details the vegetation treatments in each enclosure for each Run, and the enclosure names. Figure VIII.2 illustrates the approx-

## EXPERIMENTAL DESIGN OF TREATMENTS
## RUNS 5 & 6 ('Barbers')

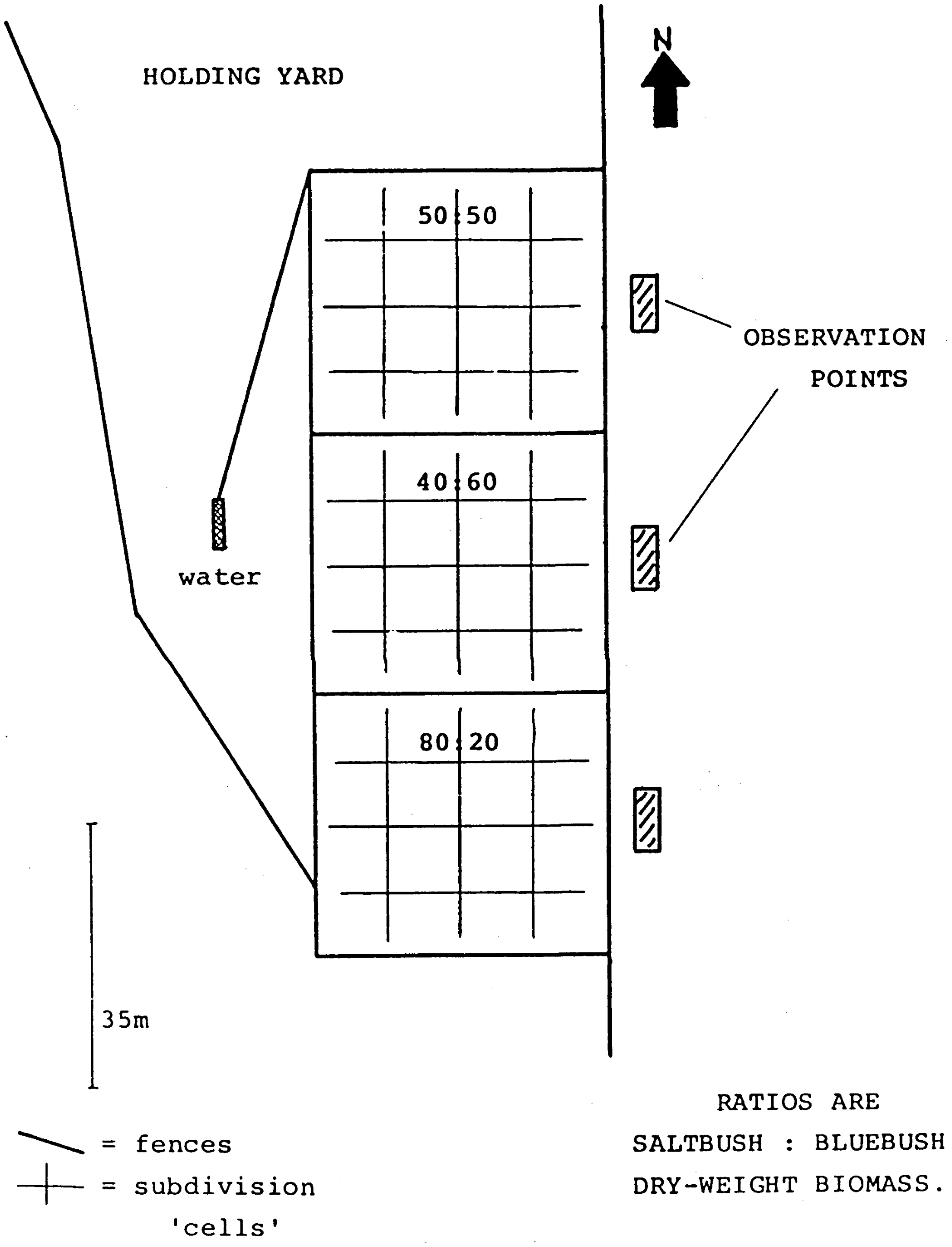


Figure VIII.1: Experimental design and layout of enclosures in Barbers paddock for Runs 5 and 6: similar arrangements were used for Runs 1, 2 and 3. (Temporary gates used for mustering and penning animals overnight by water are not illustrated). The subdivision into 'cells' was used in Run 6 (see Chapter IX(a.i,b.v)).

imate biomasses for each set of enclosures. It should be noted here that this method of vegetation treatment removes biomass by reducing shrub density, which is very different to an equal amount of biomass reduction by grazing; in the latter case, a selected (most palatable) element of the vegetation is removed, both inter- and intra-specifically.

Table VIII.2

Vegetation parameters used for Runs 2 to 6: shrub biomasses were assessed intermittently using the 'Adelaide' technique (see Chapter IV(b)). All weights are kg dry weight after 60h at 80°C.

| Run no. | Enclosure name | Numbers of shrubs | Bluebush | Saltbush | Total shrub | Approx ground | Total biomass |
|---|---|---|---|---|---|---|---|
| 2 | NW1 | 180 | 18.0 | - | 18.0 | .5[1] | 18.5 |
| | NW2 | 269 | 14.3 | 14.7 | 29.0 | .5[1] | 29.5 |
| | NW3 | 224 | - | 15.6 | 15.6 | 2.0[1] | 17.6 |
| 3 | NW1 | 180 | 14.0 | - | 14.0 | - | 14.0 |
| | NW2 | 269 | 13.8 | 10.7 | 24.5 | - | 24.5 |
| | NW3 | 224 | - | 11.6 | 11.6 | 1.0[1] | 12.6 |
| 4 | West End | 153 | 41.5 | - | 41.5 | - | 41.5 |
| | Depot | 461 | - | 29.0 | 29.0 | 3.6 | 32.6 |
| | Chyds | 286 | 14.7 | 5.2 | 20.5[2] | 4.1 | 24.6 |
| 5 | North | 460 | 10.1 | 13.7 | 23.8 | - | 23.8 |
| | Mid | 421 | 10.6 | 9.0 | 19.6 | - | 19.6 |
| | South | 445 | 3.3 | 16.4 | 19.7 | - | 19.7 |
| 6 | North | 446 | 10.1 | 10.6 | 20.7 | 1.0[3] | 21.7 |
| | Mid | 400 | 12.6 | 8.1 | 20.7 | .9[3] | 21.6 |
| | South | 445 | 3.3 | 15.1 | 18.4 | 1.0[3] | 19.4 |

[1] post hoc estimates to nearest .5 kg

[2] includes 0.6 kg Chenopodium ulicinum

[3] green, newly germinated, mostly eaten in the first trial in each enclosure: all other ground material was dry, mostly grass and bassias, except for some green grass in Run 4 Chyds.

Sheep were obtained from an open paddock, and marked so as to be individually identifiable. They were allowed several days in which to become used to the holding yard and water arrangements. Then they

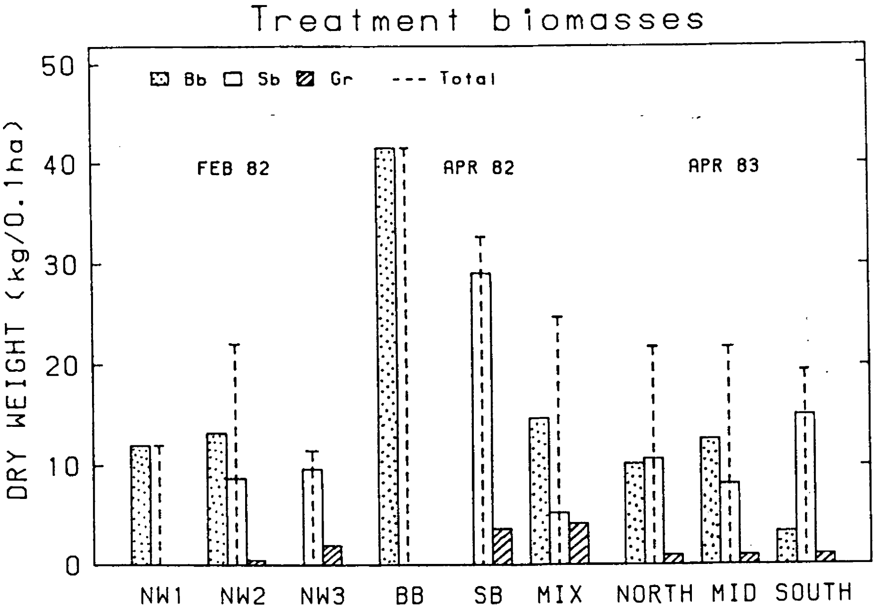


Figure VIII.2: Estimated biomasses in each enclosure used for the small enclosure work (variations between Run not illustrated). Dashed lines show total biomass for each treatment. 'BB', 'SB' and 'MIX' refer to the West End, Depot and Chyds enclosures of Run 4 respectively.

were mustered several times, and observed in an enclosure similar to the treated ones; they soon became indifferent to my presence and that of the Toyota, providing that I did not move significantly. Any exceptionally nervous or aggressive animals were removed at this stage (if they had not already departed over the fence). This was usually one or two sheep out of about 15, so it is not considered to have affected the data with regard to the 'average' sheep.

Each trial in a Run consisted of the observation of the entire early morning grazing period on one day. This grazing period was more easily synchronised with open paddock behaviour, and some observations that were made of afternoon grazing periods suggested that there were no qualitative differences. The three sheep to be watched were penned just before last light on the previous evening. Overnight they had water available ad lib, but usually no food. They were released as soon after first light as the vegetation was visible, usually within 20 minutes of the departure from camp by sheep in the open paddock. They would graze for between one and three hours, during which time watering was not permitted.

The general Latin Square observation design is shown in Figure VIII.3. Statistical analysis of previous studies (Dudzinski, pers.comm.) had suggested that cycling on a longer than three-day period for a given group of sheep should result in no auto-correlation with regard to memory in trials of this sort. The sheep could then be regarded as being drawn at random from the population, although fixed inter-individual differences could not be discounted. For Runs 2 and 3, therefore, 9 sheep were used in three fixed groups; each group was watched in each enclosure, leaving a day between each set of three trials to guarantee the three-day gap. During each trial, I would observe each animal for 10 minutes in turn, in strict cycle (also cycling between the first observed in replicate trials), or watch one animal throughout (cycling through animals between trials).

In the first three Runs, I found no evidence of inter-individual differences. I performed various ANOVA tests, based on the Latin square design, which showed no significant differences between replicates, between animals or between groups of animals either in time spent in major activities or on transition matrix patterns, and I do not discuss these further. As a consequence, in Runs 4 and 6 I used only three sheep. This permitted stricter replication. In Run 5, I was helped by Dr Imanuel Noy-Meir and Mr Peter Cochrane, and we used 9 sheep again since three trials were run simultaneously. Again no differences in the major activity parameters could be found (in

| | Replication of given enclosure | | |
|---|---|---|---|
| Enclosure | 1 | 2 | 3 |
| 1 | 1<br>1 | 2<br>5 | 3<br>9 |
| 2 | 2<br>2 | 3<br>6 | 1<br>7 |
| 3 | 3<br>3 | 1<br>4 | 2<br>8 |

Figure VIII.3: Idealised Latin square design used for replication on each each enclosure within one Run. First number in each cell is sheep group (Runs 2,3,5) or sheep individual (Runs 4,6) being watched; second number is overall day of observation (one day was usually also left between sets of replicates), except for Run 5, where the added complication of three observers is not shown.

transition matrix or stationary analysis) which were attributable to individual animals or observers, although one group of sheep grazed consistently longer than the other two in Run 5.

The sheep were watched until they stopped grazing. Where possible this was defined by the time at which they lay down; sometimes they did not do so, and I had to use my judgement. Most of the following discussion is concerned with the earlier part of the grazing period for which the preciseness of the definition does not matter. Near the end of a grazing period, the amount of time spent inactive rises rapidly. Where I discuss the whole grazing period, therefore, I usually describe its length in terms of the total time spent active, which minimises errors due to the inaccurate determination of the cessation of activity.

After the end of records, the sheep were returned to the holding yard. The time to this release was varied by several hours to avoid the development of any learned expectations which might have shortened subsequent grazing periods.

(ii) Activities and data-handling.

Throughout the grazing period, the animal under observation was assigned into one of 5 main activities, each of which could be subdivided further. The activities, and the names used below, are given in Table VIII.3. For Runs 1 to 4, these codes were typed directly into a handheld, battery-driven data-storage device. This unit, a NORAND 101XL ALPHA1, could store up to about 5000 entries, and possessed an internal time-base. When 'enter' was pressed, the previously keyed activity code was stored with the time spent since the previous 'enter'. This record could then be dumped directly to a Horizon NorthStar micro-computer which was kept on mains power at the field centre.

For Runs 5 and 6, the grazing period was described on a cassette tape recorder. Later in the day, this record was replayed at the field-centre, and converted into the same codes using the internal time-base of the Horizon. Tape-recording was more discriminatory of short activities, but required two processings, and well over twice the data collection time per day.

Once on the computer, the data was annotated and saved on discs immediately. It was then available for analysis that same day. A considerable number of display and data handling routines were written in Horizon NorthStar BASIC. The two general analysis approaches, used

Table VIII.3

Activity codes and definitions used in small enclosure observations.

| Code | Name | Activity description |
|---|---|---|
| N | NULL | animal inactive: includes brief inactivities, ruminating, lying down, watching galahs, etc. |
| M | MOVE | moving without eating (may include chewing): numbers were usually appended to indicate estimated distance of movement in m. MOVE must be >.5 m to over-ride any simultaneous activity. |
| A | TRY | sniffing at vegetation without eating (second letter gave vegetation type, as for EAT). |
| C | CHEW | chewing, with head away from vegetation, movement <.5 m |
| B | EAT | actually biting at vegetation (second letter gave type of vegetation: main categories, G=ground, B=bluebush, S=saltbush). |
| BGM | | continuous nibbling along ground whilst moving, where no movement between nibbles exceeded .5 m, but total distance moved did. |

in this chapter and the next, are a static analysis of time spent in different activities during different intervals of the grazing period, and a transition matrix or Markov chain approach which permits the examination of dynamic pattern during the grazing period. Transition matrices are not easy to treat statistically. Information statistics may be used to check the significances of different orders of transitions, and special versions of $\chi^2$ tests can compare between or within matrices. I was helped in developing programs for these by Dr Kim Malafant, and the literature of Anderson & Goodman (1957), Macrae (1971), Chatfield & Lemon (1970) and Thomas & Barr (1977). I do not refer to these sources again.

## (b) Grazing: the major activities.

In this section I first examine the influence of conditions on total grazing time. I then turn to the coarse division of grazing into the activity categories of NULL, MOVE, EAT, CHEW and TRY, and show how the time spent in these varies through the grazing period. In doing so, I sometimes assume that time is useful as a measure of successful effort in eating; this assumption is justified in the next chapter.

### (i) Total active grazing time.

As mentioned above, the total time spent active (that is, total observation time less time spent NULL) is an indicator of total time spent foraging which minimises the errors in determining the end point of grazing. I soon noticed that the sheep seemed to graze for a shorter period in summer observations than in autumn. This might have been due to a shorter penning time and consequent shorter starvation time in summer: however, the grazing periods were shortest in early February, whilst penning was shortest in December. Alternatively, Noble (1975) had reported less intake when there was very little vegetation available.

I examined the effect of season (which is centred in January) as opposed to time of overnight penning (related to daylength and centred on December 22), as well as environmental and vegetation parameters, on active grazing time for all the records. No causation can be inferred, of course, but the correlation with season is the strongest ($r=-.79$, $n=53$, $p<.0001$), as well as with seasonal temperatures. Within season (e.g. Nov-Dec or Apr-May records), there is no significant effect of any climate parameters (temperatures, cloud, wind), nor vegetation quantity (biomass of shrubs, saltbush alone, ground material or total biomass on offer in the enclosure) nor phase of the moon. Multiple regressions confirm this pattern.

I conclude that length of grazing period is more-or-less independent of day-to-day climate, and of vegetation availability, provided that a reasonable quantity is available. Some trials in smaller enclosures with much less vegetation resulted in shorter grazing periods, but the quantities present in 0.1 ha seem to be adequate for normal behaviour. Over three trials in one enclosure, the three sheep would typically eat 3 to 4 kg, or at most 25% of the biomass on offer; this proportion was smaller in the later Runs. The variation in length of early morning grazing periods may be related to physiological adjustments in metabolic heat production as a response to mean temperatures. I do not have data to quantify the effect.

(ii) Major activities: the whole grazing period.

Figure VIII.4 shows the mean proportion of observed time spent in each major activity, averaged over the trials of each Run. The pattern is consistent between Runs except that time spent inactive (NULL) varies. This inactivity shows no significant correlation with any climatic, seasonal or vegetational characteristics; it is probably largely dependent on how easy it was to be sure that grazing had finished, which in turn depended on chance observational events which influenced whether or not the sheep lay at the end of a trial.

The righthand column of each plot shows the division of the active time into MOVE, TRY, CHEW and EAT. Again the division between

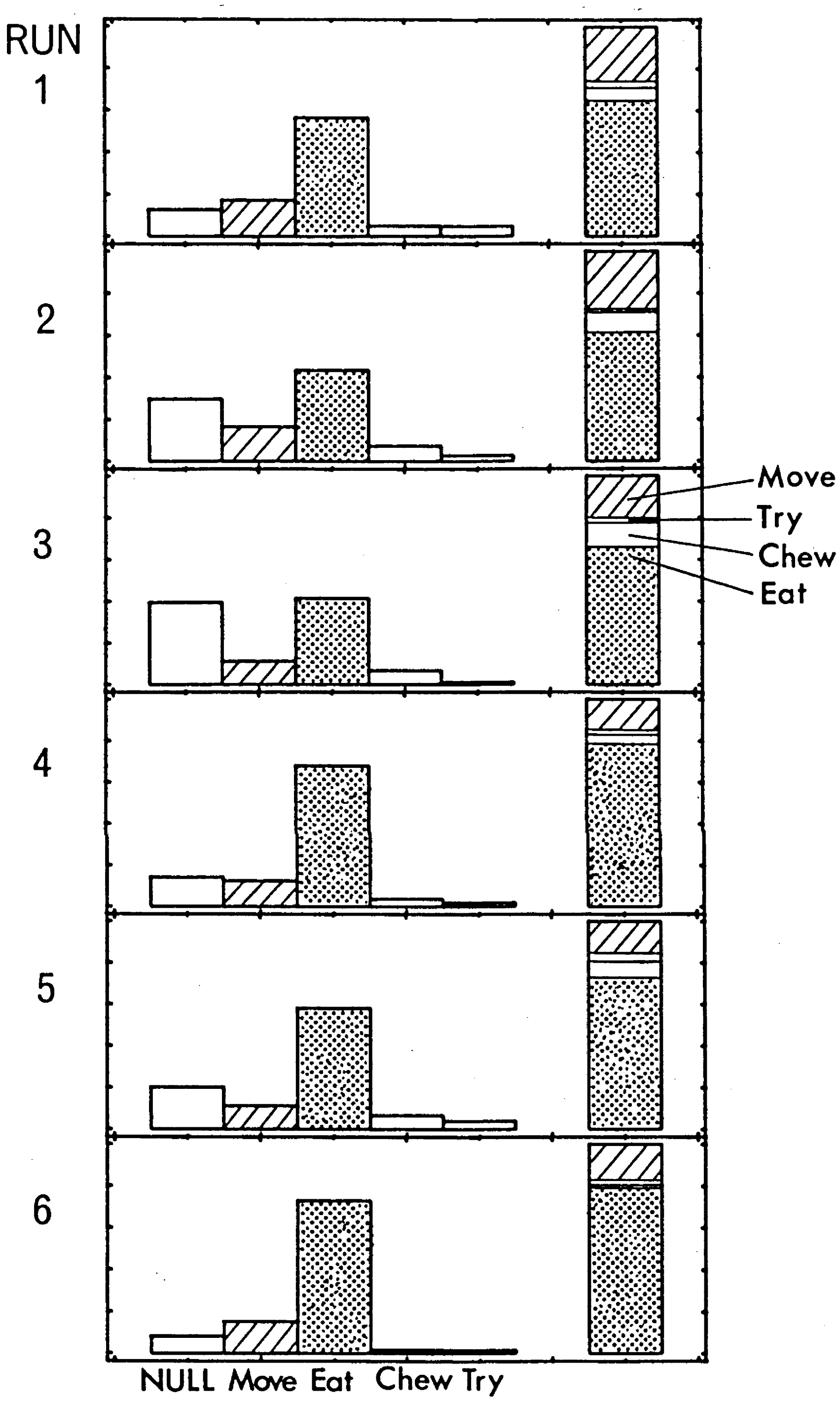


Figure VIII.4: Distribution of time between major activities over the whole grazing period, for each Run. Lefthand histograms show the percentage of total time time spent in each activity; righthand column shows how active time (total time less NULL) was apportioned between activities. (Y-axis scale is 0-100).

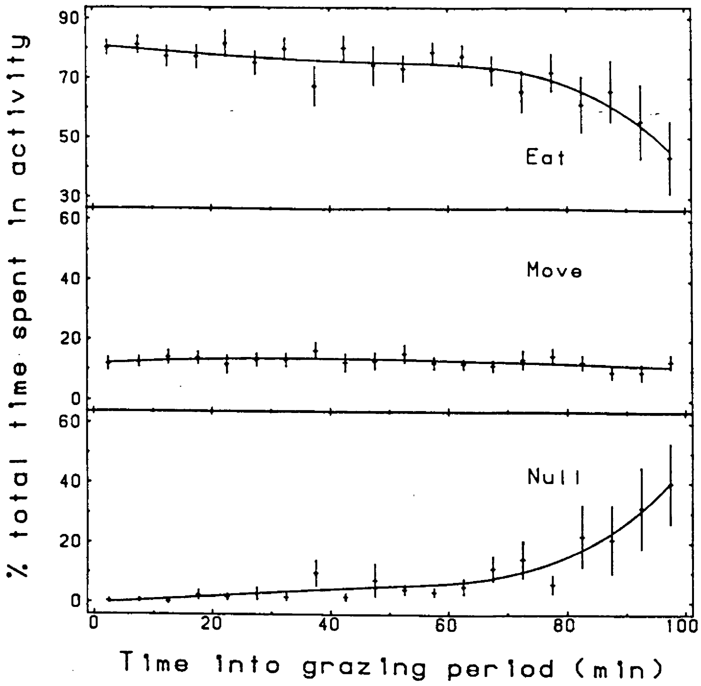
movement and eating-associated activities is very consistent: time spent moving is highly correlated over all trials with active time (r=.73, n=53, p<.0001). A mean 18% of active time is spent moving, or 14% of total time.

TRY and CHEW account for a small and variable proportion of active time, 1-10 and 1-16% respectively (means 7 and 3%, n=53 trials). Much of this variation probably depends on vegetation type and visibility from the Toyota. Either activity could occur during eating whilst the sheep's head was ensconced in a shrub; under these circumstances these activities were indistinguishable from eating and they would have been included in the EAT record. They do not vary consistently with parameters of climate or vegetation. These two activities are not discussed much further below, but are sometimes included with EAT as eating-associated activities.

### (iii) Major activities: time courses through the grazing period.

Regardless of how intake rates and selection change during a grazing period, net intake per unit time will be constrained by the time spent actually eating. Similarly, total movement will be constrained by time spent moving as well as movement speeds.

Figure VIII.5 shows the mean percentages of time spent in the activities NULL, MOVE and EAT in each 5-minute period for all trials of Run 4 and 5. The general pattern, shown by the spline-fit curves, is a gradual increase in NULL, compensated more-or-less by declines in EAT or MOVE. The full grazing periods are truncated in these Figures to the length of the shortest trial in the Run, so the end of the grazing period is not illustrated. Figure VIII.6 shows the trials in the (a): Run 4



(b): Run 5

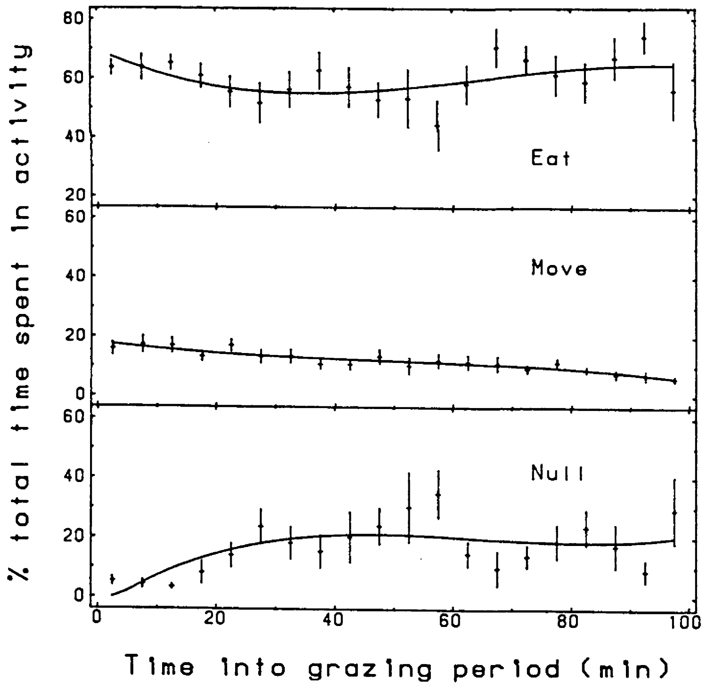


Figure VIII.5: Mean time courses of the activities EAT, MOVE and NULL through the grazing periods of (a) Run 4, (b) Run 5 and (c) Run 6. Points show mean percentage of total time spent in the given activity and one standard error for 9, 12 and 6 trials per Run respectively; line is spline fit to these points. Only the first 100 minutes of the grazing period are shown. (Continued on next page).

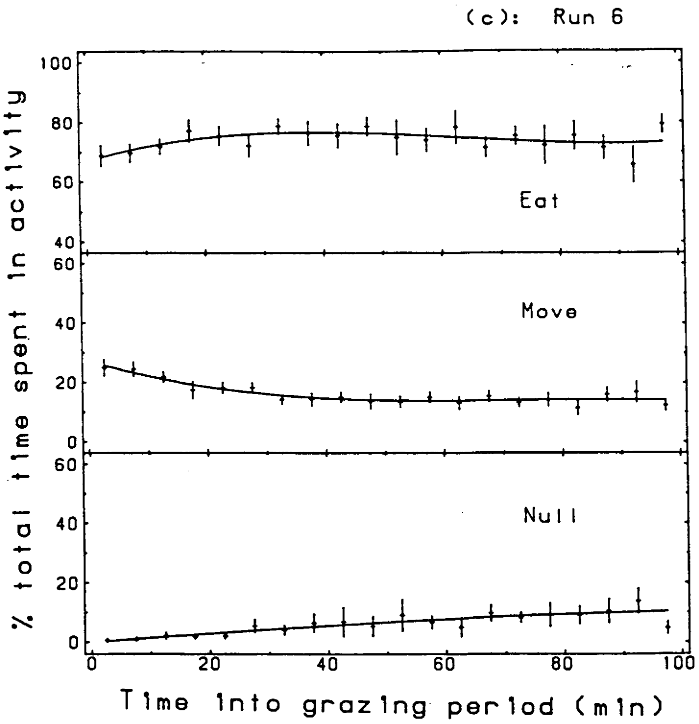
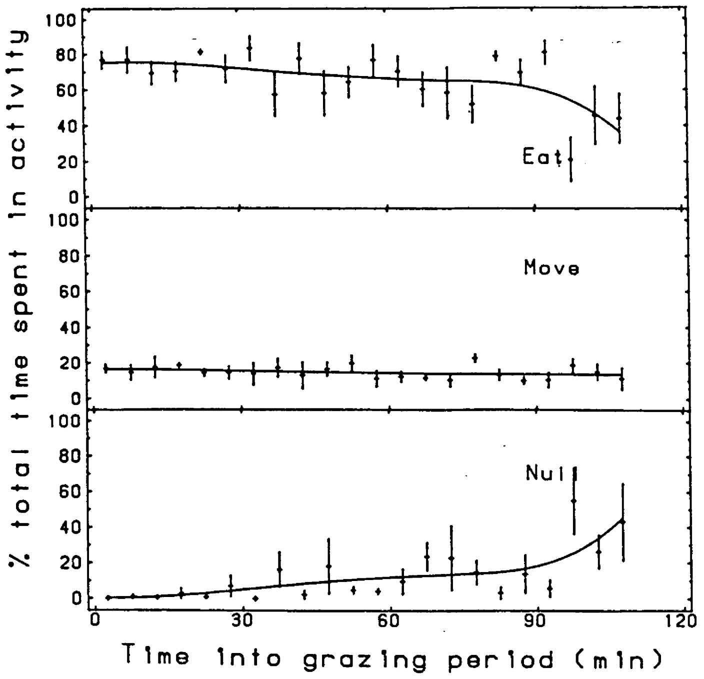


Figure VIII.5 (ctd): (c) Run 6; see previous page for details.

Depot enclosure of Run 4, and one of these trials in more detail, to give an impression of within enclosure and within trial variability. At the very end of the grazing period, NULL increases rapidly to 100%. As can be seen from Figure VIII.6(b), this is usually associated with a break in gradient from a gradual rise in NULL to a rapid change to total inactivity. These general patterns were very consistent in all Runs, although there were variations in rates and asymptotes.

It is apparent from Figure VIII.5 that there is usually some decline in MOVE during the grazing period, but that this is not necessarily linear. Over all the Runs, regressions of time spent moving in each 5-minutes against total time into the grazing period

(a) Run 4, Depot enclosure.



(b) Run 4, 3rd trial in Depot

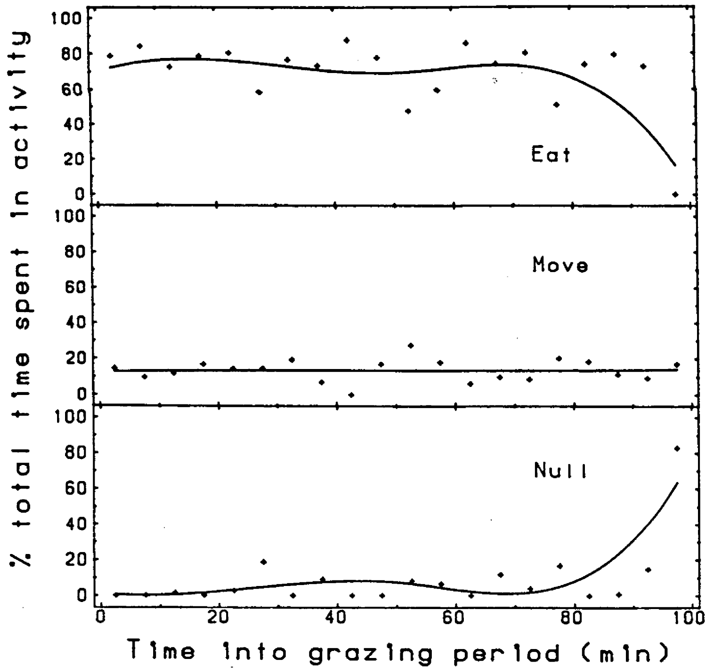


Figure VIII.6: Time courses of major activities through the grazing periods of (a) all 3 trials and (b) the 3rd trial only in the Depot enclosure of Run 4 to illustrate daily variability. Details as Figure VIII.5, except that no error bars are plotted on the single day.

sometimes show significant declines, but regressions against active time do not. In Figures VIII.5 and 6, 'EAT' refers to eating only; regressions of all time associated with eating (i.e. EAT+CHEW+TRY), however, show the same pattern as MOVE. Clearly the data contains non-linear variation, but, in general, the decline in active time through the grazing period is absorbed approximately proportionally by movement and activities associated with eating.

### (iv) The cyclic nature of inactivity.

It may have been noticed that the spline-fit curves of Figure VIII.5 hide a cyclical variation in the actual values, which is superimposed on the trend. When it is recalled that each point is an average over nine trials, the remarkable regularity of the cycles becomes apparent. Plots of EAT or MOVE as proportions of active time remove this effect, so it is due to cycling in inactivity. It may be seen in the data of most of the Runs, with a consistent period of between 20 and 25 minutes. During the observations, it was noticed as an increase in standing around, and sometimes ruminating, about every 20 minutes, being more apparent towards the end of the grazing period. It may be related to physiological function in the rumen, or digestion. It is insignificant at the time scale of the model, but it reinforces the need to use proportions of active time in the next chapter.

### (v) Summary: major grazing period activities.

Total time of grazing is related to seasonal variations, probably in metabolic requirements; early morning grazing periods are shortest in late summer. Total time spent in different major activities (NULL, MOVE, EAT, CHEW, TRY) is largely independent of external factors of climate or vegetation. Time spent moving is about one fifth of time spent active in the grazing period as a whole. Time spent inactive increases slowly through the grazing period, increasing more rapidly only at the very end of grazing. Concomittantly, time spent moving and eating decrease proportionally.

## (c) Movement speeds.

Foraging models generally predict that an animal should modify its rates and patterns of movement to match the foraging conditions that it is experiencing. In this section, I describe evidence that, in small enclosures at least, sheep do move faster in poorer foraging conditions, thus potentially searching a larger area. In these trials, however, it seems that this may only be a response to greater mean free path between food items. Attempts to confirm these findings in the open paddock have already been described (Chapter VII(b.ii)). I also examine changes in movement speeds through a grazing period.

### (i) Movement speed and forage condition.

In all trials of Runs 2, 3 and 4, the distance that an animal moved was recorded at the same time as recording the time taken in moving. I estimated these distances by eye, but the estimates appeared both reasonably accurate (±1 m each time) and consistent. They could be checked against the regular 5 m spacing of the fenceposts, and with pegs put in at the 5x5 $m^2$ cell boundaries within each enclosure. Absolute accuracy is not important to most of the argument below, but should, in any case, be improved after averaging over a whole grazing period.

Firstly, using the Latin Square design described in the previous section, I found no differences attributable to individual animal, day of replication or section of grazing period (comparing the 1st, 2nd and 3rd third of each grazing period). ANOVA's of animals x treatments, animals x third of grazing period, or treatment x day of replication all showed no interactive effects, and no differences which were not solely a result of treatment type (all p>.10).

Because the grazing periods are not necessarily of the same total time, I compare now the mean speed for the trial, defined as the total estimated distance moved during the period divided by the total time spent in the MOVE activities. Table VIII.4 presents these mean speeds for each treatment in these Runs; the data are also plotted in Figure VIII.7. In general (as Chapter IX will show), ground material is preferred by sheep over saltbush, which is greatly preferred over bluebush. In all three Runs, the 'bluebush-only' enclosure contained the least preferred species at the lowest density of individuals, though not necessarily the lowest total biomass (cf. Table VIII.2, in particular, Run 4, West End enclosure). There are significant differences between the enclosure treatments over all the data (ANOVA, between treatment, $F_{2,18}$=5.6, p=.012) but not between the Runs ($F_{2,18}$=1.2, p>.10, and no interactions). Evidently the state of the forage on offer has some effect on the animals' movement speed.

It is not clear what may cause this change in speeds from the biomasses as presented. In particular, the treatments other than 'BB' in Figure VIII.7 all contain more preferred species, more variety of species, a higher density of individuals, and a greater quantity of ground material than the bluebush-only treatment.

From the original data, I have calculated the mean length of each movement; Table VIII.4 shows this, and the mean distance between shrub centres for each enclosure. Again there is a significant difference in mean movement length between enclosures (ANOVA $F_{2,18}$=10.8, p=.001) but not between Runs ($F_{2,18}$=0.8, p>.10). Furthermore, the correlation between mean length of movement and mean inter-shrub distance is almost

## Table VIII.4

Mean movement speeds for each treatment of Runs 2, 3 and 4: also given are mean length of movement, and mean distance between shrub centres (D), calculated by assuming random distribution of the shrubs in the treatment (when the mean distance is given by $1/(2\sqrt{\rho})$, $\rho$=mean shrub density).

| Run no. | Enclosure name (treatment) | Mean speed (m $s^{-1}$) | Mean distance moved (m) | D (m) |
|---|---|---|---|---|
| 2 | NW1 (Bb) | .449 | 3.02 | 1.18 |
| | NW2 (Mix) | .419 | 2.15 | 0.96 |
| | NW3 (Sb) | .393 | 2.04 | 1.06 |
| 3 | NW1 (Bb) | .439 | 2.70 | 1.18 |
| | NW2 (Mix) | .403 | 2.01 | 0.96 |
| | NW3 (Sb) | .362 | 1.92 | 1.06 |
| 4 | West End (Bb) | .470 | 2.68 | 1.28 |
| | Chyds (Mix) | .411 | 1.75 | 0.74 |
| | Depot (Sb) | .411 | 1.98 | 0.93 |

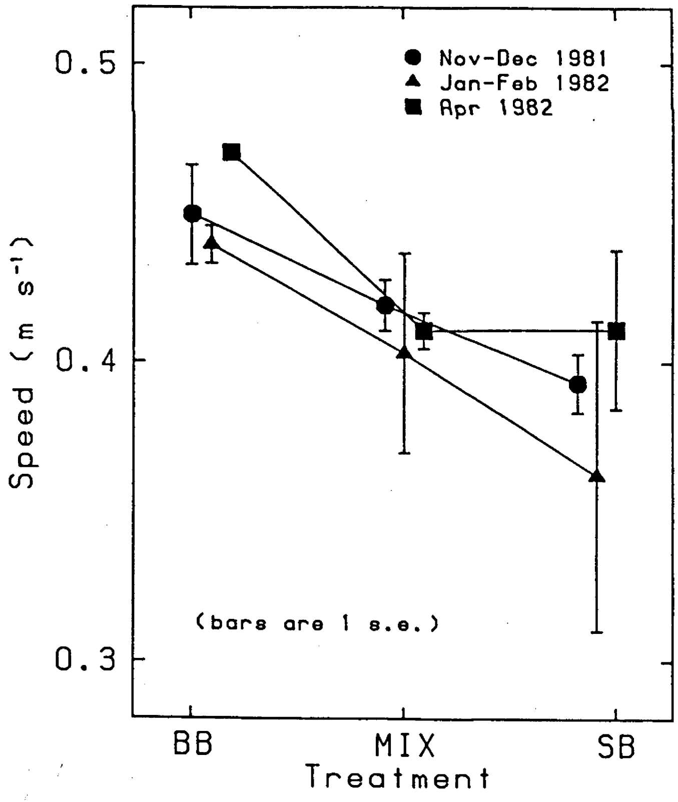


Figure VIII.7: Mean and standard errors of speed of movement in three replicates for each enclosure of Runs 2, 3 and 4, plotted against general vegetation type.

significant (over all trials, r=.39, d.f.=7, p=.07). Thus higher speeds occur with longer movement distances in enclosures with greater distance between shrubs. This may be interpreted to imply that longer movements permit the attaining of a higher speed.

The forage condition correlates for this change in movement speed were further investigated in Run 6, where all three enclosure treatments contained both a similar total biomass and a similar number of individuals. Each enclosure was broken into 16 cells, however, and these contained a considerable range of different biomasses and numbers. There is the inevitable correlation between biomass and numbers of plant individuals in a cell although this was better for saltbush alone (r=.85, n=48, p<.001) than for all shrubs (i.e. bluebush and saltbush, r=.59, n=48, p<.001). The task of estimating movement distances as well as tracking the animals' movements between the 16 cells of each enclosure proved too much, so here I recorded only the time spent moving.

The correlations between mean duration of each movement and various vegetation parameters are shown in Table VIII.5. During these trials, there was some ephemeral biomass, and over 90% of shrub foraging was on saltbush (see Chapter IX(b)). The results suggest that the relatively non-preferred food-types (here the bluebush) are not important in affecting the movement parameters. However, because the saltbush numbers and biomasses are so highly correlated, it is not possible to confirm the importance of shrub density as opposed to total biomass.

If movement speeds in undirected grazing are primarily determined by distance between potential food items, variation in speed is not

Table VIII.5

Correlations between mean time in each move and vegetation parameters for the 16 cells of each of 3 replicate trials in the 3 treatments of Run 6. n=144 throughout.

| Vegetation parameter | r | p |
|---|---|---|
| total biomass (Sb+Bb) | -.13 | .116 |
| saltbush biomass | -.48 | <.001 |
| total no. of shrubs | -.38 | <.001 |
| no. of saltbushes | -.50 | <.001 |

likely to be significant in an open paddock when grass is common. This may also be the reason why no single vegetation parameter appeared to explain the differences between the treatments of Run 2 to 4, since quantities of ground material and shrub densities were confounded in many cases.

(ii) Movement speed through the grazing period.

Two alternate effects on movement speeds might be expected during a grazing period: a decrease in speed might occur due to more careful searching for small food items, or an increase might result from the acceptance of fewer food types as satiation proceeds, thus increasing mean free paths between acceptable food items.

Using the data collected on movement speeds as described above, I tested for these possible changes during the grazing periods of Run 4. The mean speed was calculated for each 20-minute period in each trial, up to 100 minutes (this being the length of the shortest grazing period). Although speeds varied from .302 to .539 m $s^{-1}$ during different 20-minute periods, no significant correlation (or even trend) could be found with time for the whole run, or within individual treatments. The only significant differences were those between treatments, as discussed above.

Movement also occurs in the special 'lawn-mowing' activity of BGM (see Table VIII.3). This activity usually increases during the grazing period. I have no exact data on movement speeds in BGM, but they are very much slower than MOVE (by definition). Its increase might therefore be seen as supporting the first alternative above, of movement speeds declining later in the grazing period. It is, however, linked to increased foraging on the ground (discussed in Chapter IX(b)), and should probably be regarded in the light of this, rather than movement speeds per se.

### (iii) Summary: movement speeds.

Movement speeds in grazing in small enclosures differ significantly in different forage conditions. Higher speeds seem to result from increased mean distances between food items in poorer forage. Movement speeds do not change during grazing periods independently of forage conditions. Instantaneous speeds of movement in small enclosures varied from .3 to .54 $m\ s^{-1}$ over 20-minute periods, corresponding to .15 to .27 $k\ h^{-1}$ in overall activity, if 14% of total time is spent moving. This is at the lower bounds of typical subflock speeds in undirected grazing in the open paddock, but does not include a small amount of movement in the activity 'BGM'.

# Chapter IX.

## The grazing period: intake rates and selection.

The previous chapter has examined movement in grazing, and has discussed how the amount of time spent actually eating declines during a grazing period. In doing this, I have implicitly assumed that time spent eating is a good indicator of net intake. This requires that intake rates be constant. In this chapter I first show that intake rates are indeed consistent between trials and plant individuals, and then examine whether they change within a grazing period. I then turn to diet selection, and discuss how it may vary during the grazing period. Finally, I touch briefly on a number of aspects that are important to individual plants, but are shown to be relevant at too fine a scale to be significant in the model.

## (a) Intake rates.

My small enclosure work has examined grazing by recording the time spent in different activities. A requirement of this approach is that time spent should be a reliable indicator of success or effort expended in an activity. This is particularly important in the interpretation of time spent eating different food items in terms of diet. In this section I therefore demonstrate that the net intake of a given species in a given condition is accurately related to time spent grazing that food type, for the shrub species at least.

It is important to know whether intake rates change during the grazing period with satiation. I therefore also show that there are no significant changes, and that eating seems to be an on/off activity.

### (i) Consistency between plants and within trials.

During Runs 3 and 5, some mornings were given over to a different observational setup. For these trials, 10 plants each of saltbush and bluebush were cut and weighed to the nearest 0.1 g close to sunset on the evening before the trial. Eight plants of each species were then wired on to pegs scattered around a small (0.05 ha) enclosure, whilst the other two were wired outside the enclosure to act as controls for loss of moisture before reweighing (which was usually slight). The measured plants accounted for about 1/5th of the biomass on offer in the enclosure.

Next morning, three sheep were let into the enclosure, following the normal routine of other small enclosure trials, and allowed to graze until they sat down. Although the enclosure was only half the size of that used for the other trials, the sheep were well acclimatised to my presence and behaved as if undisturbed. Occasionally one of the test 'plants' would be a trifle unstable, but this did not worry the sheep.

Instead of recording the activity of one sheep, I recorded the time spent eating each of the test plants, which were individually identifiable by letters scratched in the ground beside them. When the sheep had finished, they were released as usual, and the 20 plants reweighed as soon as possible. The weight loss was then determined and corrected by the weight loss per unit weight of the controls. A few plants were trampled by the sheep, and these were omitted from analysis, so that intake rather than plant damage is recorded: the latter was too variable to be examined in this way. The weight change for each plant was then regressed against the observed time spent eating that plant to obtain an intake rate for each species, with an indication of variability.

For Run 6, I made biomass estimates in 16 cells within each of the three treatments before and after the nine trials (Figure VIII.1 showed the spatial layout of the enclosures). During the trials, I recorded not only the activity of the sheep under observation, but also the cell in which it was. I therefore know the total time that was spent eating each of the food categories in each cell by one sheep throughout the trials: this time can be used as an estimate of grazing time by all three sheep, on the assumption that the observed sheep at any time reflected the behaviour of the other two both in space and activity. An intake rate can then be obtained by regression, with an estimate of variability between the cells.

The results show that there is a good correlation between measured offtake and time spent eating for each shrub species. Figure IX.1(a-d) are plots of time spent against offtake for all the data of trials from each of Runs 3 and 5, where each point represents one plant individual, being grazed by one to three sheep. I did not record which sheep individual was grazing at a given time, but from the tightness of fit there is little variation in intake rate between either plants or sheep. Some plants were grazed much less than others, and some were clearly rejected on the basis of smell alone.

For Run 6, Figure IX.1(e) shows the plot of saltbush biomass change against three times the total time spent eating saltbush in the 44 cells of the three enclosures that contained any of the species. This estimating method has greater scatter due both to the less accurate estimate of biomass change, and the assumption that all three sheep behaved identically. Too little bluebush was eaten in this Run to obtain a reliable estimate for its intake rate.

Table IX.1 shows the resulting intake rate estimates. Time is a good measure of intake rate on specified bushes: it is also a good measure when averaged over many bushes or days within a short period. There is also a reasonable consistency in dry weight intake over longer period. There is a much greater variability in 'wet' weight intake rates, especially in Run 6. Plants in this Run, which followed rains after a dry summer, had a high water content but had not put on much new growth. This suggests that the spatial patterning of leaves on the shrubs may be a more important factor in determining how much a sheep can cram into a mouthful than the contents of the leaves themselves. As bushes dry out into summer most years, and in periods of drought, they have a lower density of leaves, and this may result in

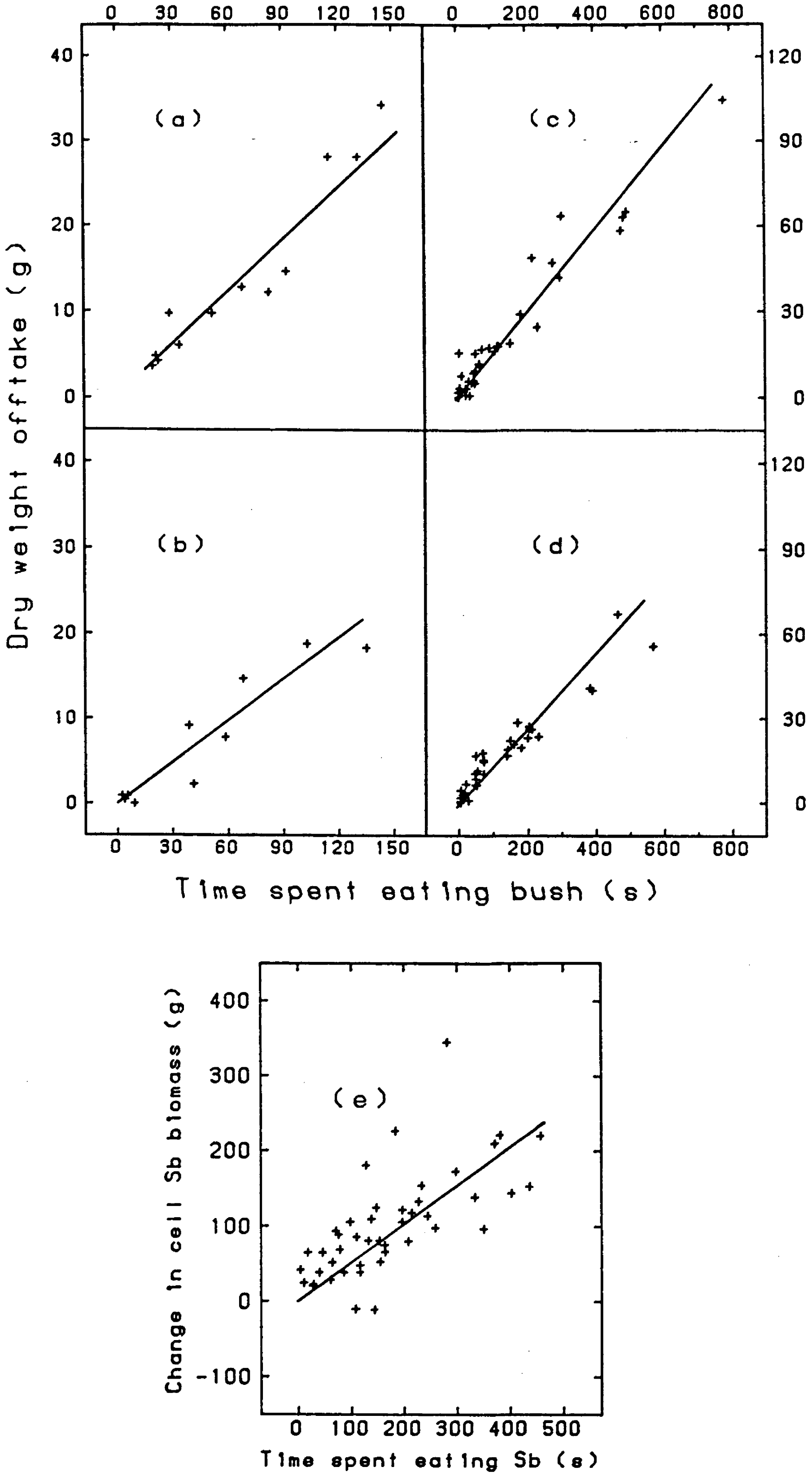


Figure IX.1: Plots of dry weight offtake against time spent eating for intake rate trials of (a,b) Run 3 and (c,d) Run 5, where each point represents a single plant, and (e) Run 6, where each point represents a cell within one of the enclosures. (a,c,e) are for saltbush, (b,d) are for bluebush. Some negative changes in (e) relate to the accuracy of biomass estimation (Chapter IV(d.i)).

Table IX.1

Mean intake rates estimated during Runs 3, 5 and 6 (see text for methods). Dry weights relate to oven drying at 80°C for 60h. n is number of shrubs (Runs 3 and 5) or cells (Run 6). 's.d.' is standard deviation on the origin regression coefficient; all $r^2$ are significant, $p<.001$. 'Wet' weight intakes were obtained by correcting dry weight rates for mean foliage water content at the time.

| | | Intake rates (g $s^{-1}$) | | | | | No. of |
|---|---|---|---|---|---|---|---|
| | Run | dry wt. | s.d. | 'wet' wt. | $r^2$ | n | trials |
| Saltbush | | | | | | | |
| | 3 | .21 | .011 | .34 | .92 | 12 | 3 |
| | 5 | .15 | .005 | .22 | .94 | 35 | 4 |
| | 6 | .17 | .014 | .61 | .37 | 44 | (3) |
| Bluebush | | | | | | | |
| | 3 | .16 | .013 | .35 | .88 | 10 | 3 |
| | 5 | .13 | .005 | .23 | .92 | 34 | 4 |
| | 6 | (inadequate data) | | | | | |

a generally decreased rate of dry weight intake, as seen in Run 5.

I conclude that time is a good measure of intake where many bushes are involved within a short period. However, correlated changes in vegetation condition over periods of months and longer, and potentially between sites, mean that intake rates should not be expected to be consistent between Runs, nor between spatially well-separated enclosures. Although the difference between dry weight intake rates is not great between Runs, digestibilities, water contents and salt concentrations are hidden by this measure.

(ii) Intake rate changes during the grazing period.

The above analysis could disguise changes in intake rates during the grazing period. It will be seen below (section (b)) that there was an a priori reason to suppose that the early part of the grazing period might be different to the remainder in terms of instantaneous intake rates. Animals which are hungry might be expected to eat less selectively within a bush and consequently maintain a higher intake rate; alternatively, frenetic behaviour, as is sometimes seen early in the grazing period, might be inefficient and result in dropped food.

It was not possible to design an experiment of the form above in which the offtake weight changes could be determined for different intervals within the grazing period without disturbing the sheep. (A laboratory approach could be used for this, with regularly-changed artificial food containers). However, the times spent eating each plant were recorded continuously, and could therefore be distributed amongst different portions of the grazing period. Provided there is a reasonable scatter in usage between plants and in time, it is possible to use multiple regression techniques to see whether the relation between time spent and offtake is constant during different sections of the grazing period.

Table IX.2

Intake rate in the first 30 minutes of the grazing period, as compared to the remainder. Multiple regression coefficients for linear model, offtake = A * t(30) + B * t(remainder), where t is the time spent grazing a measured plant individual during the period indicated. Constants a and b are the respective predicted intake rates, in g d.w. $s^{-1}$.

| Run | 0-30 minutes | | Remainder | | % S.S. | n | Test A≠B | |
|---|---|---|---|---|---|---|---|---|
| | A | s.e. | B | s.e. | explained | | t | p |
| Saltbush | | | | | | | | |
| 3 | .204 | .014 | .225 | .020 | 91.5 | 12 | .86 | n.s. |
| 5 | .146 | .009 | .128 | .015 | 92.7 | 35 | 1.0 | n.s. |
| Bluebush | | | | | | | | |
| 3 | .178 | .024 | .124 | .034 | 88.1 | 10 | 1.3 | n.s. |
| 5 | .120 | .009 | .118 | .007 | 88.9 | 34 | .18 | n.s. |

All multiple correlation coefficients are significant, p<.0001
All A and B coefficients differ significantly from 0, p<.001

Table IX.2 presents the results of this approach for each species in each Run, where measured total offtake is the dependent variable, and time spent in the first 30 minutes or the remainder of the grazing period on a given plant are the independent variables. The data is such that significant relations may be found in all instances, although they do not explain any more of the variability than the simple regressions described above (see $r^2$ in Table IX.1). None of the pairs of coefficients are significantly different to each other.

The analysis can be repeated for any time period division, although the partitioning of the data limits the reliability. On shorter partitionings, for Run 5, there was a significant increase in intake rate for saltbush only between the first 20 minutes of grazing and later. This effect is not large enough to affect the discussion of the next section, but may indicate that saltbush is grazed less efficiently in the earliest part of the grazing period.

In general, then, I conclude that intake rates within a species of shrub are approximately constant during the grazing period for a given vegetation condition. This suggests that eating, for shrubs at least, is an 'on/off' phenomenon, and that if an individual is to be eaten at all, it will be eaten as fast as possible.

### (iii) Summary: intake rates.

Intake rates are highly consistent between sheep and between shrubs of the same species within a trial and a locality. They differ between species and change with long-term vegetation condition. They are probably related to the physical structure of leaf display in these shrubs. Intake rates are also constant within a grazing period.

## (b) Selection: scales of change in time and space.

'Traditional' foraging theory is based on preference indices for different food types; for conditions of differing relative abundances, these result in different inclusions in the diet. Much of the optimal foraging approach is concerned with showing that these preferences do relate sensibly to measurable nutritive characteristics of the food types.

Implicitly, these preferences are often used as constants, although it is well recognised (for plants especially) that they vary continuously in time and within the food type. It is generally impossible to be sure that animals, especially herbivores, perceive their food in the same categories that the scientific observer may use: the species is often an inadequate category, as is clear from the sub-division of the cabbage or cattle taxa in our own foods. Even within what we label a single food type for our own consumption, there is continuous variation in quality. Individual plants are probably treated as 'patches' by herbivores, since different plant sections certainly have different nutritional value. Sheep are known to select young leaf over old, for example.

Despite the limits imposed by these complications (or perhaps because of them), Noble (1975) found that a simple intake selection model described his grazing trials as well as more complex versions. This was based on the intake equation,

$$c_i/C = \rho_i * b_i / \Sigma (\rho_i * b_i),$$

where $c_i$ and $b_i$ are the consumption and biomass on offer of species i respectively, $C = \Sigma c_i$, and the sum is over all food types. $\rho_i$, which he termed the preference rating for food type i, is the product of the probability of consuming food type i with the mean quantity consumed in a successful encounter: it should be a constant for given pasture conditions in this model. Noble recognised the need to allow $\rho$ to vary with pasture condition, but did not have the data to include this. Although an approach to the variation might be by water content, I have not pursued the long-term preference issue. These changes would be related to general vegetation condition, which is presumed to vary significantly only on a timescale of weeks to months.

In the shorter term, I have tested whether and how diet selection changes within a single grazing period, and related this issue to Noble's intake selection model. Additionally, I examine the spatial scale at which the sheep selects, since this affects its perceived encounter rate with food types. In this section I show that selection does change on a timescale well within that of a single grazing period, and that the spatial scale is probably sufficiently small as to be effectively random.

### (i) Changes in selection within a grazing period.

Table IX.3 shows the mean proportions of time spent on different major food types in each enclosure of Runs 2 to 6. The structure is similar to that of Table VIII.2 (the vegetation biomasses), which may be compared. The most obvious discrepancy between the two is the relatively large time spent searching on the ground even in enclosures where there was so little ground biomass as to make it impossible to estimate. In the West End enclosure of Run 4, for example, I had removed all ground material, raked and finally swept the area, yet 42% of their eating time was still spent on the ground. Despite my efforts, there were obviously small amounts of dry grass and bassia seeds available, the latter potentially having a significant protein content. Their efforts did decline over the three trial days (% of eating time spent on the ground was 56, 38 and 33 respectively). Their return rate on the ground in comparison to the shrubs was miniscule, and, on the basis of estimated intake rates, over 95% of their total intake was bluebush in this particular enclosure.

Table IX.3

Mean times spent eating the major food categories in each enclosure of each Run: times given as percentage of active time, to the nearest unit. Dashes indicate the absence of the food type.

| Run no. | Enclosure name | Eat bluebush | Eat saltbush | Eat shrub | Eat on ground | Total eat |
|---|---|---|---|---|---|---|
| 2 | NW1 | 32 | - | 32 | 20 | 52 |
| | NW2 | 29 | 20 | 52 | 12 | 63 |
| | NW3 | - | 25 | 25 | 43 | 68 |
| 3 | NW1 | 56 | - | 56 | 6 | 62 |
| | NW2 | 29 | 30 | 58 | 10 | 68 |
| | NW3 | - | 34 | 34 | 36 | 70 |
| 4 | West End | 47 | - | 47 | 34 | 80 |
| | Depot | - | 24 | 24 | 51 | 75 |
| | Chyds | 14 | 9 | 27 | 55 | 82 |
| 5 | North | 14 | 28 | 42 | 29 | 71 |
| | Mid | 18 | 16 | 34 | 41 | 75 |
| | South | 10 | 27 | 37 | 34 | 71 |
| 6 | North | 1 | 12 | 13 | 65 | 78 |
| | Mid | 2 | 12 | 14 | 66 | 80 |
| | South | 1 | 12 | 13 | 68 | 81 |

The distribution of intake through time was also not random with respect to food type availability, which is more important as far as spatial distribution of grazing impact in the open paddock is concerned. For Runs 4, 5 and 6 (2nd and 3rd replicates in each enclosure only for Run 6, for reasons explained below), Figure IX.2 shows the mean proportion of active time spent eating shrubs or on the ground for every 5 minute interval into the grazing period.

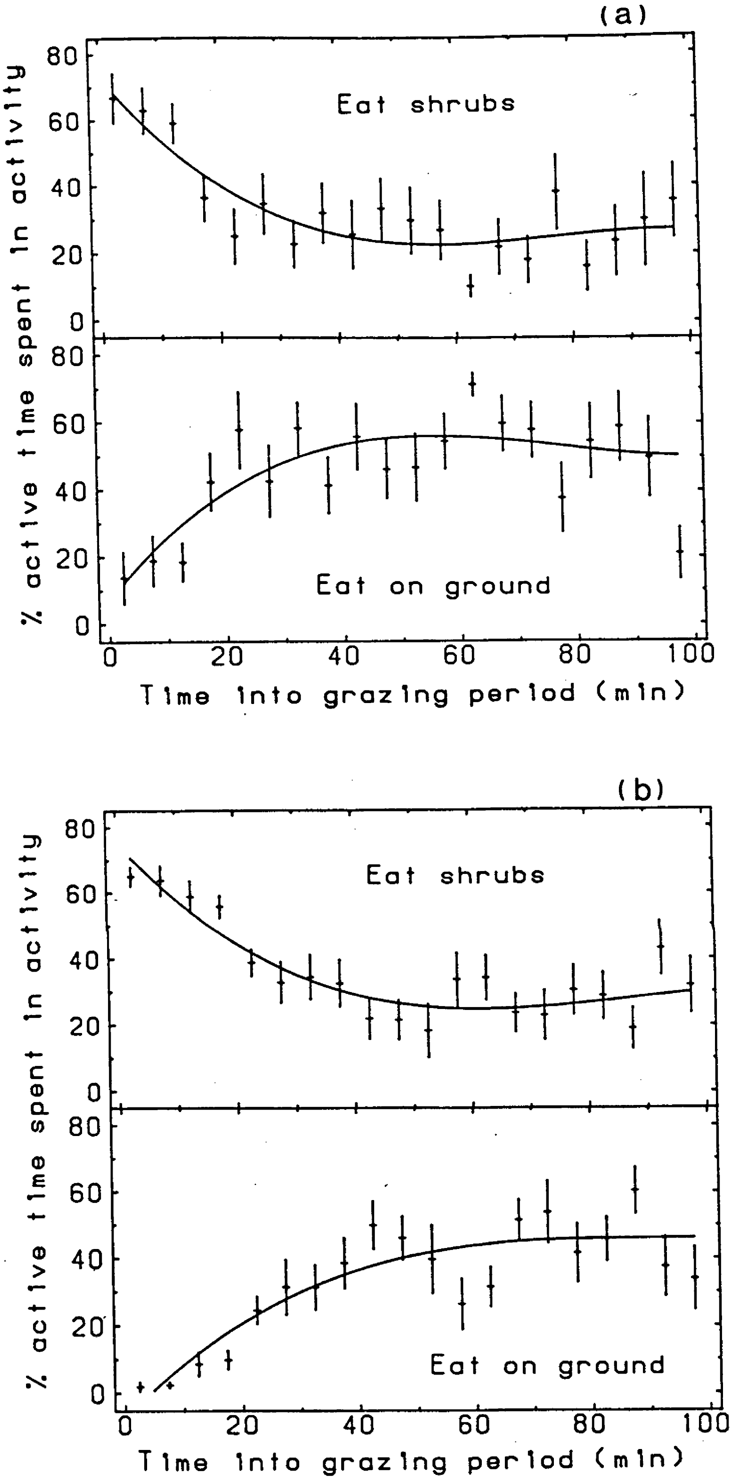


Figure IX.2: Time courses of eating activities through the grazing periods of (a) Run 4, (b) Run 5 and (c) Run 6; upper plot of each pair is for eating shrubs, the lower is for eating on the ground. Points show mean and standard error of percentage of active time spent in the activity during each 5-minute period for 9 (Run 4), 12 (Run 5) or 6 (Run 6) trials per Run. First 100 min of grazing period shown, curves are spline fits.

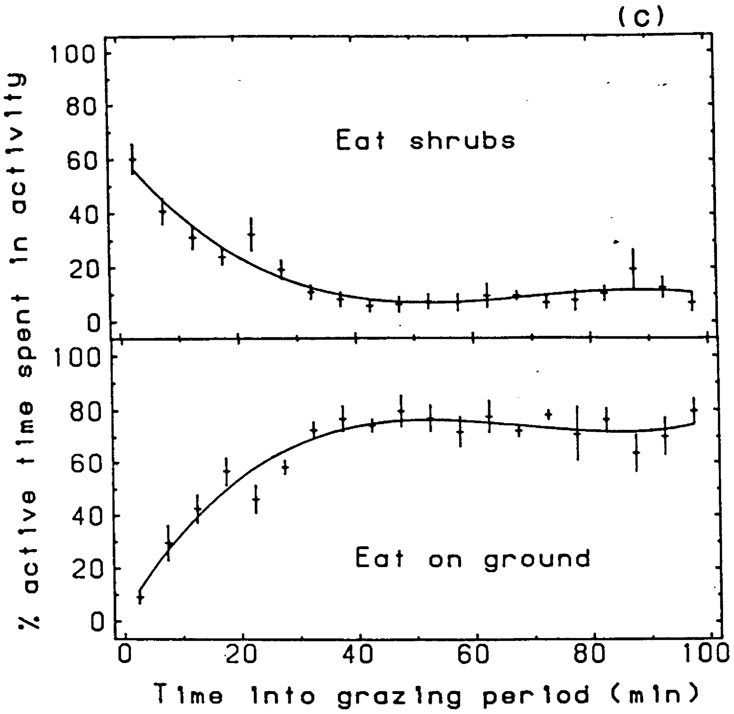


Figure IX.2 (ctd): (c) Run 6 (see previous page).

The importance of the dichotomy between shrubs and the ground layer is clear here. Over the first 20 to 40 minutes of their grazing time in this vegetation, the amount of time spent by the sheep on eating shrubs declines from an initial high level to a lower plateau that is maintained for the rest of the grazing period. Time spent eating on the ground rises to a complementary plateau.

From the previous section on intake rates, these curves may be taken as approximately equivalent to intake (with a different scaling factor for each food type). The precise fashion in which this varies for the ground category is not known, but where there is very little ground material present this does not matter. Since these curves are repeated trials within the same enclosures, the effect is not a result of changing vegetation during the grazing period. Evidently the animals are changing the criteria by which they select their diet as the grazing period proceeds.

This pattern was common to all the trials of Runs 2 to 5, and to the later trials in each enclosure of Run 6. As mentioned, I was unable to determine the intake rates for ground material by any method comparable to that used for the shrubs, but a maximal intake rate can be estimated from the loss of material from the enclosures during a Run. All the trials above are characterised by the dry weight intake rates on the shrubs exceeding those on the ground by 3 to at least 10 times. Consequently, whatever the reasons for the switch from shrub to ground material, the effective result of it was that early in their grazing periods, the sheep were preferring a diet with a high net intake rate, whilst later they accept a much lower rate despite the food still being available.

I should stress here, then, that short-term samples of dietary intake are not reliable predictors of the overall diet of an herbivore that behaves in this manner. Even unbiased sampling of the overall diet (e.g. by monitoring vegetation removal) does not give information about the temporal distribution of the diet during the grazing period. This is very important in modelling the impact of an herbivore which moves out from regular foci to graze, since the animal may be selecting by quite different criteria close to the foci than when it is further away.

### (ii) The causes of change.

Figure IX.2 showed declines in shrub intake to a plateau around which there is variation. In this section I test whether the time at which this plateau is reached is constant, or is related to a constant intake, or is related to intakes of toxins in the shrubs. I located a consistent 'inflection point' in this data by two techniques: a fitted continuous curve, and paired linear regression.

It is possible to fit an exponential decay curve of the form,

$$y = A + B\ e^{-kx}.$$

This can be achieved by computer global search techniques which adjust all three coefficients (A, B, k) to minimise some error criteria such as sum of squared residuals. A criterion such as

$$e^{-kT} = 0.1$$

will then give a consistently selected time T at which the decay has proceeded to 90%. This worked well for data with little variability, but with occasional outlier points, a machine method becomes unreliable. On the data of Run 6, this method gave very similar results to the second technique, which could be more easily monitored for odd behaviour, so I use the latter throughout.

Paired linear regression divides the time series data in all possible places and fit pairs of regression lines. I used the maximum overall F-ratio as the criterion to determine the best fit, although I sometimes had to constrain it to a sensible region where there were multiple maxima for the more variable data. The point of intersection of the two regressions was then taken as a consistent measure of the inflection point, although this is not meant to imply that the data necessarily contain a discontinuity. Some data was too variable for the approach, especially in shorter grazing periods, but I carried out the analysis for each enclosure of Runs 4, 5 and 6.

After obtaining the inflection point, I returned to the raw data

## Table IX.4

Intake rates (g $s^{-1}$) for Runs 4 5 and 6, used for the calculation of intake to the inflection point in Table IX.5. Shrubs: for Runs 5 & 6, from Table IX.1 (bluebush being increased proportionally with saltbush from Run 5); for Run 4, as Run 3 (Table IX.1), but wet weights from known water contents. Ground material: maximal rates calculated from loss of ground material (or total initial biomass where this is not known) divided by the total recorded time spent eating on the ground (allowing for 2 other animals); values for Run 5 and West End in Run 4 assume there was 200 g d.w. initially (all had supposedly been cleared from the enclosures).

| | | Bluebush | | Saltbush | | Ground[1] |
|---|---|---|---|---|---|---|
| Run | Enclosure | dry | wet | dry | wet | dry |
| 4 | West End | .16 | .35 | - | - | <.025 |
| | Depot | - | - | .21 | .34 | <.036 |
| | Chyds | .16 | .35 | .21 | .34 | <.050 |
| 5 | all | .13 | .23 | .15 | .22 | <.026 |
| 6 | all | .14 | .57 | .17 | .61 | <.052 |

[1] no estimate of ground material wet wt. intake rate possible, due to variability in drying curves.

and counted how much time had actually been spent eating different foods up to this point. From this I make an estimate of the total intake during the initial period. Intake rates used for this calculation are given in Table IX.4, together with comments on their derivation: the ground intake rates are very approximate, but all were estimated prior to the calculation of the following results.

Table IX.5 shows the times spent eating prior to the inflection points, and the calculated total intakes at this time. Time to inflection varied from 20 to 45 minutes, but there seems to be a remarkable consistency of dry weight intake by this time at around 150 g, both within and even between Runs. The wet weight intakes vary much more, even without including the ground material; Run 6, after rains, is particularly high.

## Table IX.5.

Estimated inflection point (T, min) for data from each enclosure of Runs 4, 5 and 6, with actual times of eating (sec) to the inflection per trial: estimated dry and wet weight intakes (g) are calculated from the intake rates given in Table IX.4. Wet weight intake is for shrubs only.

| Run | Enclosure | T | eating times | | | dry intake | | | wet intake |
|---|---|---|---|---|---|---|---|---|---|
| no. | name | | Bb | Sb | Gr | Bb+Sb | Gr[1] | Tot[1] | Bb+Sb |
| 4 | West End | 28 | 928 | - | 434 | 148 | 11 | 159 | 325 |
| | Depot | 22 | - | 659 | 344 | 138 | 12 | 150 | 224 |
| | Chyds | 20 | 352[2] | 265 | 349 | 112 | 18 | 130 | 213 |
| 5 | North | 32 | 288 | 712 | 147 | 144 | 4 | 148 | 223 |
| | Mid | 37 | 533 | 494 | 383 | 143 | 10 | 153 | 231 |
| | South | 45 | 186 | 768 | 574 | 139 | 15 | 154 | 212 |
| 6 | North | 38 | 0 | 553 | 1113 | 94 | 58 | 152 | 337 |
| | Mid | 38 | 114 | 554 | 1052 | 110 | 55 | 165 | 403 |
| | South | 35 | 27 | 729 | 852 | 128 | 44 | 172 | 460 |

[1] these figures maximal (see intake rates, Table IX.4).

[2] this figure includes 30s spent eating Chenopodium ulicinum.

Late in their grazing periods, as the previous section showed, sheep are prepared to spend a large amount of time obtaining very little bulk return. Sheep can certainly survive on saltbush and bluebush, although many herbs and grasses may be more nutritious. If plenty of ground material is available, sheep will eat it almost exclusively. Clearly the ground material in general is more highly preferred than the shrubs.

There are two classes of possible reasons as to why an animal should switch between shrubs and ground material during the grazing period when the former are still available. Either (1) it is switching as a result of a build-up of toxins from the shrubs, or (2) it has obtained enough bulk intake, but can still gain from the higher or different quality (in nutrition or minor elements) available in the ground material. There are two other unlikely explanations. The animal might completely forget its preferences between grazing periods, and require 20 minutes or more to re-assess the vegetation. I dismiss this since sheep are known to have long-term expectations about their surrounds (c.f. Gluesing & Balph 1980), amongst other reasons of mal-adaptation in an animal that spends a third of its life eating. Alternatively, the latter part of the grazing period could have no importance at all, but just satisfy some innate restlessness. I dismiss this possibility since significant intake does still occur during this period, and the suggestion is not compatible with the variable length of grazing activity described in the last chapter.

The consistent dry bulk intake at the indicator inflection point could support either a basic satiation of hunger or a toxin that was present in constant proportion to dry weight. Salt, oxalates and probably other secondary compounds occur in saltbush and bluebush. Salt is the obvious candidate, but its levels vary in dry weight proportion with soil moisture and plant water content (e.g. Sharma et al.1972 for saltbush). From this literature, salt intake by the inflection point varied between about 3 and 12 g: this argues against salt being relevant. The variability in the ratio of shrub to ground material intake between trials also argues against salt, or any other toxin, although interactive effects, or multiple limiting factors, cannot be ruled out.

The suggestion that the changeover is determined by bulk gut fill (rather than toxin level) might be doubted because of the wet weight intake variability. However water from the rumen can probably be absorbed over the time period (20 to 40 minutes) that is involved (e.g. Warner & Stacy 1972 show that up to 200 ml of water per hour can move across the rumen wall for suitable rumen osmolarities, and the rumen is less permeable than the omasum). The variation between trials is not consistent with increased penning time (from 10 h in November to 12 h in autumn) resulting in increased hunger: Run 6 has longer mean times and perhaps higher intakes than Run 5, but Run 4 does not parallel this. A sheep's rumen empties geometrically by about one tenth per hour (e.g. Blaxter et al.1956); if the rumen is full at about 750 g, after 10 h starvation it will contain about 262 g, and only lose a further 50 g to 212 g by 12 h. Thus it may be that two additional hours are not significant after being starved for 10 hours anyway.

As mentioned earlier, the effect of the switch between food types is that sheep are selecting for bulk early and, perhaps, quality later on in their grazing periods in this vegetation type. Two further facts suggest that the sheep may be making an active change in the criteria by which they select. Firstly, Kenney and Black (1983) have recently reported a study on laboratory sheep fed artificial diets (different hays, variously chopped, etc). When these sheep were presented with two foods simultaneously in the first one to four minutes of their grazing periods, their preferences for the foods could be predicted on the basis of the maximal intake rates of each of the foods when presented alone. They found that the preference for one food had to be adjusted by a 'palatability factor'. Within the constraints of tolerable feed acceptability, it seems that the sheep will select for maximum intake rate alone in the (very) early part of the grazing period.

Secondly, Figure IX.3 shows the eating activity curves, comparable to those of Figure IX.2, for the first use of each enclosure in Run 6. In all other Runs discussed in this section, there was little ground

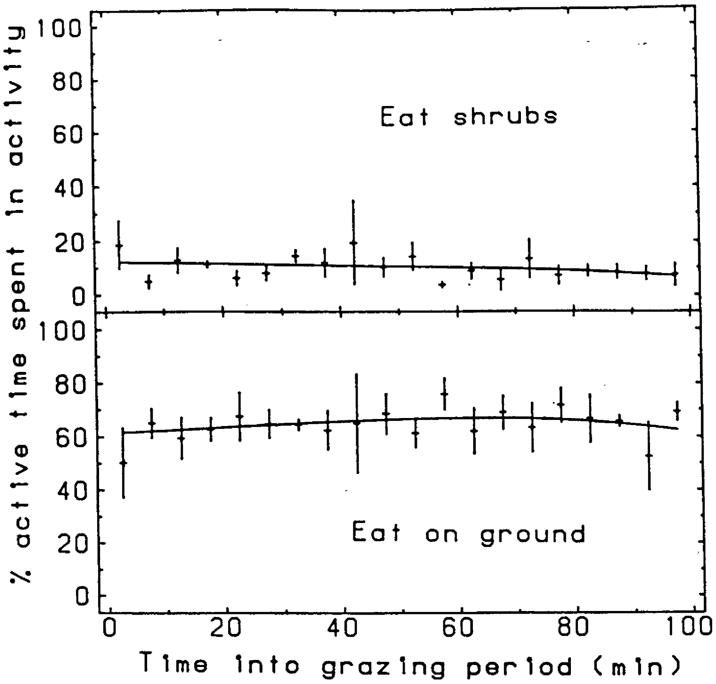


Figure IX.3: Eating patterns in the first trial in each enclosure of Run 6 only; otherwise as for Figure IX.2.

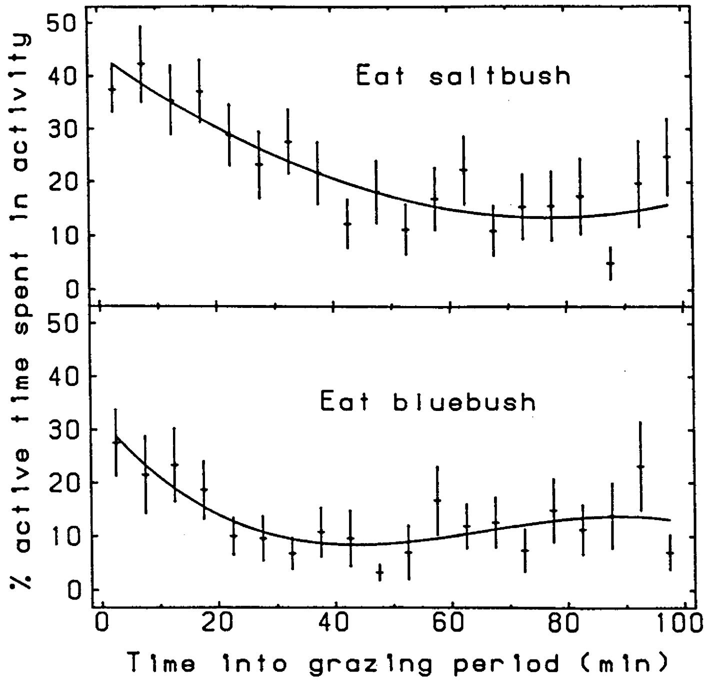


Figure IX.4: Time courses for eating the shrub sub-categories of saltbush and bluebush during trials of Run 5; details as for Figure 2. Note the earlier decline in the use of bluebush.

material available. In this set of trials, however, there had been ephemeral germination. There was only about 1 kg of ground material in each enclosure, but it was highly preferred and mostly eaten off during these first grazing periods. As can be seen, these showed no initial use of shrubs at all. Note that the levels are very similar to the plateaux levels of Figure IX.2(c).

I therefore tentatively conclude that, early in their grazing periods, sheep select the plants that they can eat at a maximal rate from the range of acceptable plant types at the time. In optimal foraging terms, this is akin to suggesting that, as satiation proceeds, their perception of the relative abundance of the minor but higher quality food types increases (e.g. Emlen 1966, Schoener 1971). This theory predicts that the easily-accessed but lower quality feeds should drop out of the diet during the course of satiation in order of increasing palatability: this order will be affected also by relative intake rates and actual relative abundances. Figure IX.4 shows how bluebush and saltbush dropped from favour in grazing periods of Run 5. Bluebush usually has a lower palatability and a lower intake rate than saltbush; it also declined in the diet earlier, which is consistent with this approach.

### (iii) Relevance to the open paddock.

I briefly discuss the wider relevance of the findings of the last two sections here because, although they certainly apply to small enclosures, there are possible criticisms of any extension to open paddock behaviour.

In general, behaviour in the small enclosures seemed very similar to that seen during sub-flock observations in the open paddock, although it was difficult to obtain any recordings of the same detail there. Obviously the enclosed sheep did not have the option of moving to alternative pasture, whilst they were not restricted from looking through the fence at it. This might have affected their movement behaviour to some extent and prevented them from making larger movements between eating bouts, for example when the vegetation seemed poor.

The major criticism, however, is that in the enclosures the animals have been penned without food overnight, and that the initial preference for high intake foods might be caused by a degree of hunger which would never occur 'naturally'. There are four counter-arguments to this.

Firstly, penning times varied from 10 to 12 hours. On hot days, I have observed undisturbed sheep in the open paddock which have stayed voluntarily in shade without eating for over 10 hours. Night-time campsites are probably occupied for similar periods in winter. This suggests that natural factors may restrict sheep to non-grazing activities for comparable periods to at least my shorter penning times, although it is possible that a very few nibbles in this period might stave off starvation.

Secondly, the intake by the inflection point described in the last section is a half to a third that of the observed grazing periods (e.g. estimated mean total intake for each trial of Run 5 was 339 g d.w., for Run 6, 432 g d.w.). Although the inflection point as assessed may not be exactly equivalent to when starvation hunger might have ended, it is unlikely that anything approaching half the grazing period intake would be necessary to return the hunger status to a 'natural' level at which ad lib grazing would begin.

Thirdly, in October 1983, I carried out three consecutive days of 22 hour observations of sheep in the Barbers paddock enclosures used in Runs 5 and 6. The sheep were free to water and graze at will within the confines of one enclosure, and were watched almost continuously. The first morning and afternoon grazing bouts were recorded on tape as for other trials, from their ad lib starting points. The data was not very satisfactory because there was not time for the sheep to acclimatise properly to my presence. However, declines comparable to, but less significant than, those described above sometimes occurred, in the afternoon grazing period as well as the morning one. Maximum gaps without any eating at all were only 5 to 6 hours: often gaps which would have been as long were broken by about a minute of desultory grazing. I do not know to what extent this was affected by the availability of water (which they used 5 to 6 times a day) and the unsettled restlessness of the sheep. Variability was such that I could not compare the time to any inflection point with the time since the previous grazing period finished, as I had hoped.

Fourthly, there is no evidence of time to the inflection point or intake up to this time being related to time of penning. That this detail did not show up may reflect differences between the vegetation types, but clearly any effect of starvation in two hours is minor in comparison to that of the natural gap between grazing periods.

For the model, therefore, I conclude that the effect is important in the open paddock. In Chapter X I shall take it to be related to the hunger trigger, and to be sufficiently important as to have a significant effect in the sheep's first hour of grazing. This will only result in a change in diet selection when there is little ephemeral material available. The basis for this approach is discussed further in the next section. I should remark, however, that a similar change in diet selection may also occur between different classes of ground material when they are available, both at Middleback and, no doubt, in more mesic pastures. This could normally be masked by the change being for different parts of one plant type, or by the difficulty of observation in such pastures.

### (iv) Relation to the previous diet selection model.

The previous sections have established how grazing effort changes during the grazing period. In this section I briefly apply a modified version of the diet selection model of Noble to my data to test its adequacy for the overall model. 'Traditionally' in the literature, such a diet selection model would be applied for an animal's total intake. The previous sections have suggested that this is unlikely to be adequate here; I show that, although the model fits the plateaux levels of grazing reasonably, a different approach is needed for the early period. I had planned to test the model in more detail in Run 6, where the location of the sheep was followed closely; one result of the breaking of the drought, however, was that bluebush was little eaten during this Run. The usefulness of these trials was therefore greatly reduced by the small number of food types being eaten. Much of my data is not ideally suited to these tests, so I restrict their ambit.

The model referred to in the introduction to this section (b) may be re-written as,

$$t_i/T = (\rho * b_i / r_i) / \Sigma (\rho * b_i / r_i)$$

where intake $c_i$ is replaced by $t_i*r_i$, the product of the time spent eating food type i with the intake rate on the food type. Combining equations for i and j, one obtains,

$$\rho_i / \rho_j = (t_i * r_i * b_j) / (t_j * r_j * b_i)$$

In an enclosure with only two species, for which t, b, and r are known, it is therefore possible to estimate the ratio of the preferences.

For Run 4, I have calculated the relative preferences of bluebush and ground material in the West End enclosure, and for saltbush and ground material in the Depot enclosure. Note that there is substantial variability between the enclosures in the use of shrub relative to the ground material. I use biomasses from Table VIII.2 and intake rates from Table IX.4. Table IX.6 presents the resulting estimates, using the mean percentage times spent eating the food types during the plateau section. As some test of the adequacy of this formulation, I then predict what the plateaux levels ought to be for the three species in the Chyds enclosure, bearing in mind that the location was different, and consequently both preferences and intake rates might also be. The use of shrub material is underpredicted, but orders are correct. The preferences are very similar to those found by Noble (1975).

In a similar fashion for Run 5, the ratio of saltbush to bluebush preferences in each enclosure can be calculated, and should be constant. Table IX.7 shows these calculated for each enclosure using time data from the whole grazing period, or from only the plateau section. Note that the latter are considerably more consistent. Here bluebush was slightly preferred to saltbush, in comparison to Run 4; this was probably due to extraordinarily low water contents towards the

Table IX.6

Predicted preference ratings, $\rho$, for the West End and Depot enclosures of Run 4, and the time apportioning predicted for the Chyds enclosure calculated from these.

| | Bluebush | Saltbush | Ground |
|---|---|---|---|
| West End | | | |
| plateau (% eating time) | 53.5 | - | 46.5 |
| biomass (kg) | 41.0 | - | 0.2 |
| intake rate (g $s^{-1}$) | .16 | - | .025 |
| $\rho$ | .036 | | 1.0 |
| Depot | | | |
| plateau (% eating time) | - | 28.3 | 71.6 |
| biomass (kg) | - | 29.0 | 3.6 |
| intake rate (g $s^{-1}$) | - | .21 | .036 |
| $\rho$ | | .29 | 1.0 |
| Chyds | | | |
| biomass (kg) | 14.7 | 5.2 | 4.1 |
| intake rates (g $s^{-1}$) | .16 | .21 | .05 |
| predicted plateau % | 3.6 | 7.8 | 91.9 |
| actual plateau % | 8.5 | 10.4 | 81.0 |

end of the drought in the saltbush (30-35%, in comparison to 40-45% in the bluebush). Thus this simple model is reasonable for the 'baseline' plateau preferences of food types.

A similar model might be applicable to the early part of the grazing period, but with different preference ratings. I calculated the preference ratios thus predicted for the first 10 minutes of the grazing periods of Run 4, in a similar fashion to that described above. The ratio of preferences bluebush:saltbush:ground material then was 0.093 : 1 : 0.074, compared to the 'baseline' ratio 0.12 : 1 : 3.4. Note that the bluebush:saltbush ratio is still similar, although the preference for ground material is reduced by 46 times.

Table IX.7

Preference ratios, $\rho$, for bluebush and saltbush in each (adjoining) enclosure of Run 5, calculated using either the plateau time apportioning or the times for the whole grazing period. Intakes rates were .13 and .15 g $s^{-1}$ for bluebush and saltbush respectively.

| | Bluebush | Saltbush | $\rho_{BB}:\rho_{SB}$ |
|---|---|---|---|
| North | | | |
| biomass (kg) | 10.1 | 13.7 | |
| % times: plateau | 48.8 | 51.2 | 1.12:1 |
| whole period | 33.3 | 66.7 | 0.59:1 |
| Mid | | | |
| biomass (kg) | 10.6 | 9.0 | |
| % times: plateau | 58.3 | 41.7 | 1.03:1 |
| whole period | 52.9 | 47.1 | 0.83:1 |
| South | | | |
| biomass (kg) | 3.3 | 16.4 | |
| % times: plateau | 27.7 | 72.3 | 1.65:1 |
| whole period | 27.0 | 73.0 | 1.59:1 |

The work of Kenney & Black (1983), mentioned above, suggests that preferences early in the grazing period should be primarily dependent on relative intake rates. They did require some 'palatability factor' as well, and this is clearly necessary here where saltbush is always greatly preferred over bluebush in Run 4. The inaccuracies associated with both biomass and intake rate of ground material make its value uncertain. However, the ratios above are wholly consistent with relative preferences early in the grazing period being biased from the 'baseline' preferences by the relative intake rates. This approach even explains the slightly reduced preference for bluebush relative to saltbush in the first 10 minutes (the ratio change is .78 compared with the ratio of intake rates which is .76); and it is consistent with the reduced preference for the ground material, although the estimated difference in intake rates is not as large as the reduction in the preferences.

Normally no model should be tested in isolation, since its adequacy of fit must be compared with another. In this instance, however, the simple model is clearly a better predictor than any null model of random selection, and the form of the data does not justify testing any more complex models. It is worth noting that an approach to the early part of the grazing period based solely on biomass availability and random encounters (i.e. assuming that the hungry sheep will eat anything it encounters) is definitely not supported by these data, nor by Kenney & Black's work (where equal biomasses of all their artificial foods were available).

### (v) Spatial scale of selection.

In Run 6, I attempted to examine at what scale the sheep were reacting to the vegetation. Some workers assume a knowledge by the feeding animal of its entire surrounds, whilst others assume that selection is based only on the area immediately available to the sheep's senses. Long-term preference ratings are presumably built up by the sheep over many days of experience, but it is important to know whether instantaneous selection is based on a cumulated impression of what is available gained during the grazing period, or simply on a moment-by-moment basis.

The enclosures of Run 6 were divided in 16 subcells (see Figure VIII.1), each of which was monitored separately. As mentioned above, the breaking of the drought restricted the usefulness of the trials, and it was not possible to apply the model detailed in the previous section to them. However, I present some findings on the patterns of use of the subcells.

Although the overall biomasses in the enclosures of Run 6 differed little, there was a 50-fold variation in biomass between different cells (of about 8x8 $m^2$), as well as great variety in the proportions of shrub species. I had hoped, therefore, to show that vegetation variation at the finer scale predicted sheep behaviour better than at the enclosure scale of 30x35 $m^2$. Because bluebush was little eaten during these trials, I was unable to do this on the basis of the diet selection model. However, I present here a few data which suggest that activities are determined by the fine scale of vegetation pattern.

The total time spent in each cell was correlated well with the total biomass of the cell (r=.14, n=48, p=.006), as was the total time spent eating in the cell (p=.44, n=48, p=.002). The time spent eating saltbush correlated well with saltbush biomass per cell (r=.55, n=48, p=.0001), and better than it did with numbers of saltbush in the cell (r=.44, n=48, p=.0018). By enclosure, these correlations were stronger in North and Mid, where the vegetation was more mixed, than in South (see Table VIII.2). Similar correlations may be found for ground material, and weaker ones for the little-used bluebush.

These correlations support the proposition that the sheep's minute-by-minute grazing activity is determined on a fine scale, at least as fine as 8x8 $m^2$. In fact, the area may be no more than that immediately available to its senses. This results in the sheep encountering a highly randomised series of vegetation sets, and justifies the use of gross biomass totals as an estimator of these random encounters.

### (vi) Summary: scales of selection.

When there is little ground material available, sheep in small enclosures still spend large amounts of time foraging for it. The majority of their intake is, however, obtained from shrubs under these conditions. The proportions of their time that they spend foraging for different categories are not constant with time. They eat far more of the shrub category, at a much higher intake rate, than the ground category in the first 20 to 40 minutes of the grazing period. Later in the grazing period, they concentrate on the lower intake rate category. The time to this changeover may vary from 20 to 45 minutes, but estimated dry weight intake up to this time is remarkably constant at about 150 g. With some evidence against shrub toxins being important, this is hypothesised to be a genuine change from selecting for high intake rate when hungry to high quality when partially satiated. This finding is important to experimental design of diet selection experiments, oesophageal fistulation, and to the distribution of grazing impact in the open paddock. A modified version of Noble's diet selection model explains time apportioning between foods by sheep reasonably; 'traditional' preference ratings predict the plateau time apportioning, and a preference rating modified by intake rate ratios may be suitable when the sheep are hungry.

## (c) Other impacts on plant individuals and species.

The amount of time that a sheep spends on one individual plant will have obvious importance to that plant, and to the distribution of grazing between plants. The frequency with which the animal switches between species in its diet will similarly be important to the distribution of impact between species in the area through which a subflock is travelling. These factors are likely to act at a scale far below that of the model operation, so I only touch briefly on them in this section to confirm this.

### (i) Time spent on an individual plant.

When faced with a saltbush, sheep do not eat it to the ground, which perhaps they should do if all parts of the bush had equal palatability. Optimal foraging patch theory (e.g. MacArthur & Pianka 1966) suggests that the animal should cease to eat it when its marginal return rate from that patch falls below the mean marginal return rate to be expected by moving to another (although there are other possible approaches, e.g. Janetos & Cole 1981). This must be estimated from previous foraging experience, in either the short- or the long-term. It is probably naive to expect to be able to apply such theory in any simple form to a herbivore which has only small costs in moving to another bush, for which the palatabilities of different plants and plant parts fall on a continuum, which may need to sample, and on which added complications are imposed by sociality. A sheep rarely removes all the feed in one category (e.g. young leaves) from a bush on one occasion.

I tested whether offtake from an individual plant was related to its size on two occasions. In the collection of data for the intake rate measurements (section (a.i)), there was slight effect of the mean length of eating bout being longer for larger test 'plants' (r=.71, n=9, p=.03 for saltbush, non-significant for bluebush, in one trial); however, there was only a small variation in size of plant in these trials. Therefore, in Run 6, I compared the mean size of saltbush individuals within each cell (see Figure VIII.1) with the mean duration of a bout of eating on a single bush (this was defined as the time spent eating before either a movement, or a switch to another food type). The mean plant size per cell ranged from 10 to 55 g, and the mean length of eating bout from 1.4 to 39.8 s, but there was no correlation between the two (r=.00, n=48, p=.98).

If there is a genuine lack of correlation between offtake from an individual shrub and its size, then a large plant is likely to sustain a smaller proportional amount of damage in a grazing event than a small plant. Although large plants may have a higher encounter rate with sheep than small plants, this may still mean that large plants will sustain smaller proportional damage in light to moderate grazing pressures. This could certainly be important to the plant, and to the population structure of the pasture in drought years, but is below the scale of the model.

### (ii) Switching.

The concept of a search image, first studied in birds, involves the active seeking out of one cryptic prey type (Dawkins 1971). However, a weaker form of temporarily-heightened recognition for one food type, or an undue preference for locally common food types (e.g. Murdoch 1969), can cause correlated bouts of feeding on one food type, followed by abrupt switches to another. This could be significant in the pattern of grazing impact if the animal concentrated on a single species for long enough.

Table IX.8 shows the total number of transitions between the major food types in Run 5. This simple transition matrix can be tested against the mean expected values obtained from the column sums. The resulting $\chi^2$ values and probabilities are shown. In total for the enclosures, the ratio of saltbush individuals to bluebushes was 1067:224, so one would expect saltbush to be more frequently encountered (although their mean size was also smaller), as well as being more likely to be accepted because of being preferred by the sheep.

Table IX.8

Actual and expected transition matrices between food types for all the data of Run 5. $\chi^2$ tests are given for the comparison of actual and expected rows (i.e. transitions from the present food to the next), where the expected value is conservatively estimated as proportional to the column totals. All $\chi^2$ values are significant, d.f.=2, p<.0001.

| | Actual | | | Expected | | | |
|---|---|---|---|---|---|---|---|
| Next food:<br>From: | Bb | Sb | Gr | Bb | Sb | Gr | $\chi^2_2$ |
| Bb | 61 | 50 | 73 | 25 | 55 | 104 | 62 |
| Sb | 60 | 208 | 150 | 60 | 124 | 237 | 89 |
| Gr | 70 | 161 | 577 | 110 | 240 | 458 | 71 |
| Total | 191 | 419 | 800 | | | | |

(Bb = bluebush, Sb = saltbush, Gr = ground material)

There is a bias towards remaining with the shrub type just eaten for both bluebush and saltbush. Although this data records a transition only if a movement or a type switch has occurred, this bias may be partly due to sheep moving around to another part of the same shrub, especially for the larger bluebush. For saltbush there is often a spatial association of several individuals, so that the immediate environment may be locally dominated by saltbush. The effects are interesting, but not highly relevant, therefore. Many other analyses can be carried out on the transition data, but their impact is clearly at a scale that is not needed in the model.

# Chapter X.

## The new behavioural model: structure, validation and prediction.

In this chapter, I draw together the various lines of study previously discussed in this thesis, and build a new model of sheep behaviour in the large open paddock. Some sections of Noble's model have been validated and are retained, others have been validated in modified form, and some approaches have been completely replaced. In the first part of this chapter, I outline how I have rebuilt the model. I do not describe some details where they follow the approach of Noble (1975), except where they are relevant to an understanding of the major changes, or important in the ensuing discussion. Thus, for example, the submodel dealing with body and wool growth is not mentioned, since its formulation has not been altered.

The latter half of this chapter is concerned with testing the model. There are many problems and a variety of different approaches associated with testing complex models of this type (e.g. Shechter & Lucas 1978). The first step is verification - that is, ensuring that the model and its coding carries out the operations that were intended, irrespective of their validity. Validation approaches include 'informal verification' to confirm that the model behaves sensibly in the opinion of someone who has experience in the system that has been modelled; 'sensitivity analysis' to test whether the model is unrealistically sensitive to small changes in particular variables; and predictive tests of 'goodness-of-fit' to real data that were not used to build the model. A considerable amount of data from my main study paddock, Jervoise, has been used in this thesis so far, and is therefore of limited value for validation of the model, although it may be used in verification. Independent data, in particular from dung surveys and the vegetation exclosures, is used for validation in Jervoise, and I also run the model for Wizzo North paddock. Finally, an important test of a predictive model is to try to look into the future, so I finish this chapter with two predictive runs.

## (a) Remodelling.

In Chapter III, I pointed out three components of Noble's model that were deficient either in approach, or because of lack of validation. These were the physiological indices that determine the sheeps' behaviour, the selection of sites of non-grazing activity in the movement model, and the form of the grazing intake model. Additionally, I remarked that the interactions between the physiological threshold levels were over-simplistic, partly because directed grazing was not permitted. In this section, I discuss briefly how I have tried to redress each of these components, and I then describe how they are linked together, and into the structure of the overall model.

The spatial representation of the pasture in the new model is very similar to the old, and was described in Chapter III(b). In brief, the modelled paddock is divided into cells (500x500 $m^2$ in Jervoise); the runoff, soil moisture and plant growth is modelled on a daily time-step for each cell. There are six categories of plants modelled for growth and grazing: these are grasses, 'bassias', standing dead and dry ephemerals, saltbush, bluebush and blackbush. A number of sheep subflocks move between the cells on an hourly time-step, with movement being determined by their activity during that hour. Grazing takes place within a cell, and intake is constrained by the vegetation available in that cell. The impact of the sheep on the paddock is determined by nitrogen re-distribution and grazing offtake in the cells that they visit.

### (i) Physiological triggers.

The four 'triggers' used in Noble's model were a heat-loading index, thirst (as a body water deficit), hunger (as rumen fill) and night-time. The interactions of these resulted in seven trigger conditions (see Table III.1), which gave rise to the eight activities of grazing, 'shading', camping, resting, moving to shade, to camp or to water, and watering. This subsection describes the determination of the trigger levels; their integration is discussed in the next.

The heat-loading index has been the most successfully developed and validated of the triggers in this thesis. Chapter VI(b) and the Appendix describe how the physically-determined respiration index can predict movement to shade. This respiration index is used in the new model, and is calculated from the equations given in the Appendix. For a given day and hour, these equations require the climatic inputs of air temperature, wind velocity and cloud cover; they also need the body length and radius of the sheep, its wool length and body weight (only the latter two vary in the model). From these parameters, respiration indices for sheep in the shade and in the open are calculated, and one or other is used for a given subflock depending on its activity.

In addition to predicting movement to shade, the respiration index is also used to determine aspects of the sheep's energy balance. It is not allowed to fall below a minimum value (20 $\text{min}^{-1}$) for lung aeration; below this value, an increase in metabolic rate to maintain body temperature is assumed to occur, and the extra energy is taken into account when calculating the daily live-weight changes. When the sheep are hot, the index is not permitted to rise above the maximum value recorded for sheep (300 $min^{-1}$), at which body cooling begins to fail; energy which cannot be lost from the sheep is stored in the body tissues, so that the body temperature begins to rise. Both of these approaches follow Noble (1975). The fourth use of the index is to predict water loss in respiratory cooling for the water balance accounting.

The water balance sub-model for the sheep is calculated hourly as a body water store; this store may be replenished by drinking. Other sources of water are metabolic water and water from food intake, whilst losses are incurred during respiration, in the faeces and urine, and to dispose of salt absorbed from the food. This approach follows Noble, and is described in more detail in Chapter VI(c). Salt and water contents in the food are determined from grazing intake. Using this approach, Chapter VI(c) showed that observed watering peaks occurred in a consistent range of predicted water deficits, although this submodel is not validated as thoroughly as the respiratory index.

The rumen-fill index for hunger is discussed further in subsection (iv) which deals with the grazing model; this index also operates as a store. Decline in rumen fill, by outflow to the omasum, is taken to be by a constant factor of 0.9 per hour, after Blaxter et al.(1956). Finally, the night-time camping trigger is set an hour after dusk and lifted in the hour before dawn. As discussed in Chapter VI(d), the strong urge that sheep have to camp seems to be genetically imposed and not amenable to process-modelling.

## (ii) Activity transitions and the interaction of triggers.

Noble's model did not permit directed grazing, and was simpler in its heirarchy of trigger thresholds. Chapters VI and VII have shown that grazing does occur en route to water, and perhaps to shade and campsites. The behavioural categories of 'gm' and 'mg' (see Table IV.4) are important parts of grazing and movement behaviour, and are allowed for in the structure of the new model. As was shown in Chapter VI, other interactions also occur, such as with the heat index.

It is not possible to make the threshold levels of the index continuously interactive with each other, as they probably should be, because their functional relationships are not known in this much detail. However, I now have enough information to be able to divide the ranges of the trigger indices in more places than the old model, and thus permit more interaction. These indices are examined every hour for every subflock in the model, so that it must be possible to operate the chosen method of implementation quickly.

I have therefore adopted the approach illustrated in Table X.1. Each trigger has several threshold levels, with the order of dominance being thirst, heat, hunger and then night-time. This heirarchy normally determines the next activity on the basis of the previous activity, the dominant current trigger and its threshold level (1-3). This permits implementation using the same decision table method of the old model, which is very rapid, although this table is now three dimensional. If all triggers are at the zero level, then the animal will rest; all other possibilities are illustrated in Table X.2. As can be seen, I have retained the eight basic activities of the old model, but once the main decision has been made, the subdominant

Table X.1

The new heirarchy of trigger level conditions: the conditional entries are explained below. A dash indicates that the entry is irrelevant in determining the dominant trigger, which is underlined.

| | Trigger levels | | | |
|---|---|---|---|---|
| | Thirst | Heat | Hunger | Night |
| ranges | 0-3 | 0-3 | 0-2 | 0-1 |
| Next activity | | | | |
| To water[1] | $\underline{3}$ | - | - | - |
| To shade[1] | ≤2 | $\underline{3}$ | - | - |
| To water[2] | $\underline{2}$ | ≤2 | - | - |
| To shade[2] | ≤1 | $\underline{2}$ | - | - |
| Graze[3] | ≤1 | ≤1 | $\underline{2}$ | - |
| (Drink)[4] | $\underline{1}$ | ≤1 | ≤1 | - |
| (Shade)[5] | 0 | $\underline{1}$ | ≤1 | - |
| (Graze)[6] | 0 | 0 | $\underline{1}$ | - |
| To camp[7] | 0 | 0 | 0 | $\underline{1}$ |
| Rest in situ | 0 | 0 | 0 | 0 |

[1] movement is exclusive
[2] hunger level 2 will induce some grazing during movement
[3] any trigger level 1 will induce directed grazing
[4][5][6] these activities are conditional
    [4] drink if near water
    [5] stay in shade if already there
    [6] keep grazing if already doing so
[7] except that, once in camp, sheep cannot leave till morning unless a trigger reaches level 3

triggers may interact to modify the chosen activity.

The interactions between triggers primarily concern directed grazing. In particular, hunger may cause some grazing during movement (i.e. 'mg') to shade, camp or water, providing the trigger instigating movement is not at the extreme level 3. Low levels of other triggers may cause grazing to become directed (i.e. gm) providing the potential destination has not been reached. Other conditional decisions are mentioned in Table X.1. In particular, the camping impulse, which is subdominant before arrival at camp, does not allow departure from camp

## Table X.2

The decision table for primary activities, described in the text: on the basis of the previous activity (row, with identifying number) and the dominant trigger and its threshold level (columns), a new activity is chosen (entry in table). Two conditional decisions are corrected after using the decision table, and interactions with subdominant triggers are handled separately.

| | | Dominant trigger and threshold level | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Thirst | | | Heat | | | Hunger | | Night |
| | | 3 | 2 | 1 | 3 | 2 | 1 | 2 | 1 | 1 |
| Previous activity | | | | | | | | | | |
| 1 | Graze | 7 | 7 | 1[1] | 5 | 5 | 1[1] | 1 | 1 | 6 |
| 2 | Shade | 7 | 7 | 2 | 2 | 2 | 2 | 1 | 4 | 6 |
| 3 | Camp | 7 | 7[2] | 3 | 5 | 5[2] | 3 | 1[2] | 3 | 3 |
| 4 | Rest | 7 | 7 | 4 | 5 | 5 | 4 | 1 | 4 | 6 |
| 5 | Move to shade | 7 | 7 | 4 | 5 | 5 | 4 | 1 | 4 | 6 |
| 6 | Move to camp | 7 | 7 | 6 | 5 | 5 | 6 | 1 | 6 | 6 |
| 7 | Move to water | 7 | 7 | 7 | 5 | 5 | 4 | 1 | 4 | 6 |
| 8 | Water | 8 | 8 | 8 | 5 | 5 | 4 | 1 | 4 | 6 |

[1] rest if hunger trigger is not above level 1
[2] stay in camp if still dark

until the hour before dawn unless an extreme (level 3) trigger threshold is exceeded (in practice this only occurs with thirst). There are a number of other minor complications; for example, the heat index only influences grazing movement if it has risen since the previous hour, so that movement to shade does not occur on a hot evening. Similarly, on very hot days, sheep will not stay in shade after the hour before sunset; this event occurs very rarely.

The threshold levels of the indices are mostly obtained from earlier chapters. The hunger trigger levels are discussed in subsection (iv) with the grazing model. The night-time trigger is turned on in the hour after dusk and off in the hour before dawn; sheep were rarely seen in camp outside this period. Level 2 of the heat index ('hot') is set from the less-stressed values in Table VI.2, with allowance for wool length. The relationship was obtained from regression on the original data, after rounding, as,

trigger level = 185 + 650 * wool length (min$^{-1}$)

The higher threshold ('extremely hot') is set if body temperature begins to rise (see previous section). There could be a higher level still, of heat exhaustion, where the body temperature rises above a critical level: this was the upper trigger in the old model. However, this occurs too rarely to warrant the extra code for the sake of symmetry in the decision table, and in test runs the 'extremely hot' threshold had invariably already caused movement to shade. (The calculations of rising body temperature are retained since they allow the sheep to tolerate high air temperatures with less water loss). The lower or 'warm' threshold level is taken to be 20 min$^{-1}$ below the 'hot' level, which typically results in an hour's warning for the grazing sheep. This value results in a small effect of the need for shade on grazing movement, as suggested by Chapter VI(b).

The threshold levels for the thirst index are set on the basis of Chapter VI(c). The maximum drink size permitted on one occasion is 5 l, but drinking may occur again in the next hour. The first level of mild thirst is taken at a body water deficit of 2.75 l, which was approximately the minimum calculated deficit at which animals returned to the waterpoint in West End. The second level, thirsty, is taken as 4.25 l deficit, which was the modal level at next watering, and the highest level at which sheep might miss a modal watering time in West End (Figure VI.8(c,d)). Level 3, or 'dehydrated', is set at 6 l; sheep did tolerate more than this occasionally in West End, but that was in an extreme summer. In the model, the notional body-water store for the sheep is taken to be 6 l, so that drinks will not be taken to exceed this level; the dehydrated threshold is then at a body water store of 0 l.

To what extent does this approach accord with the data of Chapters VI and VIII ? In Chapter VI, it was shown that hunger could delay entry to shade, and thirst could advance departure. In the model, sheep will depart shade for water before they will leave to graze (although they may then graze a little en route if very hungry). Arrival at shade will be delayed if the animals are hungry because they will graze en route and therefore move more slowly (see next section). Chapter VI also showed that the need to water might affect grazing directions early in the day, even though a period in the shade intervened. The timing of these interactions are not coded into the model, but the structure will allow them to occur. Watering in West End rarely took place at night (Figure VI.8(a)), and then not after the middle of the night; in Jervoise, sheep were occasionally heard at the waterpoint several hours before dawn, so that extreme thirst had overriden the camping impulse. Again the structure is compatible with reality.

### (iii) Movement and selection of destination.

In this section, I discuss movement speeds and movement directions. The activities that involve movement are grazing and movement to shade camp or water. Grazing may be directed (gm), and movement may include some grazing (mg).

Speed of movement and grazing 'intensity' in the activities g, gm, mg and m are set by derivation from my definitions (see Table IV.4), where a mean 12.5, 37.5, 62.5 and 87.5% of the time is spent moving respectively, in a ratio 1:3:5:7. 12.5% of the total time spent moving is similar to the proportion found in small enclosure grazing periods (Chapter VIII(b.ii)). Taking 0.3 km $h^{-1}$ as the net movement speed in grazing (at the upper end of the values found in small enclosures), this results in speeds of 0.3, 0.9, 1.5 and 2.1 km $h^{-1}$ for the activities respectively; these values accord well with the values observed in the open paddock and with ranges quoted in the literature. Correspondingly, grazing 'intensity', or the effective proportion of time spent eating, declines in the ratio 7:5:3:1, except that, in the model, no grazing is permitted in 'm' sensu stricto (intakes would be very small, but computing costs are very high, since the grazing model must be run for every cell that is passed through).

Chapter VIII(c.i) showed that movement increases in low shrub densities (when there was little forage available on the ground). Observations aimed at quantifying the relationship between movement speed and vegetation quality in the open paddock were unsuccessful (Chapter VII(b.ii)). Sheep clearly do not graze much in areas where there is no vegetation, so a realistic model must permit them to leave a cell that is devoid of forage. One approach to this requirement would be to set a threshold level of forage availability below which a subflock tends to move faster in grazing. Another approach, adopted in Noble's model, is to increase a subflock's speed if its intake in the current hour is less than in the previous hour; this is not satisfactory where more than one cell may be traversed in an hour, as is the case with the smaller grid size used in Jervoise in comparison to Wertigo, nor does it result in an increase in movement speed if the sheep have started their grazing in a poorly-vegetated cell (near the waterpoint, for example). A third alternative is to increase the subflocks's speed if the forage available to it at its present position is less than the mean availability in the paddock.

Since I have no data on which to reliably base any threshold, I adopt the third approach. This approach assumes that the sheep range over the paddock sufficiently to visit cells which are not severely affected by any grazing impact, and that they have some memory of the quality of these cells. This is effectively invoking some learning on the part of the sheep, a process which has generally been avoided in the model, although the response could also be based on smells wafting in on the wind. Rather than using the total available forage in a given cell, I use the total effective forage ($\Sigma \rho_i b_i$), since it is biased in favour of preferred feeds and may therefore be more relevant to the sheep.

Movement directions are determined for directed movements by the 'choice' of a shade, camp or waterpoint location. There is only one waterpoint in Jervoise, and the use of water in Wizzo North is discussed further in section (c). Chapters VI and VII have suggested that the choice of camp and shade sites may be more important than movement in grazing in determining the area of a paddock in use, and that this choice may be affected by wind direction. The old model selected the nearest camp or shade site for this purpose. In the new model, the nearest shade or camp site in the direction of the wind is selected as required, except that a site which is only one cell away will be chosen in preference to one in the direction that the wind is coming from if the latter is more than two cells distant. For speed of implementation, this choice is coded as a matrix of nine possible destinations (one for each wind direction, and one for calm conditions) for each cell in the paddock. For Jervoise, only the major campsites shown in Figure VI.9 are used.

Movement in grazing was shown to be little affected by wind direction in Chapter VII, except perhaps in stronger winds. Once a subflock has started moving in some direction, therefore, its movement direction in the next hour is selected randomly with bias towards the previous direction (as it was in calm conditions in the old model). Movement in the first hour of grazing is still selected as it was in the old model, that is, as a random direction biased by the wind direction, the bias being stronger in stronger winds.

The final effect to discuss with respect to movement is that of 'contagion'. The model runs on a fixed number of subflocks, whilst Chapter V showed that group size varied with a number of conditions. Some of the variation may be related to the physiology of lambing, and I do not attempt to model this; however, other aspects were probably dependent on the time since subflocks last met up, and grouping of subflocks is included in the model as follows. From Chapter V(c), the maximum 'core group size' in Jervoise was about 10 sheep, and for most purposes I run the model with 260 sheep in 20 subflocks. Real groups were larger at campsites and the waterpoint, and broke up during extensive movement on departing these locations. The old model permitted subflocks grazing in the same cell to move together at times; I adopt the same approach, where the probability of 'contagion' for two such subflocks is given by p, where p (=.77) was the probability of a group not breaking up during a given hour of grazing as calculated in Chapter V(c.i).

### (iv) Diet selection.

The diet selection and intake submodel used in the old model has already been described (Chapter IX(b)). The equations used in it require an independent estimate of hourly total consumption, which was derived from a Holling-type equation, adjusted by a satiation factor. As Chapter IX showed, selection as well as total consumption changes at an hourly timescale, and within a grazing period.

The approach intimated in Chapters VIII and IX is developed as follows. The actual time spent eating per hour is modelled first, rather than total intake per hour. Chapter VIII showed that there was an inconsistent decline in eating activity with satiation, which was slow relative to a rapid cessation of grazing at the end of the grazing period. From mean values, I take this to be a linear decline in time spent eating from 75% to 65% of total time, from when the sheep are very hungry to when they are sated. If these two states of rumen fill are respectively $F_0$ and $F_T$, time spent eating per hour is given by,

$$T_F = 0.65 + 0.1 * (F - F_0) / (F_T - F_0) \quad \text{hours}$$

This total time is divided amongst the food types available by the modified version of the previous model that was discussed in Chapter IX(b), so that,

$$t_i = T_F * (\rho_{i,F} * b_i / r_i) / \Sigma (\rho_{i,F} * b_i / r_i) \quad \text{hours}$$

where $t_i$ is the time spent eating food type i, of biomass $b_i$, intake rate $r_i$ and preference rating $\rho_{i,F}$ at this hunger status F, and $\Sigma$ is over all food types.

Evidently $\rho_{i,F}$ cannot be regarded as constant for all F. Chapter IX(b.iv) suggests that, if $F_p$ is the hunger status at the 'inflection point' described in the previous chapter, then $\rho_{i,F}$ for all $F>F_p$ should be constant and equal to the 'baseline' preference ratings. At $F_0$, it also suggested, $\rho_{i,F}$ should be given by the product of the baseline preference rating and the relative intake rate. I take this tentatively to be an adequate description for this model.

I can find no satisfactory suggestions in the literature as to what the functional form of any influence of hunger on preferences should be, so I assume a linear interchange between $\rho$ at $F_0$ and $F_p$, resulting in,

$$\rho_{i,F} \begin{cases} = (\rho_i * (F - F_0) + \rho_i * r_i * (F_p - F)) / (F_p - F_0) & \text{for } F<F_p \\ = \rho_i & \text{for } F \geq F_p, \end{cases}$$

where $\rho_i$ is the baseline preference rating for food type i. Intake rate, $r_i$, may be expressed in any consistent units, since these divide out in the equation for $t_i$ above.

This model can now be used to predict the observed time distributions in the small enclosure Runs. I assume the sheep to have been at status $F_0$ when released; then, using the known biomasses and intake rates, Figure X.1 shows the modelled times spent eating shrubs and ground material for trials in the Depot enclosure of Run 4 compared with the observed times. The selection model underpredicts the initial extreme value, and overpredicts the rate of changeover between food types. However, in the overall model, grazing intake is calculated on a time-step of 15 to 60 minutes (depending on the numbers of cells traversed during the hourly time-step of activity selection), so that underprediction of the effect of the hunger status at the start of the time-step satisfactorily approximates the average value of the declining hunger status as the animal grazes.

In the full model, actual intakes per hour are now calculated as the product of the time spent on each food type and its intake rate. Several values must be known, namely, the intake rates and the baseline preferences for each food type, and the three critical levels of rumen

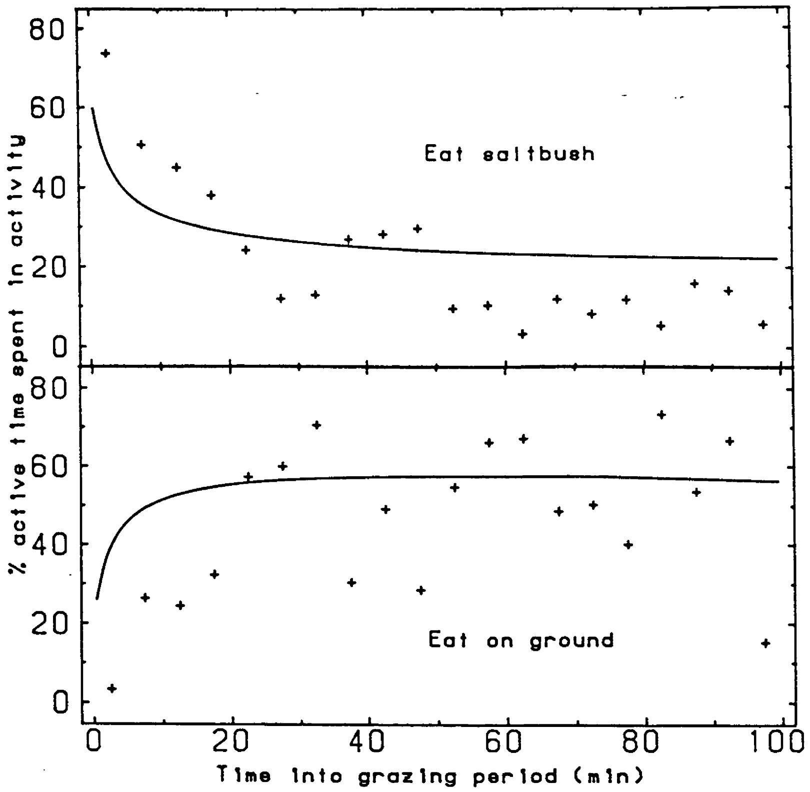


Figure X.1: The observed time courses of eating shrubs and ground material (points) compared with the modelled time courses (solid line) calculated for every five-minute period, for trials in the Depot enclosure, Run 4 (c.f. Figure IX.2).

fill ($F_O$, $F_p$ and $F_T$). As with the original model, it is clear that preferences do change during the year (e.g. the increase in preference for bluebush relative to saltbush from Run 4 to 5). In the shrubs, this might be related to water content at Middleback, but there is not enough data to vary these at present. The values found by Noble correspond well with my values for Run 4, when weather conditions were moderate, so I retain them for the shrubs (Table X.3). I have increased the preference ratings for ephemerals, since my trials showed much higher values than were found by Noble.

The sheep's intake rates of the shrubs also vary; this probably is a result of the physical structure of the shrub, and may also correlate with water content at Middleback. Again I have inadequate data to adjust the rates reliably, so I adopt mean values after Table IX.1.

The variation in preference ratings with intake rates described above is most importantly affected by the intake rates of the ground material. These too probably vary continuously through the year, although some of the variation is taken up in the model by the separation of dry from living ephemeral material. In order to be able to model the increased preference for shrubs when the sheep are hungry, I assume a step function where ephemeral intake rates have one value when they are plentiful, and a lower value if their biomass falls below a critical value in the cell being grazed. These are derived as estimates based on the small enclosure trials, although the grass intake rates are comparable with those described by Allden & Whittaker (1970); all the values used are listed in Table X.3.

Table X.3

Values of baseline relative preference ratings and intake rates used for the vegetation classes in the new model, with the critical levels of ephemeral biomass below which intake levels are reduced (see text).

| | Preference rating | Intake rates ($g\ s^{-1}$) | | Threshold biomass ($kg\ ha^{-1}$) |
|---|---|---|---|---|
| | | normal | reduced | |
| Ephemeral classes | | | | |
| Grass | 5.0 | .10 | .04 | 20 |
| 'Bassia' | 1.5 | .09 | .03 | 20 |
| Dry | 2.0 | .08 | .03 | 25 |
| Shrub classes | | | | |
| Saltbush | 1.0 | .18 | - | |
| Bluebush | 0.1 | .15 | - | |
| Blackbush | 0.025 | .12 | - | |

The remaining parameters are those of rumen fill. $F_T$, for the sated sheep, is taken as 0.75 kg d.w. after Noble (1975). $F_0$ is assumed to be the approximate state of rumen fill for a sheep after 10 h penning, which, on the basis of a 0.9 rumen-emptying factor per hour (Blaxter et al.1956), is 0.26 kg d.w. The setting of $F_p$ should be about 150 g d.w. above this according to Chapter IX(b.ii). Equally, on the basis of the total intakes of the observed grazing periods being 350-400 g d.w., it should be 0.2-0.25 kg d.w. below $F_T$. In fact, the inflection point as defined in Chapter IX may not be the end point of extreme hunger if the change in preferences is considered as a smooth curve, and the rumen probably empties a little more slowly when low in contents, so the value may be more than 0.15 kg d.w. above $F_0$; contrarily, the grazing periods as described from the small enclosures do not include possible residual grazing later in the morning, which may have been delayed because of 'jaw fatigue' or other food processing factors. In consequence, $F_p$ is defined as 0.5 kg d.w. rumen fill, and is also taken as the 'hungry' trigger level (i.e. level 2 at which, if no other urge prevents them, sheep will start grazing). The level 1 hunger threshold occurs whenever rumen fill is below $F_T$.

The sheep ingest water and salt in their food, and these affect the water balance of the body. The old model had no provision for variation in these. During the drought that occurred during this study, plant water content dropped drastically, and, to be realistic in validation runs, I include a simple descriptive relationship based on soil moisture to determine these parameters for the shrubs. Sharma et al. (1972) show a reasonable linear relationship between the salt content of saltbush leaves (as $Na^+$ or $Cl^-$) and soil moisture, and a quadratic relationship between salt content and relative leaf water content; the latter is almost linear for higher values of water content. This work was carried out on <u>Atriplex vesicaria</u> and <u>A. nummularia</u> on clay soils in the Riverina Plain. I measured water contents of saltbush forage (by dry weight) on five occasions and compared them with soil moisture values predicted in the the deepest of the three soil layers treated in the runoff submodel during the increasing drought of 1980-82. In the first four cases, water contents decreased in parallel with the predicted soil moistures. The fifth was measured in April 1983, when rain had saturated the upper soil layers, but had not reached the deep layer; here the plants had a high water content, showing that the shrubs can tap sources at both levels.

On the basis of my results, and by comparison with the work of Sharma et al. (1972), I use the following linear relations to describe the water and salt content of saltbush forage for validation runs prior to March 1983. I emphasise that these are merely descriptive relationships for this period:

water content of saltbush = 400 - (27 - SM3) * 27.4 (% d.w.)

salt content of saltbush = 6 + (27 - SM3) * 0.45 (% d.w.),

where SM3 is the mean soil moisture (cm) in the deepest soil horizon, and the expressions are not allowed to exceed 400 and 12 % respectively. A slightly different relationship is used for bluebush,

water content of bluebush = 400 + (SM3 - 27) * 24.5 (% d.w.)

There is little available data on the salt content of bluebush, but on the basis of Lange (1967) and Noble (1975), I have taken it to be 75% that of saltbush. A few samples of blackbush have contained water in similar quantities to saltbush, and I take its salt content as 50% that of saltbush; it is a minor dietary component so that these approximations are insignificant. These values are set daily in the model.

## (v) Structure and implementation.

In this section, I describe how the new behavioural model fits together, and how it is linked to the plant growth model and the run control system. The control system is a group of subroutines that I have written to make the model interactive in use (the old model was designed to be run in batch mode only); this permits much greater flexibility in the control of output quantity (at any time interval from hours to years) and type (various summary parameters of climate, vegetation or behaviour, and behavioural details including ranging patterns and hourly activities). In common with a number of other routines, such as those controlling time incrementation, weather input from file records, and many output routines, the coding details of the control system are irrelevant to the model itself, and I do not describe them.

- AA interactive control routine + own summary structure
  - YRSIM - simulates each day of the year
    - TIMER - time keeping
    - WEATHR - obtains or generates weather
    - WATVB - runoff, soil moisture and evaporation
    - PGROW - plant germination, growth and dieback
    - HRSIM - hourly sheep behaviour, called 24x a day
      - HEAT - respiration index for hour
      - GMOVER - movement and grazing
        - GDEST - destinations and directions of movement
        - GRAZE - diet selection and intake
        - GWATER - watering
    - SHPHYS - daily sheep growth
    - ZUMARY - summaries as required

Figure X.2: Simplified structure of subroutines in overall model. 'AA' is actually a group of several routines, handling commands, initialising runs, and making available its own summaries.

```
Daily   Hourly   By subflock

Heat trigger settings
Fixed heat balance calculations
Call hourly simulator for each hour

      Hourly heat balance calculations

             Assess physiological status / time of day
             Select new activity
             Modify main activity by subsiduary triggers

             Set up contagion matrix for grazing groups

             Carry out activity
                   Graze or move
                       Obtain destination/direction
                       Set speed and grazing intensity
                       Determine route and time in each cell
                       Graze visited cells if necessary
                       Distribute nitrogen on visited cells
                       Water if at waterpoint and thirsty
                       Adjust status of any linked subflocks
                   or shade or camp or rest or water
                       Water if at waterpoint and thirsty
                       Distribute nitrogen on cell
                 Adjust rumen fill and water status
                 Store extra energy requirements
                 Adjust body temperature if cooling inadequate

      Hourly summaries, if necessary

Body and wool growth
Daily summaries, if necessary
Adjust or zero various daily stores
```

Figure X.3: Detail of new behavioural model structure; the program cycles through each block daily, hourly or by subflock.

The structure of the new model is summarised in Figure X.2, and the behavioural section is shown in more detail in Figure X.3. Each day, any factors which remain constant for the day are determined; this includes the day's weather, and the soil moisture and plant growth in each cell of the paddock. For most of the runs described in the chapter, I have used real weather data from Middleback (temperatures, wind speed and direction, cloud cover) and Roopena (rainfall), although longer predictive runs use simulated weather sequences based on Noble's model. The consequent determination of soil moisture and plant growth also uses Noble's submodels. Some adjustment of growth parameters was made after model runs with no sheep to fit the vegetation exclosure data from Jervoise (Chapter IV(d.ii)) over the study period. Initial biomasses in Jervoise were those recorded during the vegetation survey of 1980 (Chapter IV(d.ii)). The growth model fitted the vegetation conditions in Jervoise adequately for the period of the study; for longer predictive runs, results are always described in terms of the difference between model runs with and without sheep in the paddock, thus reducing the impact of the vegetation growth model on any conclusions drawn.

Certain factors which are constant for the behavioural model are also calculated at the start of the day, including dawn, dusk, solar azimuth, heat trigger levels (based on wool length), and mean effective forage availability in the paddock. An hourly simulation routine is then called for each hour of the day.

Each hour (Figure X.3), certain fixed parameters are first calculated, such as respiration rates in the shade and the open. The status of the triggers for each subflock is then examined, and this hour's activity is selected. Next, all subflock pairs are checked, and, if two are grazing in the same cell, they may be linked together in a group on the basis of the probability described in the previous section; if this occurs, then intakes and movements of the first of each tied set of subflocks are automatically applied to the others in the group in later routines. The activity of the hour is now carried out for each subflock, including any movement and grazing; at the end of the hour, various physiological triggers and stores are adjusted, and summaries output if necessary. At the end of each day, wool and body growth is calculated for the day from the sheep growth submodel.

The coding of the programs are such that the model may be adjusted to run on a different paddock with minimal effort. All alterations may be made in one data element, which includes information on the spatial design of the paddock, its grid size, and the distribution of its vegetation, run-off, campsites, shade and waterpoints. The largest matrix to be entered is one which describes movement between cells; for this, the cell nearest in each direction (NE,E,...,N) must be specified for movement from each cell. This matrix requires considerable storage, but greatly speeds up the execution of the movement subroutine, as well as taking account of fenceline effects. The model as described in this section uses about 60 s of central processor time on the Univac 1100/80 at the A.N.U. for each simulated run-year, including plant growth and the behaviour of 20 sheep subflocks in the 53 cells of Jervoise. By comparison, about 38 s is used when modelling only 10 subflocks, and 7 s when no sheep were present (i.e. run-off and plant growth models alone).

## (b) Model runs in Jervoise.

This section describes a series of runs of the model on Jervoise paddock, using the weather data from the period of my study. These runs all start in May 1980, using information from the vegetation survey that was carried out during that month as a baseline for plant distributions in the paddock.

In Jervoise, the model operates on the 53 cells shown in Figure IV.9(a). The sheep behaviour section of the model invokes a random function for two purposes - determining whether grazing subflocks will move as a group, and to select movement directions in grazing; for most of this section, therefore, I compare the observed data with that predicted by model runs with five alternate 'seeds', or starting values, in the functions that generate the random numbers. The difference between these runs gives a good indication of how sensitive the model is to chance events.

### (i) Activity patterns in different seasons.

A basic verification of the model is to ensure that it predicts sensible daily patterns of activity. Figure X.4 shows the predicted patterns for 60 day periods at various times. These patterns parallel those reported in the literature (see Chapter II) and earlier in this study (Chapter V(c.iii)). There are morning and afternoon grazing peaks, watering is usually bimodal, and shade is used in summer and autumn only. Watering frequency is reduced in winter relative to summer, and some grazing occurs throughout the day; the subflocks in the model grazed less in the middle of winter days than did real sheep, however (Figure V.7). This implies that the modelled subflocks are

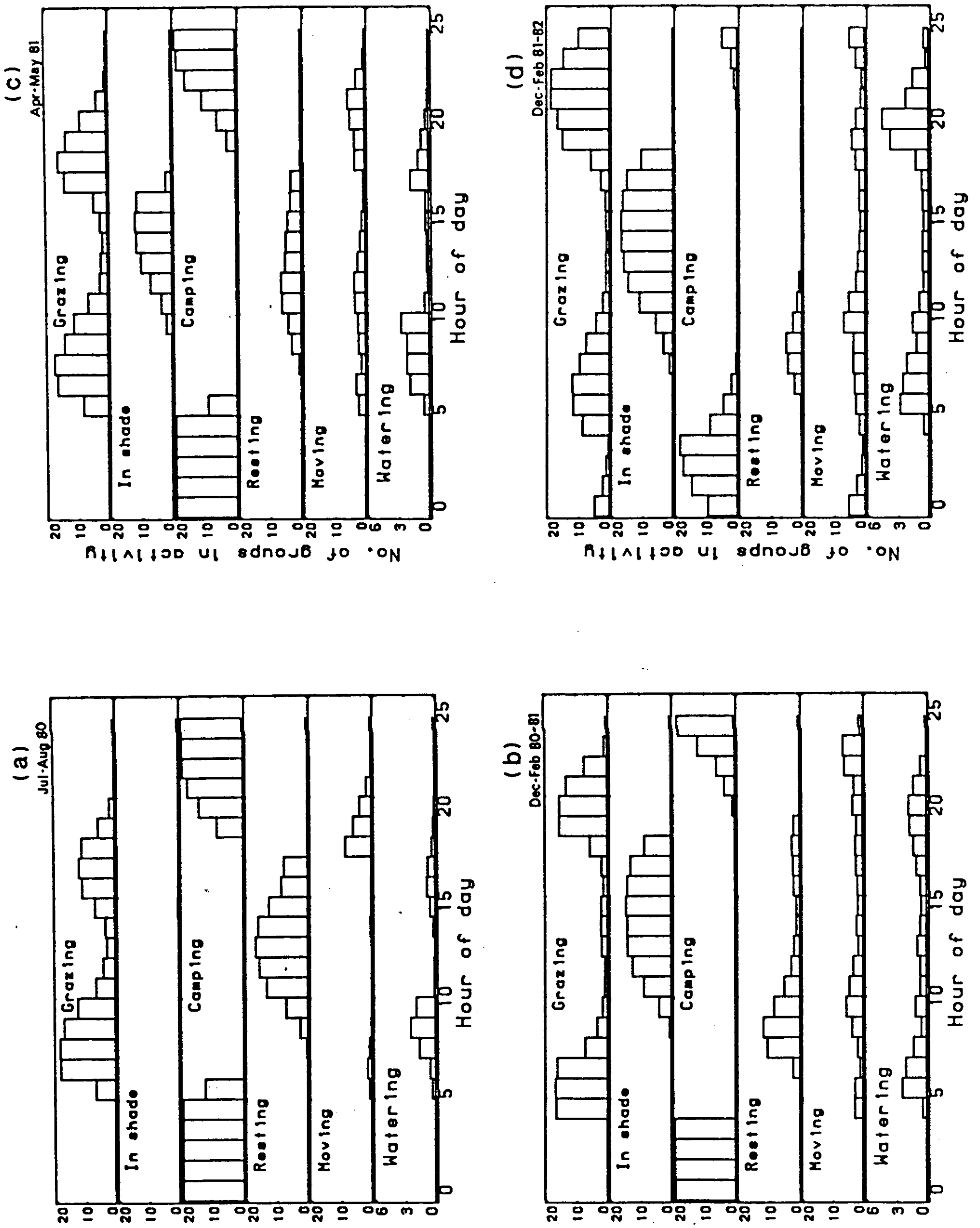


Figure X.4: Predicted hourly distributions of activities through the day for 60-day periods in (a) Jul-Aug 1980, (b) Dec-Feb 1980-81, (c) Apr-May 1981 and (d) Dec-Feb 1981-82. Ordinate is the number of the 20 modelled subflocks in the activity.

more synchronised in their behaviour patterns than are real sheep in winter. Movement in winter is primarily movement to camp in the evening, whilst in summer it is also associated with water and shade usage.

Conditions during summer 1980-81 at Middleback were not severe; the vegetation was in good condition, and a total of 94 mm of rain fell during the period represented in Figure X.4(b). By summer 1981-82, vegetation condition had declined (Table V.2), and only 2 mm of rain fell during this two month period. This change is reflected in differences between Figure X.4(b) and (d), with increased watering frequencies, greater synchrony of day-time activities, and substantially more night-grazing. These differences were all seen in the field, although the night-time activities were not well-documented.

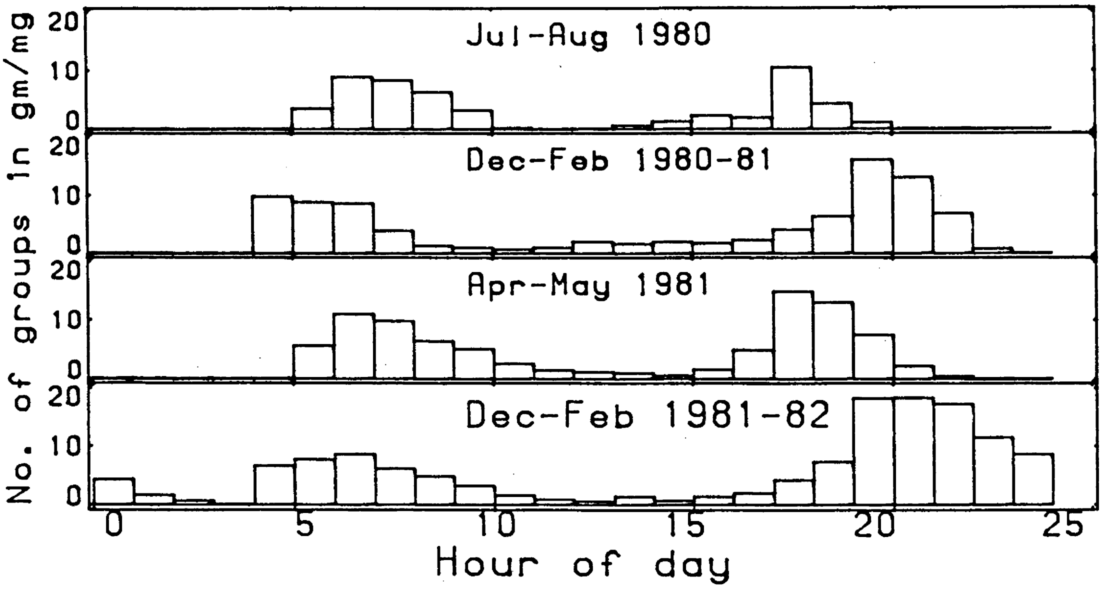


Figure X.5: Predicted numbers of subflocks in the activities 'mg' or 'gm' during the day, for 60-day periods at various times of year. Ordinate as for Figure X.4.

An important aspect of sheep behaviour which was included in this model is directed grazing. Figure X.5 shows how the numbers of groups in the activities 'gm' and 'mg' (Table IV.3) were affected by season in the model. In summers, the patterns are very similar to those shown in Figure VI.6(a), with peaks in the morning associated with movement to water and some movement to shade, and in the late afternoon again related to watering. The model also predicts directed grazing to campsites after dark, which I never had the opportunity to observe, but could sometimes infer from dusk and dawn locations of sheep in Jervoise. The model also predicts substantial directed grazing in winter; some of this is towards campsites, which may occur, but in the morning it is a response to thirst which was rarely seen in Jervoise (Figure VI.6(b)). The relationship between thirst and hunger in the model may be too sensitive to thirst.

Use of water is very important to the predictions of the model. The threshold levels for the thirst index were set on the basis of the observations in West End which were described in Chapter VI(c.i), which may have been in unusually extreme conditions. Figure X.6(a) shows the predicted daily water intakes for the modelled sheep during the same period as is illustrated in Figure VI.7; there is good agreement throughout the run, even in details such as the decline in drinking in early 1981 (as a result of rains), except that the model underpredicts the intake in the latter stages of the drought. Additionally, the model fails to show the extra increase during late winter in 1982, which, as previously noted, may be a response to lactation requirements which are not modelled here. The underprediction of water use is surprising since, as the next section will show, the model overpredicts the impact of the sheep near water in the drought conditions.

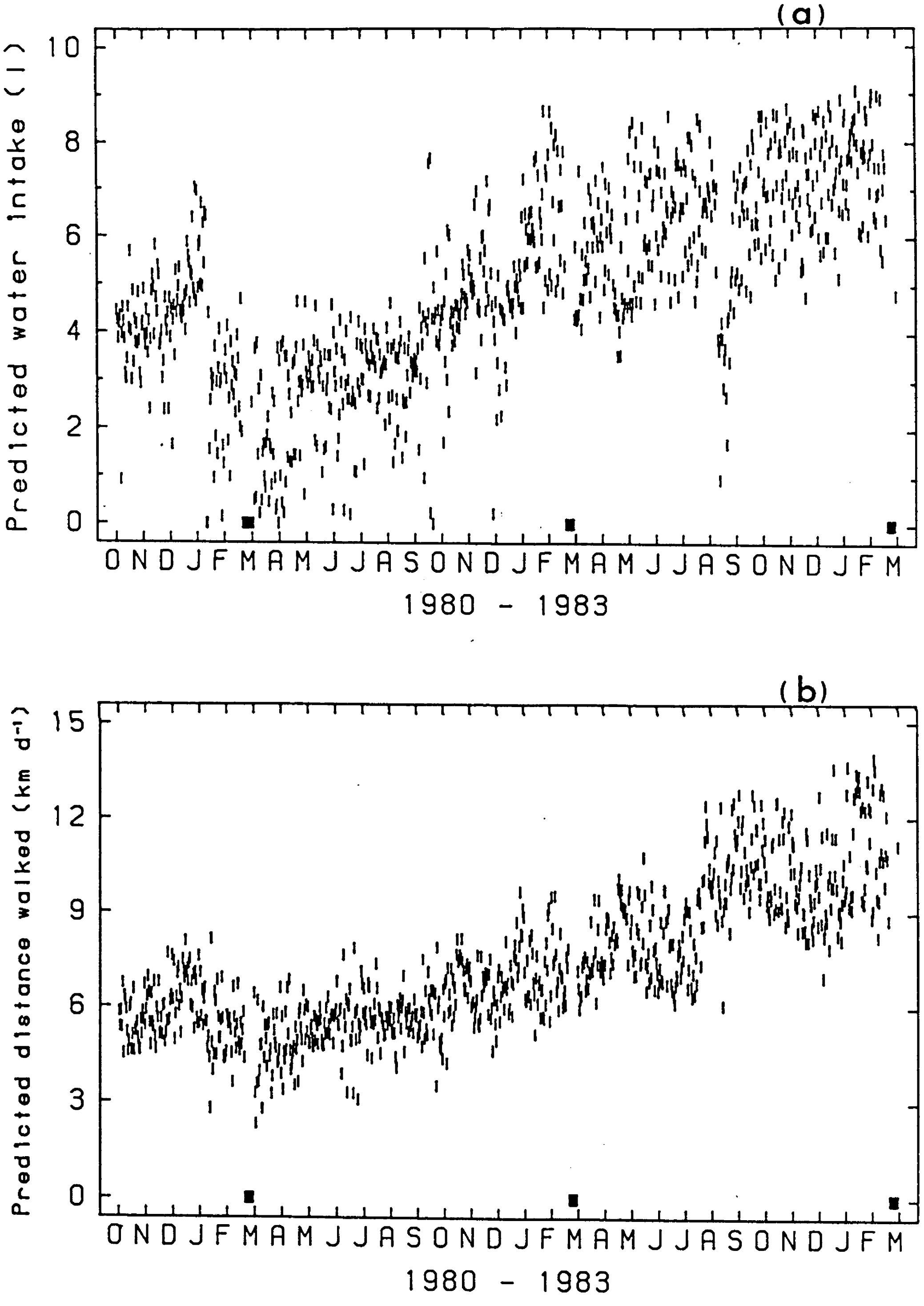
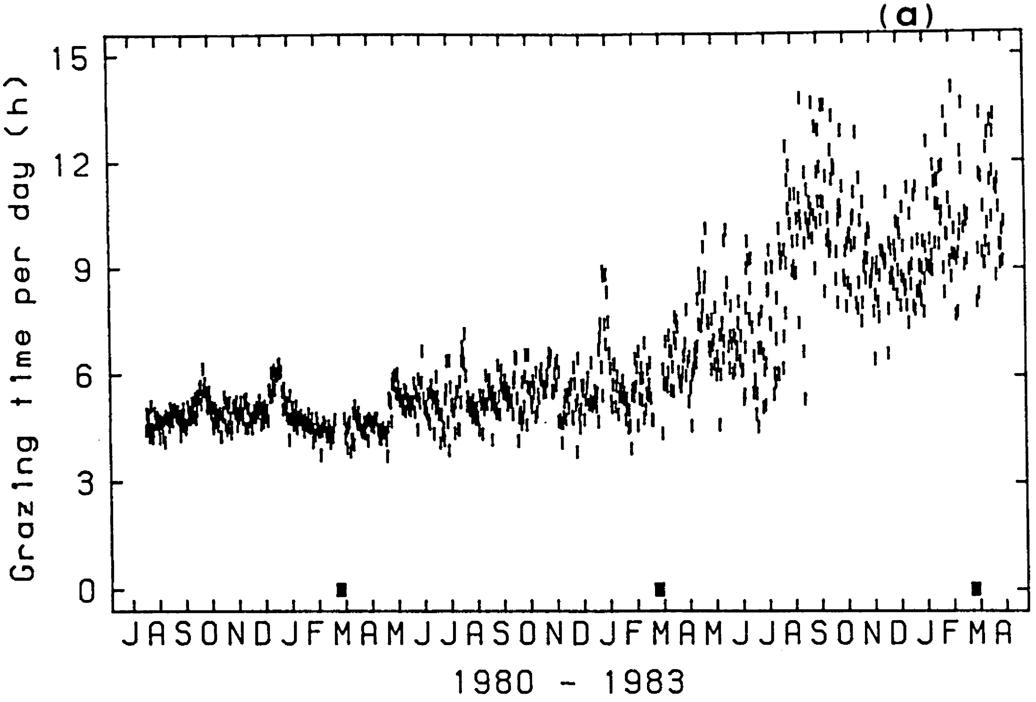


Figure X.6: Predicted daily activities in Jervoise, 1980-1983, (a) mean daily water intake per head, (b) mean distance walked daily by a subflock. Solid blocks on the x-axis indicate times of shearing.



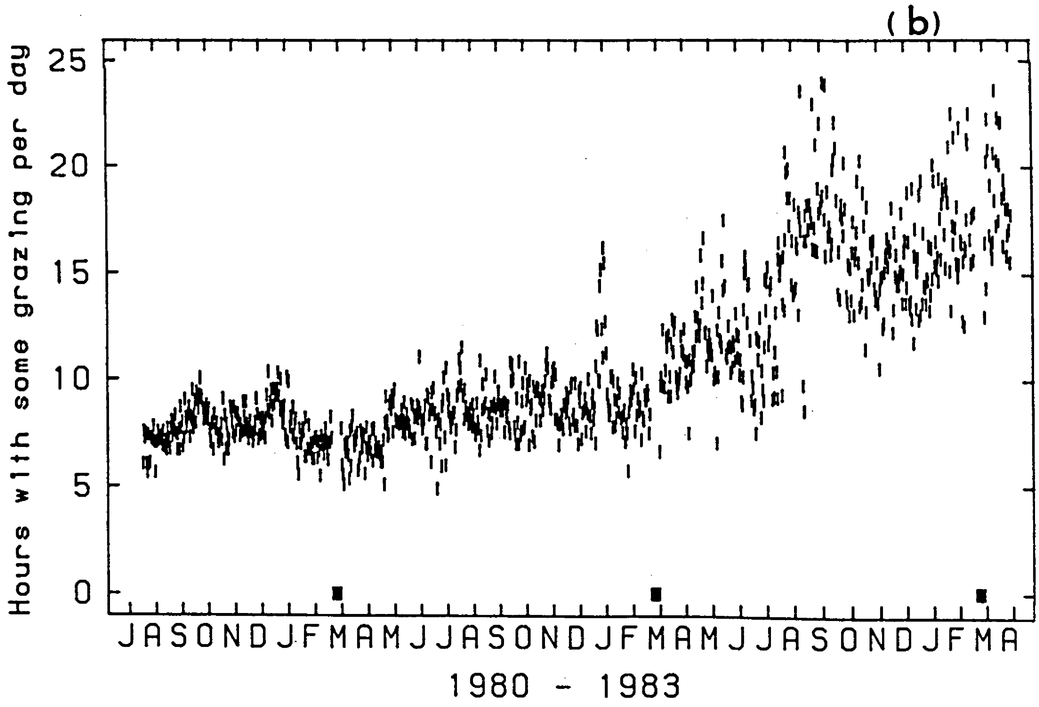


Figure X.7: Predicted mean grazing times per subflock per day in Jervoise during 1980-1983; (a) time spent actually grazing, (b) number of hours in which some grazing occurred. Solid blocks on the x-axis indicate times of shearing.

Figure X.6(b) shows the predicted variation in the mean distance walked per day by a subflock during the study period. These records are comparable to distances recorded in the literature (see Chapter II(b.ii)), with distances in the drought period reaching the maxima recorded by Squires et al. (1972). The model therefore appears to predict a sensible amount of movement on the part of the sheep; the next section examines to what extent this movement is to the correct areas of the paddock. The model predicts a much greater scattering of subflocks in winter than in summer (e.g. Figure X.15(b) in Wizzo North), and correspondingly smaller 'linked' groups. Thus it is possible to predict some seasonal reduction in group sizes simply because of less synchrony in behavioural patterns, especially in the use of waterpoints and camp sites, as was suggested in Chapter V(c).

Predicted daily intakes of the modelled sheep varied from 1.4 kg $hd^{-1}$ in 1980 down to 0.95 kg $hd^{-1}$ in late 1982. This reduction was associated with greater movement, as Figure X.6(b) shows, but was also caused by attempts to graze in cells near the waterpoint which contained little or no vegetation by the end of 1982. These daily intakes are within the range found by Noble (1975) in grazing trials at Middleback, although they do not fall as low as those that he recorded in poor vegetation. This is a result of the model being purely time-limited in attempting to maintain the intake of the sheep, whereas real sheep eventually reduce their total intake in response to very poor forage conditions.

In correspondence with the drop in predicted daily intake, there was a major rise in time spent grazing. This may be expressed either as the number of hours in which grazing occurred (including hours of 'mg' and 'gm'), or as the actual time of grazing (i.e. the time for which the grazing sub-routine is called, corrected by the reduced grazing 'intensity' of 'gm' or 'mg' (see section (a.iv)). The latter measure reflects pasture availability and net rates of intake, whilst the former increases with increasing movement. Figure X.7 shows the predicted variation in both of these parameters.

The number of hours of grazing in 1980 was low. Grazing times described in the literature would correspond best to a measure which is intermediate between the two measures that I have shown; Allden & Whittaker (1970) found that sheep would graze for 6 to 13 h per day, depending on pasture condition. In good conditions, therefore, the modelled sheep are probably obtaining their daily intake too quickly; this could result in less ranging movement in the model. In poor conditions, grazing times were much more variable and often excessive. This is due to the over-utilisation of cells with very low biomass; some extreme values of hours with some grazing (e.g. 24) towards the end of the simulation resulted from the unrealistic event of subflocks becoming 'stuck' in the eaten-out cells of the north-eastern corner - by this stage, the model predictions are breaking down in this particular paddock design, because of accumulated errors resulting from the overprediction of grazing near the waterpoint (see next section).

In summary, the activity patterns are generally predicted well, with some underprediction of watering at the height of the drought. Grazing intakes are realistic, but are obtained a little too fast in good conditions. This is probably because real sheep switch between categories of ephemeral material in the later parts of their grazing periods, in the same way as they switched from shrubs (which could be eaten quickly) to ground material (which could not) in the trials of Chapter IX(b). This switch-over can only occur between shrubs and ground material in the model, but a similar change within the latter category could result in net intake rates declining late in grazing periods, even in good pasture conditions. I had little opportunity to examine responses in good pasture conditions during this study.

### (ii) Dung surveys and vegetation quadrats.

The best validatory data that I have for runs in Jervoise paddock are the distribution patterns that were obtained from the dung surveys, described in Chapter IV(c.iv); although these reflect the mapped behaviour patterns, they have not been used in building this model. In conjunction with the dung survey data, I discuss the trends that were shown by the vegetation quadrats (Chapter IV(d.ii)); these were positioned at 125, 250, 500, 1000, 2000 and 4000 m from the waterpoint. These showed a grazing impact that was superimposed on the general decline in vegetation condition that was observed in adjoining exclosures. This impact differed in timing depending on the location of the quadrat, and these differences can be related to subtle shifts in the dung distribution patterns.

To compare the model output with the dung surveys, I made five model runs using different random number sequences, in which the total predicted extensive behaviour (i.e. including grazing, movement and resting, but excluding shade use, camping and watering) was summarised for the 30 days prior to the date of each dung survey. Cumulated over this many days, the model output from separate runs differed little from each other (in all cases, Spearman's rank correlation test comparing the predicted use of each cell gave $r>.88$, $n=53$, $p<.0001$: usually $r\approx.95$), so that I describe and illustrate only one run in each case. In statistical comparisons with the survey data, I exclude the waterpoint cell since my surveys actively avoided the area close to water, whilst the model includes resting by the waterpoint itself; the surveys underestimate the use of cell 1 in this respect throughout.

Figure X.8 shows the surveyed and predicted distributions of dung and animal activity respectively for July 1981 and February 1982; these agree reasonably (Spearmans' rank correlation excluding cell 1, r=.76, n=46, p<.001 and r=.80, n=46, p<.001 respectively; the reduced n is because some edge cells were not surveyed). In July 1981, use of cell 12 is overpredicted; together with cell 17, this constitutes the main northern campsite, and in reality the sheep use cell 17 more. For sheep arriving from the north in the model (as they often do from water), cell 12 is reached first and consequently used; this may significantly affect the predicted use of the north end of the paddock. It is very clear from the maps of February 1982 that the model greatly overpredicts the use of the east side of the paddock; south-east winds are common, but the real sheep tended to use the south-west of the paddock more during this summer. This may reflect camp-site preferences, since the observed usage of the south-east campsite (cells 36 and 40) varied substantially over the three years.

Although the model performs reasonably in both winters and summers in which conditions are not too severe, its prediction of the later dung surveys is markedly worse. Figure X.9 shows the surveys of September and December 1982, at the 'height' of the drought, for which the correlations are poor to non-existent (r=.36, n=46, p=.013 and r=.02, n=46, p>.10 respectively). In both cases the model is substantially underpredicting the use of the south of the paddock and greatly overpredicting the use of cells near the waterpoint (e.g. cell 3). This is despite the fact that the previous section showed

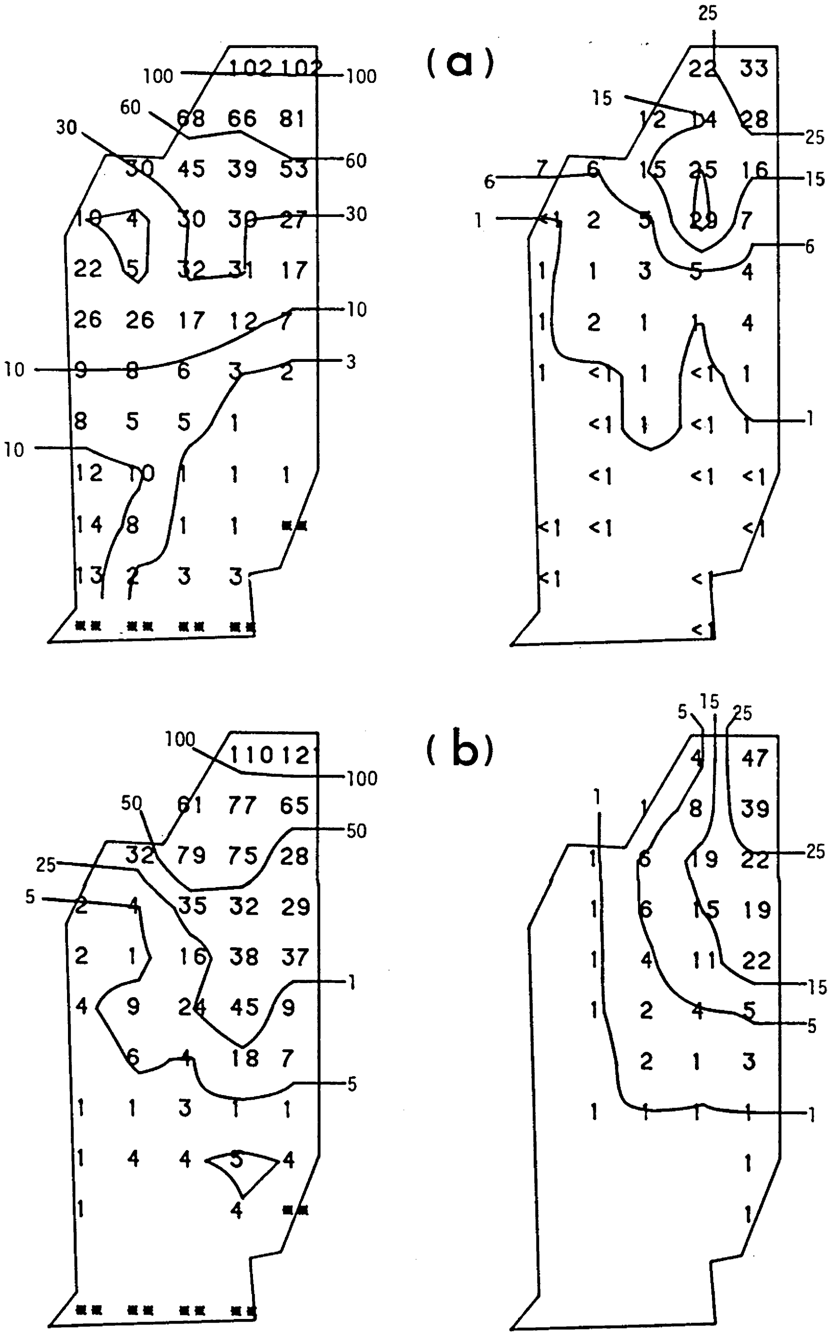


Figure X.8: Dung survey data and predicted distribution of extensive behaviour in Jervoise for (a) July 1981 and (b) February 1982. Lefthand map of each pair is dung survey (numbers are thousandths of whole paddock 'egestion event' totals), righthand map is predicted distribution of extensive behaviour for the 30 day period prior to the date of the dung survey. Contours are drawn on the data as shown; asterisks mark cells that were not surveyed.

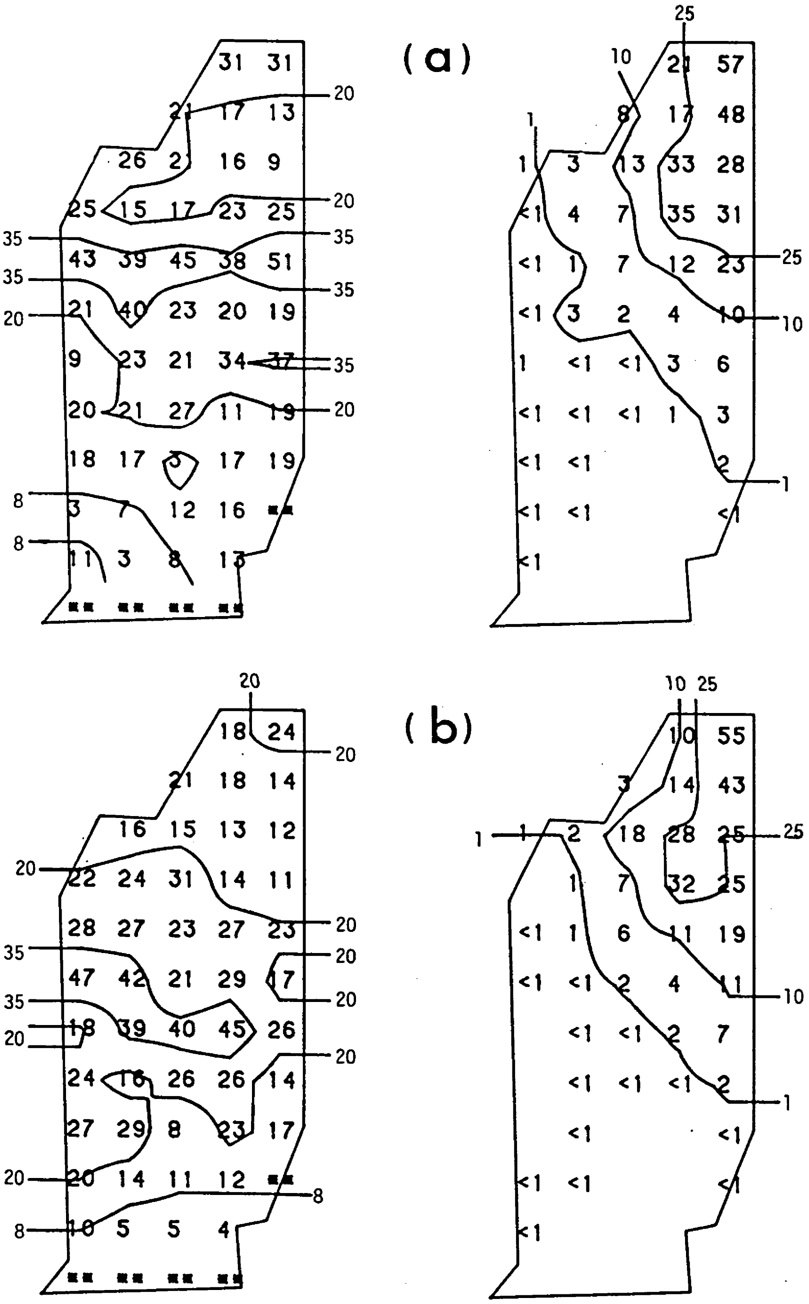


Figure X.9: Dung surveys and predicted distribution of extensive behaviour in Jervoise for (a) Sept 1982 and (b) Dec 1982. Other details as for Figure X.8.

that it is, if anything, underpredicting water intake at these times. In December, the model is still predicting similarly to the previous summer, whilst the sheep were behaving very differently.

During 1982, the condition of the vegetation in the cells near the waterpoint in Jervoise declined to a very poor state, even in comparison with the universal decline in condition during the drought. This is reflected in the differences between the dung surveys of Figure X.8 and X.9; in these, it can be seen that the area of highest usage, which is usually near the waterpoint, gradually moves south (it shows as a band between the 35 mil isopleths of dung density), as was mentioned in Chapter V(c.ii). The area immediately adjacent to the waterpoint remained greatly used as a shade or rest location, but, as mentioned, the dung survey did not include this micro-site. Since the use of water increased during this period, it is clear that this pattern was a result of the sheep moving through the zone of depleted vegetation much faster than the model predicts. Although the movement speed of the grazing sheep is increased in cells of below-average pasture condition in the model (section (a.iii)), it is apparent that the predicted distribution of grazing pressure is too localised around the waterpoint.

The result of overpredicting grazing in the area near to water is that the waterpoint and adjacent cells are invariably eaten out completely by summer 1982-83 in model runs. Figure X.10 shows the decline in vegetation index at five of the vegetation quadrat sites in Jervoise compared with the predicted decline in biomass of saltbush at these locations. There were drastic decreases at all sites except that furthest from the waterpoint, and these decreases are predicted by the model; however, whereas in reality there was still some vegetation

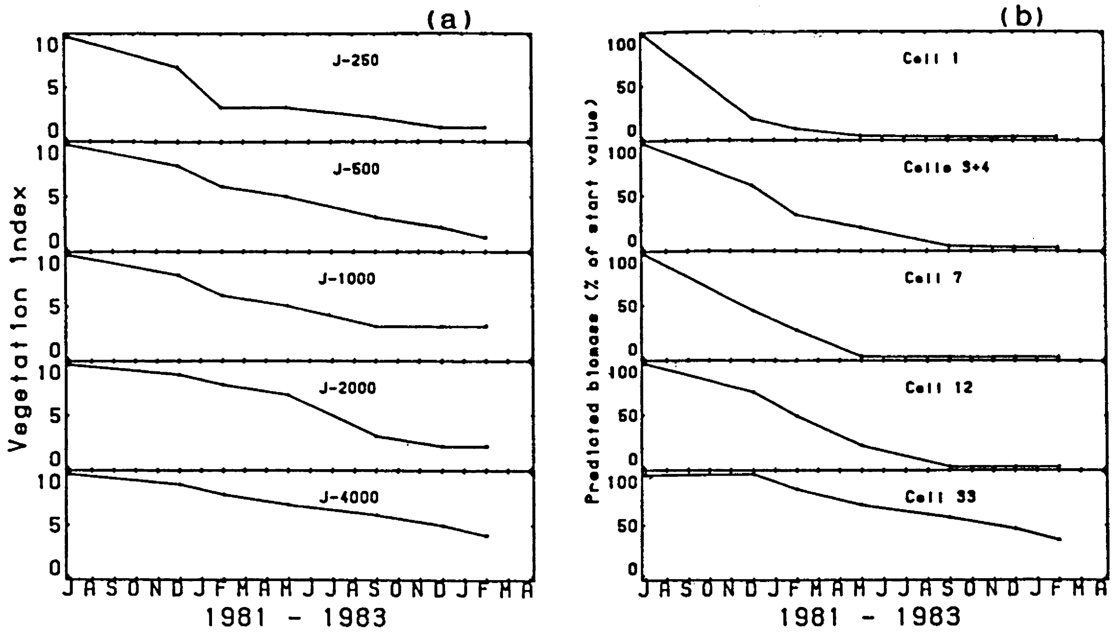


Figure X.10: Decline in vegetation at various positions out from the waterpoint during the period of the study; (a) changes in the index obtained from the Jervoise vegetation quadrats (the names, e.g. J-500, indicate distances from the waterpoint), and (b) the predicted decline in saltbush biomass in various corresponding cells ('cell 3+4' indicates the mean value in these cells, since J-500 was on their boundary).

left at all sites, the model predicts total removal at most. This is associated with the failure to predict the movement down the paddock that is shown in Figure X.9.

The explanation for the overuse of depleted cells is probably that, in the model, the preference ratings and digestibility of the feeds do not decline as their total biomass does; in reality, in an area in which the biomass is declining as a result of grazing impact, the best vegetation is likely to be consumed first, and that remaining will be both less-preferred, and composed of lower quality material. Under these circumstances in real life, sheep evidently respond by reducing their grazing in the area if there is a better alternative; in other words, the approach to increased movement speeds in poor vegetation described in section (a.iii) is insufficient, and the modelled sheep cannot adjust their diet selection within one cell by taking account of others where forage may be better. Although Chapter V showed that sheep seemed not to be responding to vegetation type in Jervoise, they must have been responding to vegetation quality. As described in Chapter VII(b.ii), I was unable to investigate this in the field, so I do not follow the point further here.

Although the model overpredicts the rate and extent of vegetation decline in the cells near the waterpoint, it does predict some aspects of the sequence correctly. Not surprisingly, the waterpoint cell is eaten out earliest in both real-life and the model, as Figure X.10 shows. However, quadrat J-2000 in real-life and cell 12 in the simulation both decline at about the same time as locations nearer the waterpoint. This was a consequence of the proximity of the northern campsite and illustrates the importance of campsites as foci of grazing impact other than the waterpoint.

To recapitulate, Noble (1975) found that his model tended to predict too much piosphere development in Wertigo; the same model run on Jervoise, which evidently has a more critical paddock layout in terms of testing the adequacy of a model, predicts the destruction of the vegetation around the waterpoint in about six months, and very rarely predicts any use of the south end of the paddock. The new model is a considerable improvement; evidently it still overpredicts grazing near a waterpoint in drought conditions, but it is much better at predicting the spatial use of a narrow paddock such as Jervoise in good years. The next section will show that the new model also produces reasonable predictions in the very different paddock design of Wizzo North.

### (iii) Map patterns in Jervoise.

To close this section on tests in Jervoise, I briefly compare some modelled sheep distributions with 'real life' at a particular time. During verification of the model, I followed many modelled days in detail to ensure that the programs were running as intended; I do not describe this process here. However, I present a few separate observation maps of sheep in Jervoise to compare with the predictions for the same day and hour by the model, in order to elucidate the limitations of the model that were described in the previous section.

Figure X.11 shows the actual distribution of sheep in Jervoise as mapped around dawn on 7th December 1980, and five alternate predicted distributions for the same time (all runs commenced in May 1980). Needless to say, there is no reason why any particular randomly-generated run should exactly agree with reality, and there is indeed a considerable variability between predictions, depending on previous patterns of grazing and watering. However, the dominant use of the northern campsite is correctly predicted by all runs; the secondary use of the south-west site is only shown in one run and there is a tendency to predict some use of the south-east campsite which did not occur. The winds on the previous day were southerly, and this frequently causes the modelled sheep to occupy the closer south-east campsite in preference to that of the south-west. In reality, sheep did not frequently use the south-east campsite, and it is apparent that the use of campsites may be more affected by learned preferences or quality differences between campsites than is permitted in the model.

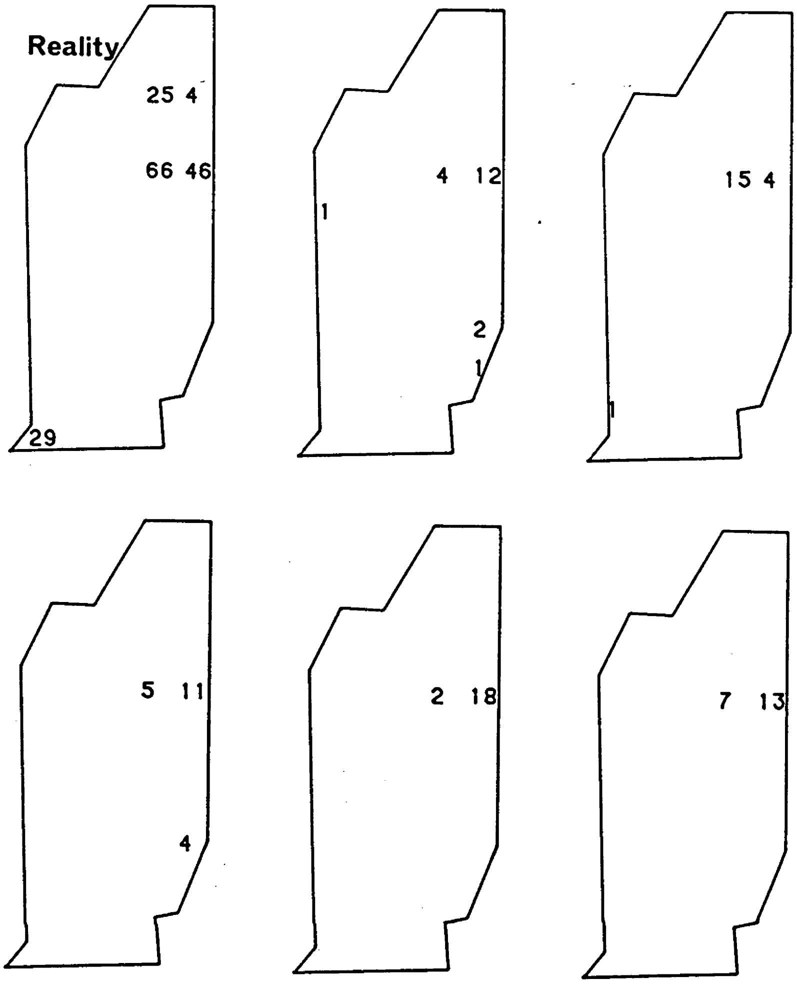


Figure X.11: Observed and predicted distributions of sheep in Jervoise at 0600 h on 7th Dec 1980: top left land map is observed distributions of sheep (numbers are sheep), all others are the predicted distributions (numbers are subflocks) from each of the 5 independent simulations.

This over-use of the south-east campsite in comparison to that in the south-west is the main factor responsible for the general overprediction of use of the eastern side of the paddock, as shown in Figure X.8.

Three further illustrative days are shown in Figure X.12, in which I include only two predictions - one which best matches reality and one that least does so. The first set, from the morning of 29th August 1980 in conditions of north-west winds, shows how the model predicts

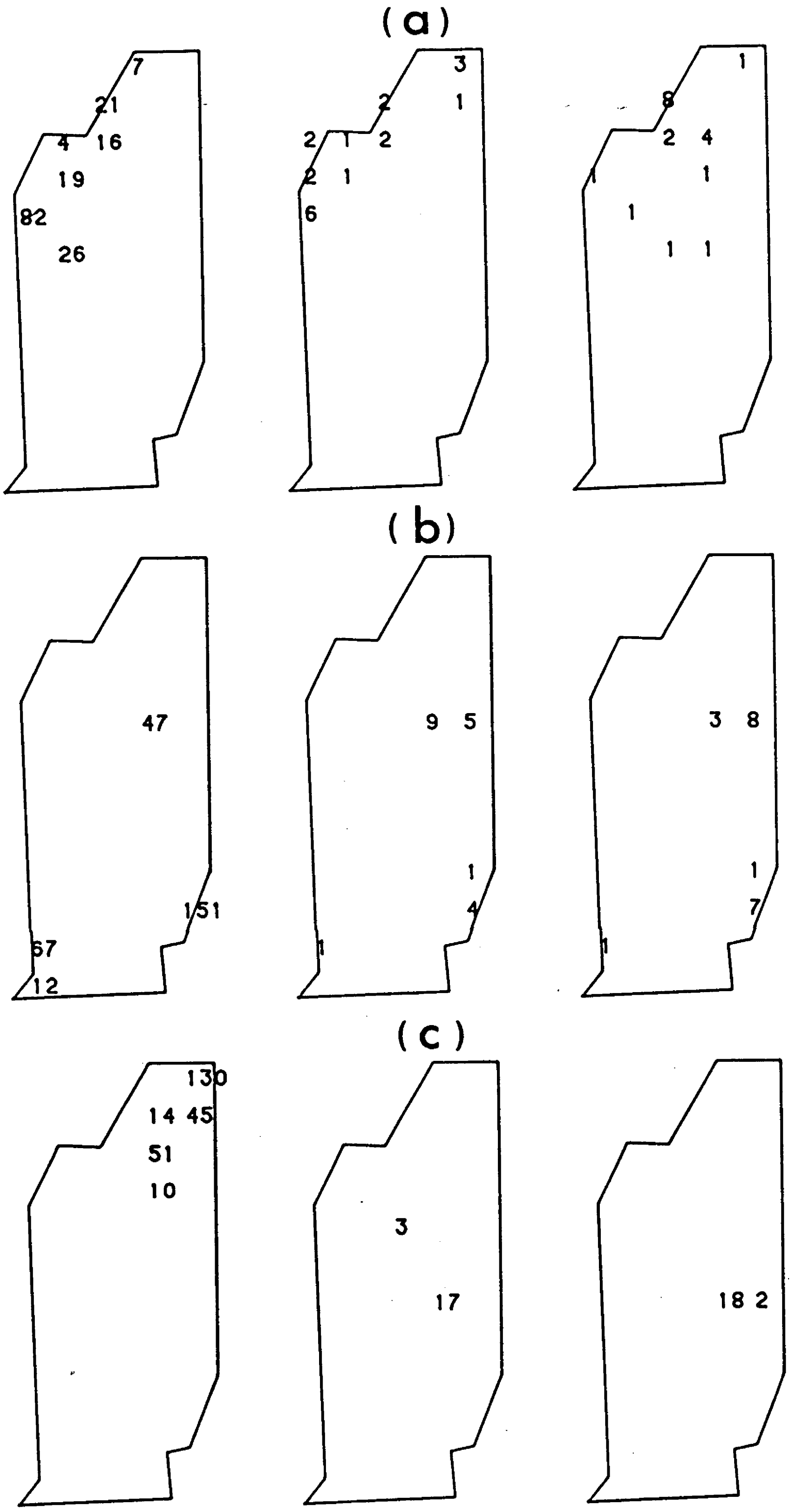


Figure X.12: Observed and predicted distributions of sheep in Jervoise, (a) 0900 h on 29th Aug 1980, (b) 0600 h on 30th Jan 1981 and (c) 1200 h on 28th November 1981. Left hand map shows the actual distribution (numbers of sheep), right hand maps show predicted distributions (number of subflocks) in two alternate simulations.

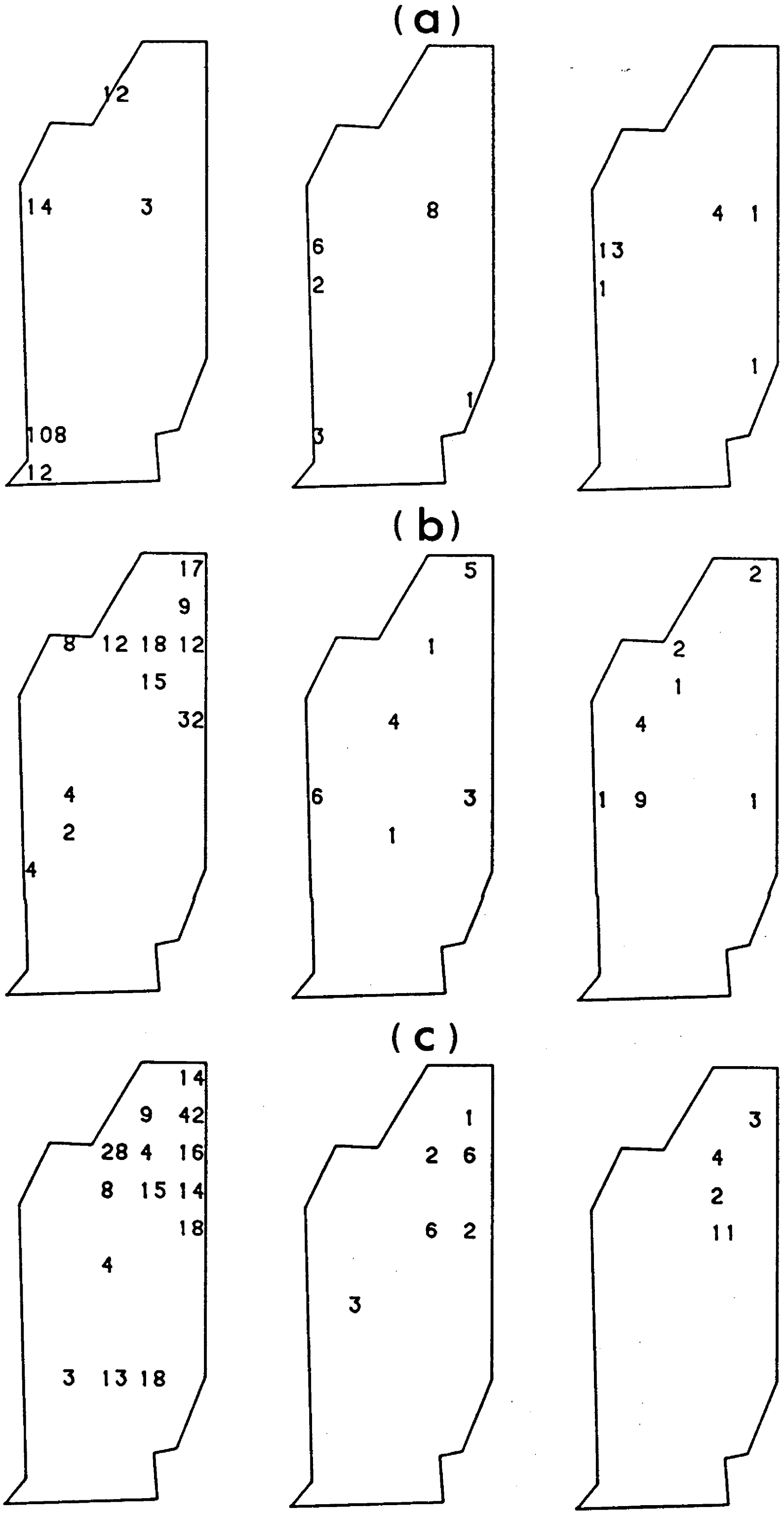


Figure X.13: Observed and predicted distributions of sheep in Jervoise, 17th April 1981, (a) 0600 h, (b) 1200 h, and (c) 1800 h. Left hand map shows the actual distribution (numbers of sheep), right hand maps show predicted distributions (number of subflocks) in the same pair of simulations through the day.

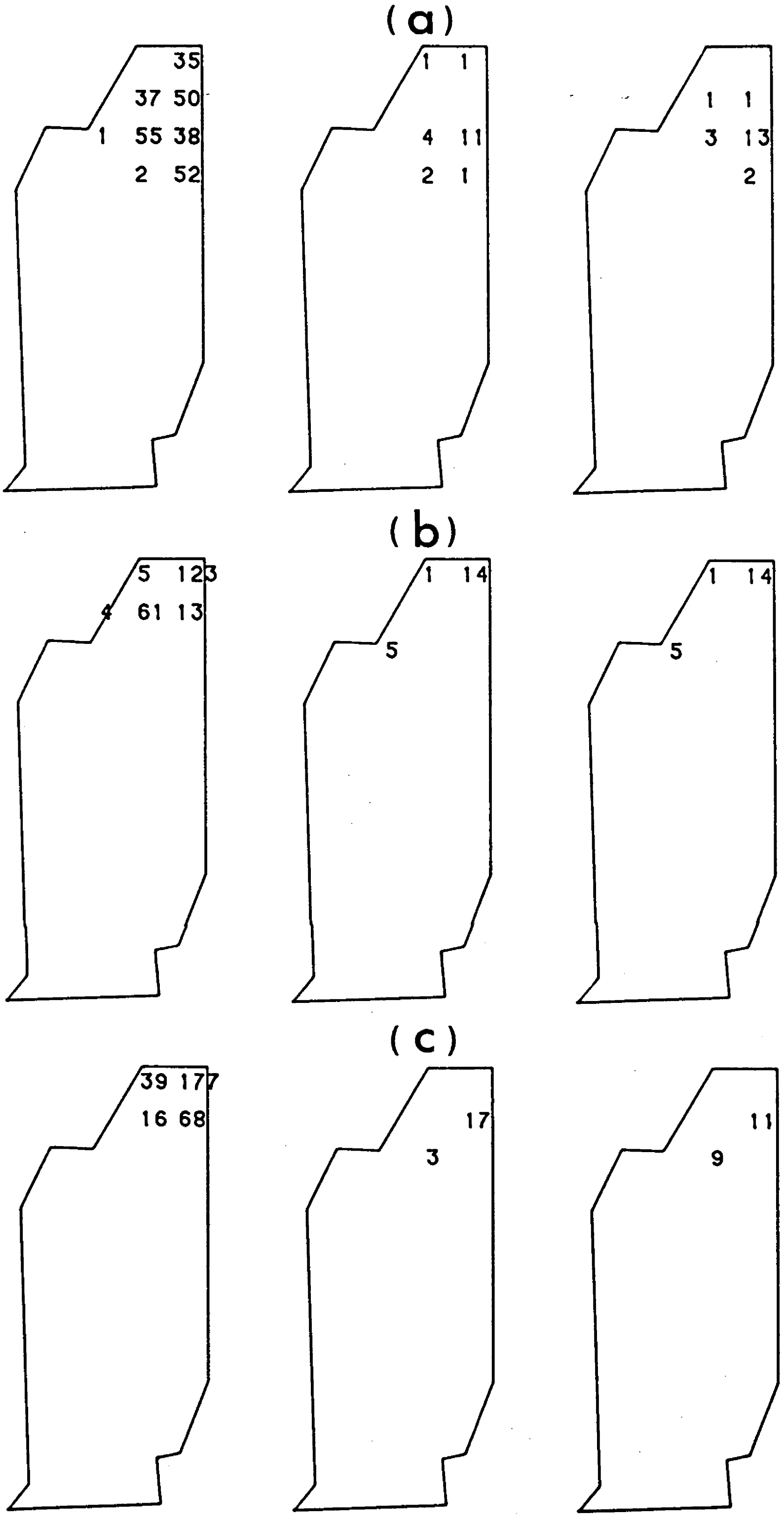


Figure X.14: Observed and predicted distributions of sheep in Jervoise, 26th November 1981, (a) 0600 h, (b) 1200 h, and (c) 2000 h. Left hand map shows the actual distribution (numbers of sheep), right hand maps show predicted distributions (number of subflocks) in the same pair of simulations through the day.

well in circumstances where the movement model is less critical. The second shows camping behaviour on 30th January 1981, which was one of the few fieldtrips during which the south-eastern campsite was used regularly. The model again predicts this usage, but most of the modelled subflocks do not come south of the northern campsite despite the south winds. On this particular occasion, the route of the sheep that camped in the south-east was still visible in the morning, since they had walked down the eastern paddock track after dark; they had apparently walked past the northern campsite, so that the factors that draw sheep to a campsite in a particular direction, or part of a paddock, may be stronger than assumed in the model. The third set of maps is from midday on 28th November 1981, and the model is consistently predicting positions too far south on this day of south winds. This illustrates the fact that the model's failings during this summer and later into the drought are not in overpredicting the use of the waterpoint, but in underpredicting the rate and distances of longer movements out from the waterpoint by sheep during poor conditions, especially to the southern campsites.

Finally, Figures X.13 and X.14 show the time-courses of two days, to illustrate the dynamic nature of the model. Figure X.13 shows records from an autumn day in south-east winds, and Figure X.14 shows an early summer day in north winds; the model predictions are from runs with the same pair of random number sequences throughout, and are, apart from reservations as expressed above, in remarkably good agreement with reality.

### (iv) Summary: Jervoise.

This section has shown that the model predicts sheep activity and watering patterns well. It may over-estimate net rates of intake in good conditions; this could result in there being fewer grazing hours available for movement. Decreases in daily intake during the declining vegetation conditions of the drought are realistic, although increases in total grazing time are excessive. Spatial use of the paddock is predicted well in moderate conditions of climate and fodder availability. In cells of poor vegetation condition, however, the model overpredicts the grazing effort by the sheep; this is probably due to the inflexible preference ratings in the model which fail to take account of the removal of preferred fodder first by the sheep, and to the assumption that sheep learn very little about the vegetation condition available elsewhere in the paddock. Invocation of learning seems to be necessary only in poor conditions. The predicted decline in vegetation state at the location of vegetation quadrats in the real paddock generally matches measured declines, although the extent of the decline is exaggerated. In particular, an area near the northern campsite is correctly predicted to be eaten out earlier than would be expected on the basis of distance from water alone. This illustrates the importance of campsites as foci of impact. Finally, predicted distributions of subflocks on particular days show considerable (realistic) variation between model runs, but often match observed distributions reasonably. They also show that incorrect, and insufficiently frequent, choice of southern campsites is the main proximate cause of the model's underprediction of the use of the extremities of the paddock, and overprediction of use of the eastern side.

## (c) Model runs in Wizzo North.

Wizzo North is a paddock of twice the size of Jervoise, with a centrally-located dam, and two permanent waters. In general, its paddock geometry is far less constricted than that of Jervoise. In this section, I describe the extra features needed in the model for it to run on Wizzo North, and I compare the output with some mapped observations.

### (i) The Wizzo model.

The main additional feature that is needed to model Wizzo North is some criterion for selecting between waterpoints. As Chapter VI(c.ii) mentioned, choice of the nearest waterpoint did not explain water use in Wizzo North; I have no detailed data on this matter, so I use a simple 'memory' model, as was suggested necessary by Chapter VI(c.ii). In this, if a sheep waters at a given waterpoint, its 'memory' of that location is set to 1.0. On each subsequent day, if not reinforced, this 'memory' declines by a factor of 0.95. When the sheep needs to go to water, the following decisions are made: firstly, if any water is in the current or adjacent cell, this waterpoint will be chosen. Otherwise, the waterpoint with the highest 'memory' value will be chosen, except that, if more than one 'memory' exceeds 0.5, then the nearest of these will be chosen. At the given rate of forgetfulness, the value of 0.5 is reached in two weeks; thus, providing a water is visited at least fortnightly, it will remain available to the sheep regardless of the animal's location. Beyond this, it will only be used if the subflock passes nearby.

This simple model predicts the qualitative behaviour seen in Wizzo reasonably. When the central dam and the eastern (McGouish's) trough are in use, both tend to be used with a preference for the dam; if sheep are 'released' in equal numbers at both in the model, it predicts visits to both, but with a tendency to drift to the central dam. Under these conditions, the voluntary use of the south-western trough is very minor. If only the south-west and eastern troughs are available to the sheep, the modelled division of visits is strongly dependent on which water is first visited after the sheep were released in the paddock, and negligible transfer occurs between the two; if all the sheep are introduced on the south-western trough in early summer, the predicted ratio of visits over the following two months is 67:1 in favour of the trough they first used. This parallels the observed behaviour in early 1982 well, when separate 'home ranges' were effectively maintained in the eastern and western sections of the paddock.

Thus the simple memory model is adequate. Other adjustments to the model for Wizzo concerned baseline vegetation distributions, run-off patterns, paddock layout and cell sizes. The grid used in Wizzo North is much coarser than that in Jervoise, with cells of 1x1 $km^2$ (see Figure IV.9(b)); the coding of the program automatically accounts for different cell sizes, however. No changes were made in any other behavioural aspects.

### (ii) Mapped patterns in Wizzo.

Predicted daily activity patterns in Wizzo were similar to those in Jervoise (section (b.i)) and I do not repeat then. Unfortuately, no dung survey comparable to those of Jervoise is available for Wizzo, so in this section I present comparisons of data from coarse mapping sequences (Chapter IV(c)) with model output. In order to smooth chance variability, I have cumulated the total observations for several days of a fieldtrip, and compared these with the day-time activity distributions predicted by the model (i.e. extensive behaviour and shade use, including grazing to and from campsites, but excluding camping itself). In general, these predict reality better than in Jervoise, even into the drought, partly reflecting the more critical paddock layout of Jervoise, and also because less detail is available on the coarser grid.

Figure X.15 shows the results of the predictions in Wizzo North. Variation between individual model runs was again considerable (cf. Figure X.11 in Jervoise), and I only illustrate one of the better predictions for each. For the period illustrated in Figure X.15(a), both the eastern trough and central dam were in use and the modelled sheep were 'released' at the E trough: the model overpredicts watering at the dam for this period, and consequently underpredicts the use of the south-east campsite area, but otherwise the pattern and dispersion is very similar (range of Spearman's correlation coefficients between the observed and five modelled patterns: r=.36 to .54, n=32, p=.04 to .002). The waterpoint model does not include any allowance for differences in water quality, and, where two waters remain within the sheep's memory, this might affect their choice between them. The observed records were obtained from 'coarse' mapping runs (Chapter IV(c.i)) so that sightings of small numbers of sheep were not reliably made. The prediction of outlying subflocks is not necessarily incorrect, but their grazing impact is minor.

Figure X.15(b) shows the situation in winter, with the dam and eastern trough available. The model predicts the increased dispersion

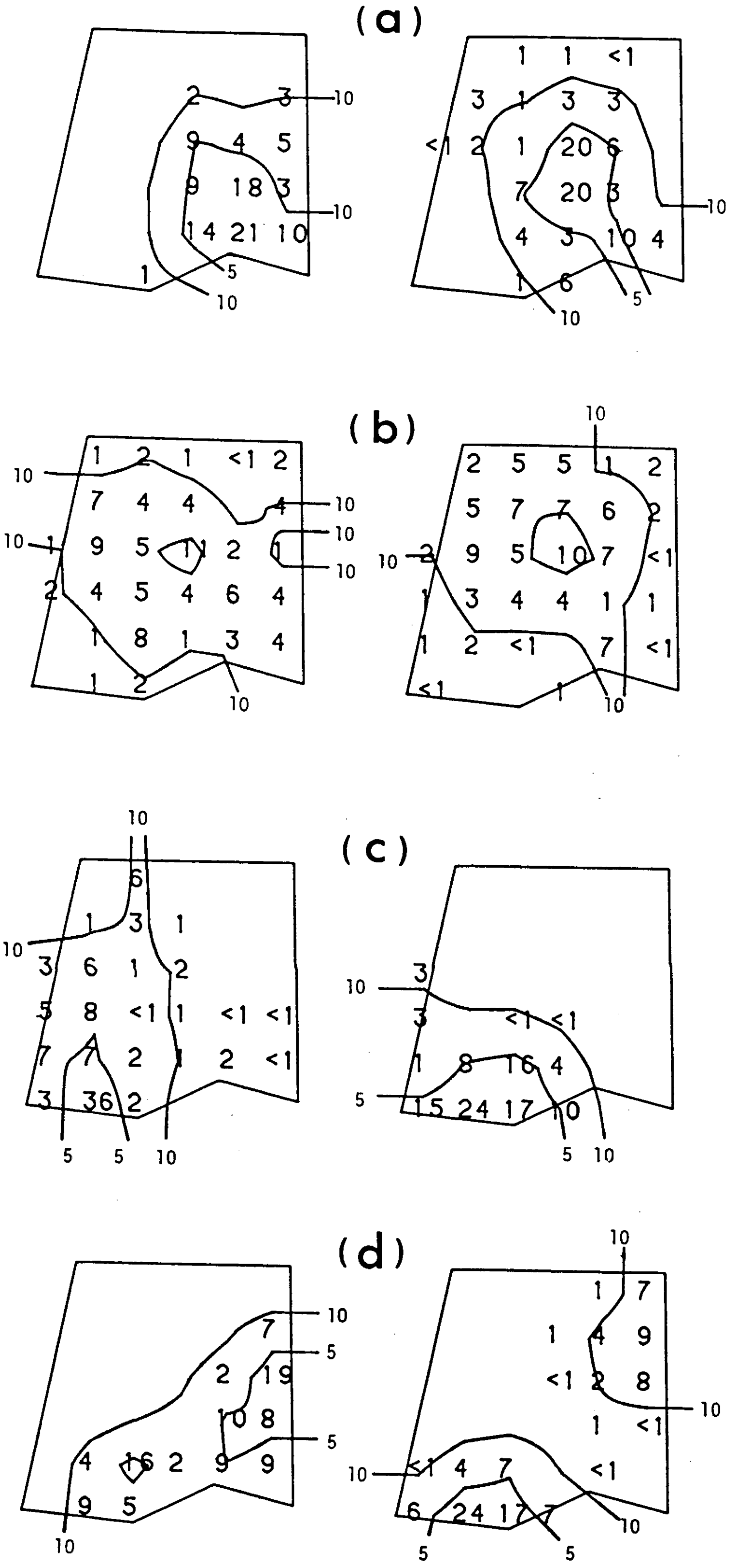


Figure X.15: Observed and predicted distributions of sheep in Wizzo North, (a) 23-25 Jan 1981, dam and E trough, (b) 11-13 Jul 1981, dam and E trough, (c) 14-16 Feb 1982, SW trough, and (d) 7-9 Apr 1982, SW and E troughs. Left hand map shows the actual distribution, right hand map shows predicted distribution in one simulation. Numbers are % animals or subflocks seen or predicted in each cell respectively; contours are isopleths of harmonic mean moments.

over the paddock in these conditions very well (range as above, r=.38 to .52, n=32, p=.03 to .002). A summer period when only the south-west trough was available is illustrated in Figure X.15(c), however, for which the sheep were 'released' in the south-west three months previously; this sequence includes north winds, and the model does not predict sufficient northwards movement over the 6 km length of the paddock (range as above, r=.01 to .53, n=32, p=n.s. to .002). This failure is comparable to the failure to predict sufficient use of the south of Jervoise, and is again related to campsite selection. Finally, Figure X.15(d) shows the predictions for autumn 1982, when both south-west and eastern troughs were available, and half the sheep had been 'released' at each after shearing in February (range as above, r=.26 to .52, n=32, p=n.s. to .002). The divided 'home-ranges', centred on each water, are shown very clearly (see Chapter VI(c.ii)), exaggerated in the model again because of underprediction of use of the south-eastern campsite area.

Figure X.15 (c) and (d) relate to 1982, towards the time when predictions became poor in Jervoise during the drought (cf.Figure X.9). The predictive capacity of the model seems to be better in Wizzo North than in the more-constrictive design of Jervoise. However, the model is deficient in both paddocks in its selection of campsites; these are evidently almost as important as the waterpoint in determining which area of the paddock is in use.

### (iii) Summary: the model in Wizzo North.

In Wizzo North, an additional model of selection between waterpoints is included. This is based on a simple 'memory', and works reasonably, although it does not allow for different water qualities. The behavioural model predicts the spatial usage of the paddock well in terms of dispersion; some failings with regard to location can be related to the same problems as discussed for Jervoise, and are primarily due to the imperfect choice of campsites.

## (d) Predictive runs.

Ultimately, the true test of any theory or model lies in the prediction of events which have not yet occurred. Furthermore, this model is intended to be a significant step in the process of producing modelling tools for management, even if, as is clear from previous sections, it is not yet perfect. In this section therefore I briefly describe two predictive sets of model runs that relate to management options currently under consideration at Middleback. The first relates to the location of a new waterpoint in Jervoise, away from the bottleneck in the north of the paddock, and the other concerns waterpoint management following the division of Wizzo North into two paddocks in the pursuance of the policy of subdivision that was described in Chapter IV(a.i).

### (i) A new waterpoint in Jervoise.

The model overpredicts offtake in the northern cells of Jervoise with the present waterpoint arrangement. However, it is clear from the vegetation quadrats that this area was damaged by grazing during the drought; with the present paddock layout, and with no relief from the pressures on the waterpoint area in good or bad times, the model is only exaggerating the inevitable results of a poor year. In consequence, the owners intend to put another waterpoint into the paddock; this will probably be fed from a bore in Adam's West paddock, about 500 m from the south-western corner of Jervoise paddock.

In this section I therefore test the effect of three alternative waterpoint locations on the development of vegetation pattern in Jervoise. Because of the local wind patterns, the paradigmatic waterpoint position at Middleback is usually considered to be about one third of the length of the paddock down from the north fence, and central on the east-west axis. I first test a location in cell 13, therefore, although this is a long way from the bore in economic terms. An alternative extreme position is in cell 45, which is close to the bore and financially attractive, but is further south in the paddock than the owners would normally choose. Thirdly, I test a location in cell 28 as a economic compromise between the first two.

Table X.4

Rainfall, vegetation and general characterisations of baseline runs used to predict the effect of different waterpoint positions in Jervoise. The initial mean shrub biomass in Jervoise was 603 kg $ha^{-1}$. The mean rainfall at Roopena is ca. 200 mm $yr^{-1}$.

| Run | Mean rainfall (mm $yr^{-1}$) years 1-5 | years 6-10 | Mean shrub biomass (Dec, kg $ha^{-1}$) year 5 | year 10 |
|---|---|---|---|---|
| 1 | 205 | 225 | 688 | 730 |
| 2 | 179 | 215 | 154 | 602 |
| 3 | 244 | 248 | 879 | 899 |
| 4 | 183 | 198 | 198 | 113 |

General description:

| | |
|---|---|
| Run 1: | 'normal' throughout. |
| Run 2: | drought years 2-5, 'normal' thereafter. |
| Run 3: | wet throughout. |
| Run 4: | mild drought throughout. |

For these predictions, I ran the model from the vegetation condition in May 1980 (i.e. from before the drought, since the vegetation model does not adequately describe re-generation of shrubs) and with no sheep for six 10-year periods with different weather sequences (simulated with the weather sub-routines of Noble 1975). From these I selected the sequences described in Table X.4, and re-ran the model for the same weather sequences with 260 sheep in 10 subflocks in the paddock. The results of the 'baseline' runs are summarised in Table

X.4, after 5 and 10 years of run. For the runs with sheep, the model is still overpredicting the use of the area near water when the vegetation condition there falls to a low state, but in Table X.5 I quote some very general statistics of the predicted effects of the sheep after 5 years in comparison to the baseline runs; the results after 10 years parallel those shown.

Table X.5

Grazing impact and sheep condition after 5 years predicted by model runs in four weather sequences for different waterpoint positions in Jervoise paddock. Vegetation parameters are: numbers of cells predicted to have less than 10 or 50% of the saltbush biomass predicted in a baseline run with no sheep, and the mean shrub biomass in the whole paddock as % of baseline run values (see Table X.4). The mean sheep body weight is given as % of the mean value from all runs.

| | No. cells with Sb biomass as % of baseline runs | | Mean shrub biomass (% baseline) | Mean body weight (% overall) |
|---|---|---|---|---|
| | <10% | <50% | | |
| Water at cell 13 | | | | |
| Run 1 | 3 | 7 | 86 | 107 |
| 2 | 6 | 20 | 69 | 87 |
| 3 | 3 | 8 | 88 | 120 |
| 4 | 2 | 9 | 83 | 88 |
| Water at cell 28 | | | | |
| Run 1 | 2 | 12 | 87 | 109 |
| 2 | 3 | 23 | 67 | 88 |
| 3 | 2 | 7 | 89 | 120 |
| 4 | 1 | 5 | 83 | 90 |
| Water at cell 45 | | | | |
| Run 1 | 3 | 10 | 86 | 105 |
| 2 | 7 | 21 | 69 | 87 |
| 3 | 3 | 6 | 89 | 120 |
| 4 | 3 | 8 | 83 | 89 |

In general the predictions show that fewer cells will be severely damaged with the waterpoint at the compromise position (cell 28); this is usually associated with a wider spread of milder grazing impact. Figure X.16 shows the typical general paddock usage for one instance in run 1 with each waterpoint, and it can be seen that the central waterpoint permits the most even usage of the paddock. Cell 13 is positioned close to both the main northern campsite and a major area of shade, and this results in the development of a large impact zone around the new waterpoint. Considering that there are only a small number of campsites in Jervoise, but that they are spread as widely as is possible (Figure VI.9), it seems unlikely that any significant changes in campsite locations would occur. Thus the position that would normally be preferred in paddocks at Middleback is not suitable in Jervoise because of its particular spatial layout.

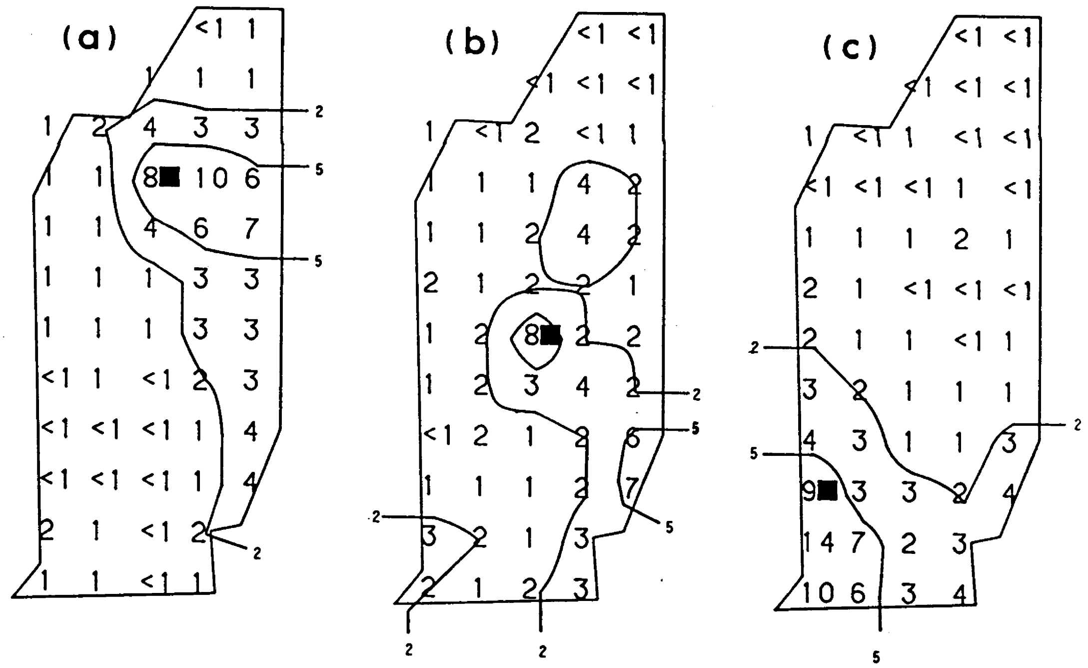


Figure X.16: Predicted mean distribution patterns of subflocks in extensive activities (g, m, r) during years 1-4 of the weather sequence of Run 1 for Jervoise paddock with a new waterpoint (■)located at (a) cell 13, (b) cell 28, and (c) cell 45. Numbers are mean subflocks hours per day spent in each cell; contours are drawn on these values.

Not surprisingly, the predictions for a waterpoint in cell 45 are also dismal as far as the south-western vegetation is concerned. The impact zone is predicted to be smaller but more intense than for cell 13, and the closeness of the south-west campsite is an important factor in this. The third choice, in cell 28, is much more satisfactory; the model is undoubtedly overpredicting the impact around the proposed waterpoint, but there is much more even use of the paddock.

In all trials there is a considerable net reduction in mean shrub biomass in comparison to the baseline run, but there is little difference between waterpoint positions in this respect. Similarly, sheep condition, as measured by body weight, is far more dependent on season than on management policy, although it is consistently slightly higher for the central waterpoint position; over many years, this might be significant to wool cuts and lambing successes. I have not discussed the possibility of continuing to use the present waterpoint intermittently, but the low use of the north-eastern corner with either new southerly position would enhance the usefulness of the old waterpoint.

One interesting, counter-intuitive result of these runs is that the grazing impact is least concentrated in the run with mild, but continuous, drought; in this run there was a regular yearly supply of ephemeral material, but the rainfall pattern resulted in a steady decline in the vegetation throughout the paddock. This highlights the influence of detailed pattern in affecting productivity, and emphasises how un-informative mean climatic data can be.

This section makes two important points. Although it is perhaps not surprising that cell 13 would not be a good location for a waterpoint given the proximity of shade and campsites, the consideration of these factors would often not occur without the analysis needed for the model. Effects such as these are usually easily explained in retrospect, and a model offers the possibility of 'pre-emptive hind-sight', even when its predictions are not quantitatively perfect. Secondly, ideal paddock layout is not simply a function of locally prevailing winds, but also of how the sheep use the landscape; if there were no hill and no campsites in cells 12 and 17 of Jervoise, patterns of use would be dramatically altered, yet the outline of the paddock on the property map would be unchanged.

### (ii) Management in 'Wizzo West' paddock.

As part of the continuing policy of subdivision, the owners of Middleback will eventually divide Wizzo North paddock down the centre. There is little choice as to where this fenceline will run, so I do not pursue this issue. As a result of the sub-division, however, the western portion of the paddock (which I have taken the presumptious step of naming Wizzo West) will contain two main waterpoints; these are the dam, halfway up its eastern fence, and the south-west trough, on the southern fence. I therefore test between two alternate management procedures with respect to these waterpoints. The first is to permit watering at either water, and the second is to permit watering at the trough only when the dam is dry. The dam is assumed to dry up if a continuous period of 6 months passes with no rainfall of greater than 20 mm in one day. I have used the same weather sequences as in the previous section, described in Table X.4.

Table X.6 presents some simplified results from this analysis. In long-term runs in Wizzo, as in Jervoise, the model overpredicts the use by sheep of cells with depleted vegetation. However, it is again possible to compare qualitatively, rather than rely on quantative values. In the different weather sequences, the dam contained water for different periods, which are shown in Table X.6.

Table X.6

Predicted impact over 10 years of two management policies with respect to waterpoint availability in the new 'Wizzo West'; analysis shows numbers of cells anywhere in the paddock in which saltbush biomass has declined to <50% of the baseline run values, and numbers of cells in the immediate vicinity of each waterpoint in which saltbush biomass has declined to <10% of the baseline values; management options considered are: only one water ever available ('managed'), or watering not controlled ('unmanaged'). The proportion of days that the dam was full in each run is also shown (for run descriptions, see Table X.4).

| | % time dam available | cells with <10% baseline Sb | | cells <50% (all paddock) |
|---|---|---|---|---|
| | | near dam | in S.W. | |
| 'Managed' | | | | |
| Run 1 | 91 | 1 | 0 | 5 |
| 2 | 77 | 1 | 0 | 5 |
| 3 | 100 | 1 | 0 | 5 |
| 4 | 74 | 0 | 0 | 5 |
| 'Unmanaged' | | | | |
| Run 1 | 91 | 0 | 0 | 5 |
| 2 | 77 | 0 | 2 | 6 |
| 3 | 100 | 0 | 1 | 2 |
| 4 | 74 | 0 | 1 | 5 |

There is little difference in the overall impact on the new paddock between the management policies, but the results show that, if given the chance, the sheep will tend to over-use the south-western trough, as is shown in Run 3, when the dam was always available (in reality this effect might be reduced since the water supplied to the SW trough is saline well water). A policy of blindly preventing the use of the trough at all times when the dam contains water would not be sensible, however, since there are occasions when it dries up for only short periods but the overall rainfall pattern is not ideal for plant growth. In these conditions, as in Runs 1-3, there is a tendency for grazing impact to be unnecessarily high near the dam. To promote even use of the paddock, the best policy would be flexible, such that the south-west waterpoint was usually turned off when the dam contained water (especially after a period of drought), but that watering was allowed there before the dam next went dry if this was a long time later. Needless to say, this model does not consider some additional issues of concern here, such as the rate of shrub re-establishment in areas that have suffered the loss of adult plants.

### (ii) Summary: predictive runs.

This short section of predictive runs has shown that, despite its failings, the model can be used to make useful comments on possible management options. In deciding where to place a new waterpoint in Jervoise, it shows the importance of considering the locations where camping and shade occur, as well as the general paddock design. The prediction that a new waterpoint in Jervoise should go in the middle of the paddock, rather than the mid-north, may have practical relevance, in addition to justifying a reduced cost of piping. In Wizzo North, water-use management in a potential new paddock has relatively slight impact on the paddock's vegetation when compared to seasonal variation. However, to maximise evenness of use, the model shows that management should control access to the south-western waterpoint at times when the dam contains water, but that this control should be flexible.

# Chapter XI.

## A retrospective.

As I have stated, the development of a model of the type that has been described in this thesis has two major purposes. For pure science, this development directs research to the areas of our knowledge which are deficient or ill-defined, and may rectify these inadequacies; in applied science, the ultimate goal is to predict the results of management decisions in real systems in a way that is useful to managers. During this study, I have had two general, personal goals: firstly, to carry out some work of pure scientific value in areas that the model of Noble (1975) had indicated that our knowledge was deficient; and secondly, to use these findings to rebuild the model, and show that it has some predictive value in a real management system.

To what extent have these purposes and goals been fulfilled ? The important areas of deficiency that were apparent in Noble's model were the lack of validation of the physiological indices used to predict behaviour, the limited understanding of how movement is determined in the open paddock, and the uncertainties in the model of grazing intake, especially with regard to the way in which selection changes during the grazing period. Chapter VI has described the validation of some of the indices, most notably and satisfactorily in the heat balance sub-model; some steps have been taken towards an understanding of how these indices may interact when animals are in a free-ranging system. Chapters V, VI and VII have examined movement in the open paddock with varying success, and have indicated the importance of movements to sites of activities other than grazing, instead of the normally assumed importance of movement in grazing itself. Chapters VIII and IX have tested how the structure of the grazing period is related to satiation, and shown that dramatic changes in diet selection occur during this period, which appear to be related to hunger. All these results are relevant to herbivores and systems other than sheep in the South Australian arid zone.

In implementing these and other findings in a new version of the model, I have shown that it is possible to predict the ranging behaviour of sheep, and their impact on a paddock, under moderate climatic conditions. In the critical paddock design of Jervoise, however, the movement model is shown to be imperfect still, especially as regards campsite usage, and more account needs to be taken of variation of intake requirements with external environmental conditions. The illumination of flaws in our knowledge is a continuing process, and the refining of the behavioural model has shown up some previously unrecognised inadequacies. From the drought years during this study, it is clear that the model requires much better information about the water and salt contents of the animals' feed, and that the decline in vegetation quality associated with selective grazing removal in a given area must be investigated and related to the preferences and learning abilities of the grazing animal.

Despite these failings, I have shown that the model has value in predicting the relative outcomes of alternative management decisions in the real world. The model highlighted factors (shade and camp locations) in Jervoise which should influence the choice of a site for a new waterpoint, and has shown that the specific design of an individual paddock is important in this type of decision. In this study, I have not attempted to extend the model to other herbivores or systems, but the structure of the model would be suitable for such an extension.

Overall, then, this study has examined some aspects of the behavioural ecology of sheep in the Australian arid zone, and produced a model that has useful predictive value, and which foreshadows paths for future investigations.

## Appendix.

This appendix presents a model of the heat balance of a sheep. This model was validated in collaboration with I.R.Noble and G.K.Jones, and has been described in a paper; the text of this paper is reproduced here in its original form, except that the references and acknowledgements have been subsumed into the bibliography and acknowledgements of this study. Note that there is a short appendix to this Appendix, which gives the deriviation of the equations used to determine the heat balance.

------------

# A general heat balance model for sheep, and its use to predict shade-seeking behaviour in hot conditions.

D.M.Stafford Smith, I.R.Noble and G.K.Jones.

Department of Environmental Biology,
Research School of Biological Sciences,
Australian National University,
Canberra, ACT 2601, Australia.

## ABSTRACT

Grazing impact in arid zones is focused around certain points which are regularily used for non-grazing activities. Amongst these are water-points and shade sites. Predicting the use of shade sites is an important component of modelling grazing impact on vegetation. We present a model of the thermal load of a sheep which has been used to predict shade-seeking behaviour by free-ranging sheep in the Australian arid zone.

We describe a generalised heat balance model for sheep and validate it in four stages:

(i) a shortwave sub-model, predicting shortwave at the earth's surface,

(ii) an approximation to ground temperature,

(iii) predicted wooltip temperatures at various positions on a sheep's torso, for two wool lengths, in shade or direct sunlight, and allowing for cloud,

(iv) a predicted respiration index correlated with respiration rate.

We demonstrate that our respiration index correlates with the proportion of sheep in a large arid zone paddock that are actually in the shade. A threshold level of the index may be used to predict under what environmental conditions sheep will go to a shade site, as well as their water usage in evaporative cooling. The effects of hunger and thirst on this threshold, and its uses as a trigger in a model of sheep behaviour in semi-arid pastures are discussed.

## Introduction.

Grazing impact by free-ranging large herbivores, or animals in large semi-arid zone paddocks, is not randomly distributed within the animals' range. Animals not only select preferred vegetation types (e.g. cattle, Low et al 1980, sheep, Squires 1976, Lynch 1974), but have certain foci in their range that are relatively over-utilised. For sheep in the Australian semi-arid zone, the paddock waterpoint is the most important of these foci, and a strong impact zone, or piosphere (Lange 1969), may develop around it. Two other significant locations of inactivity are day-time shade sites in hot weather, and night-time campsites. Being regular sites of inactivity, these are also regular starting points for grazing periods and consequent grazing impact. Squires (1975) has noted, for example, that shade location can be an important determinant of grazing distribution patterns for sheep in Australia.

Noble (1975, 1979) has described a model of vegetation growth and sheep grazing behaviour in a chenopod shrubland pasture of South Australia. Such an overall model is crucially dependant upon the modelling of the animals' use of the foci of non-grazing activities. In this paper we describe and validate a detailed heat balance model, and show how it predicts the usage of shade sites by sheep in the open paddock. It also predicts water usage in evaporative cooling by the sheep, which is part of the requirement for predicting when the sheep need to go to the waterpoint.

The merino sheep has long been recognised as being efficiently adapted to the arid zone (Macfarlane 1964). Basic physiological work has been reported by Blaxter et al (1959a,b), Macfarlane et al (1958), Macfarlane et al (1961), Macfarlane et al (1966), amongst others. Lee (1950) outlined a model of the thermal balance of a sheep standing in the sun, and this was extended by Priestley (1957). More recently, Mount and Brown (1982) have described a model of sheep heat balance which allows for cloud and rain, intended to predict energy loss by sheep in relatively cold conditions.

Lee (1972) has discussed thermal stress and strain - the disturbance experienced by an animal exposed to hot conditions. He expressed this in terms of the actual evaporative cooling rate compared with the maximum attainable by the animal. Several studies have followed Porter and Gates' (1969) approach, estimating the thermal load of animals in a particular environment and comparing this with the observed animal behaviour. For example, Porter et al (1973) modelled the environment and thermal load of an iguana in order to predict its behaviour and water requirements (and to demonstrate that such studies are important in predator-prey interactions). In Australia, various studies have compared the effects of thermal loadings with an animal's preferred shelter (e.g. Dawson & Denny 1969, Kitchener 1972). No such study has examined the hour to hour interaction between thermal load and other behavioural determinants.

## Data collection methods.

Validation data was mostly collected during January and February 1982 at Middleback Station, South Australia (33°S, 137°E). Six three-year-old Merino sheep were taken from a flock run on the station, and two of them were shorn. The relevant physical characteristics of these sheep are given in Table 1. Another ten sheep were held in a small (2 ha) paddock for less detailed observations which were taken to ensure that the close-penned sheep were not behaviourally affected by the treatment below, nor individually abnormal.

Every other day for three weeks (total 3 days for acclimatisation plus 11 days of recordings) the six study sheep were closely penned and observed. One shorn and two woolly sheep were penned in artificial shade created by a small 'barn' of reflective roofing material held high enough above the ground to allow the free flow of air. The other three were penned in the open, although the shorn individual was moved into shade when its distress became evident on the hotter days. The animals were permitted water ad lib. No animal suffered conditions that were not observably endured from time to time by undisturbed sheep in the open paddock. The weather during the observation period was typical for a Middleback summer, with minimum temperatures ranging from 12 to 34°C and maximums from 28 to 47°C. There was no rain, and six of the observation days were cloudless.

Environmental and physical measurements were taken at regular intervals. Air temperature in the shade and wind speed at the height of a sheep were recorded at the time that the observations were taken. A variety of ground and surrounds temperatures, including those under a nearby typical shade-tree, were taken using an infrared thermometer (Barnes Eng. Co., model PRT 10). Instantaneous shortwave pyranometer readings (using a LI-COR Inc. sensor LI-200S) were also taken on some days.

Wooltip temperatures were measured at various positions on each sheep's torso with the I.R. thermometer held about 0.3 m from the wool. The accuracy of these was confirmed by wool surface and wool temperature gradient readings taken with thermocouples. The respiration rate of each sheep was counted three times and averaged to give a mean respiration rate. This measure was the most susceptible to disturbance, so on some days the respiration rates of the additional 10 sheep were also monitored to ensure that our sample was representative. A small number of respiration rates measured through binoculars on undisturbed sheep in the open paddock confirmed that our other readings were not affected by the presence of the observer.

We observed a flock of fifteen sheep in the surrounding small paddock (64 ha) to obtain behavioural parameters such as time of entry to shade. In addition, on some days, we simultaneously mapped a full flock (about 400 sheep, though not necessarily all visible) in the nearby Adam's West Paddock (2400 ha). From a vantage point it was possible to determine time of entry to and exit from shade for many of the subflocks, and to see the activities of the individuals.

Model Validation.

The model is intended to be applicable to any site given certain information about location, and minimal, readily-available meteorological data. The constant inputs required for the model - location and certain physical parameters of the sheep - are listed in Table 1. With this information, the model equations as expressed in the appendix will predict values for a given day of year (D), time of day (t), air temperature ($T_a$), wind speed (V), wool-length ($\ell_w$) and, where relevant, body weight (W). Various other parameters such as body size (r,l) may be readily varied if so desired.

Our general approach has been to solve a heat balance equation at the wooltip to determine the energy flux into the body. This equation is a balance between shortwave and net longwave inputs, convective losses to the air, and conductive losses down the wool to the body (Fig.1). In the model, this equation is solved to obtain a notional 'mean wooltip temperature' from which the net heat flux into the body may be calculated. This notional temperature has no measurable meaning, so we have tested many of the assumptions involved in arriving at it by predicting wooltip temperature at various positions on the sheep's torso.

The resulting net energy flow into the body, when added to metabolic heat production, must be balanced by cooling mechanisms in hot conditions (or increased metabolic rate in cold conditions) if the sheep is to maintain a constant body temperature: this forms the basis for an internal heat balance equation. Initially we assume that all evaporative losses occur due to respiratory cooling, so that a respiration rate necessary to balance net energy inputs may be calculated. This equation could be made more complex to generate a more realistic respiration rate.

The detailed equations used in the model are derived in the appendix. In this section, we describe in four stages the main

Table 1.

Parameters and their values used in this validation.

| Parameter | Symbol | Value | |
|---|---|---|---|
| SITE PARAMETERS | | | |
| Latitude (at Middleback, S.A.) | $\phi$ | -0.576 | radians |
| Solar noon (in local time zone) | $t_{noon}$ | 12.3 | h |
| Shortwave attenuation constant | $k$ | 0.8 | |
| Mean ground albedo (shortwave) | $a_g$ | 0.25 | |
| Longwave emissivity (all surfaces) | $\varepsilon$ | 0.98 | |
| ANIMAL PARAMETERS | | | |
| Mean torso radius (no wool) | $r_b$ | 0.149 | m |
| Mean torso length | $l$ | 0.70 | m |
| Body weight | $W$ | 45.0 | kg |
| Body temperature | $T_b$ | 39 | °C |
| Mean wool albedo (shortwave) | $a_w$ | 0.26 | |
| Mean wool emissivity (longwave) | $\varepsilon$ | 0.98 | |
| Wool thermal conductivity | $\lambda_w$ | 0.064 | $W\ m^{-2}\ {}^oC^{-1}$ |
| Mean wool lengths: 'shorn' | $\ell_w$ | 0.01 | m |
| 'woolly' | | 0.07 | m |
| INPUT VARIABLE PARAMETERS | | | |
| Proportion of sky covered by cloud | $c$ | | |
| Day of year (assumed S hemisphere) | $D$ | | d |
| Air temperature | $T_a$ | | °C |
| Hour of day (local time zone) | $t$ | | h |
| Wind speed (at 0.5m) | $V$ | | $m\ s^{-1}$ |

assumptions underlying the derivations, and our validation which justifies these assumptions.

(i) Shortwave radiation reaching the earth's surface.

Since solar radiation represents a major portion of incoming radiative load on a clear day (up to 1100 W $m^{-2}$), the shortwave section of the model is the most complex, and its predictions are important enough to warrant separate validation. Hourly cumulative radiation readings have been measured at Middleback throughout the year with a silicon pyranometer (as above) attached to an automatic weather station. The cumulative radiation load on an horizontal surface for each hour on several days, scattered through the year and known to have been clear at Middleback, was

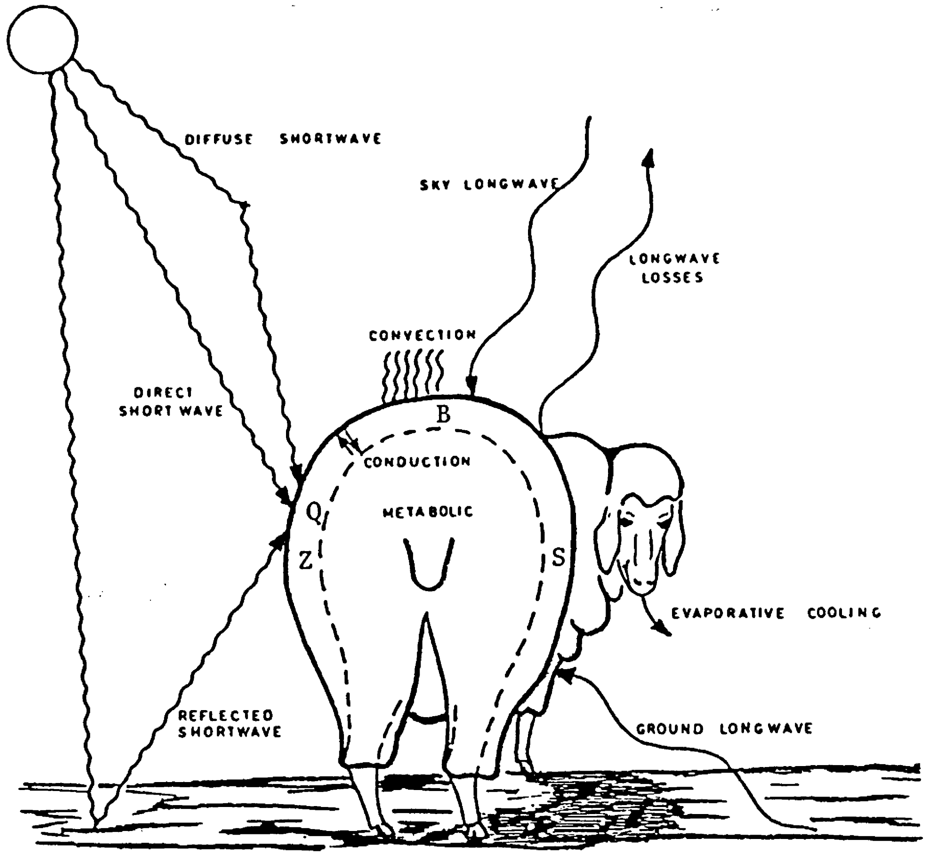


Figure 1: The heat flows estimated in solving the heat balance equations. The letters (B,S,Z,Q) indicate the points used for wooltip temperature validations.

calculated using E0.1-E0.6 (see appendix). The inputs required are the latitude of the site ($\phi$), the mean time of solar noon ($t_{noon}$) in the local time zone, the day of the year (D) and the time of day (t).

The form and magnitude of attenuation in the atmosphere is described by an attenuation function (in E0.5) which depends on the value of a dimensionless constant, k. Clear Australian skies can have a value of k as high as 0.9 (Hounam, 1963): however, we have used k=0.8 here, which is the normal clear sky value for the rest of the world, since our definition of a 'clear sky' allows up to 1/8 cloud.

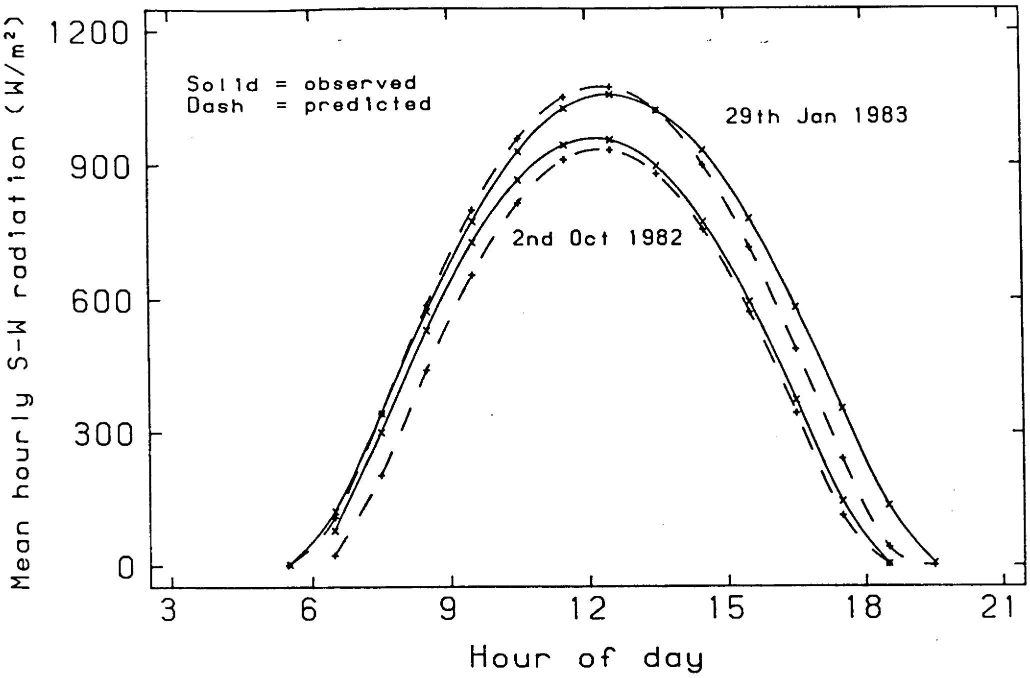


Figure 2: Cumulative hourly shortwave traces at Middleback; predicted and observed values for one winter and one summer day.

Figure 2 shows the traces for a summer and a winter's day at Middleback (29th Jan 1982, $r^2$=.987, n=15; 2nd Oct 1982, $r^2$=.993, n=13; for both p<.0001), without adjusting $t_{noon}$ for the small drift which occurs through the year. Most of the significant error is at times of low radiation input, and is due to the form of the attenuation function which causes underprediction at low solar altitudes (and also allows no light prior to sunrise). The main effect of this, therefore, is early and late in the day, when the shortwave energy input is becoming physiologically trivial. Data from Canberra and other sites gave similar regressions, so the model is taken as satisfactory for Australian latitudes. The effects of cloud and shade are discussed in the appendix.

(ii) An approximation to ground temperature.

Estimation of wooltip temperature elsewhere on the sheep than its horizontal back requires a value of ground temperature ($T_g$). We have measurements of ground temperature during our validation readings, but it is not a commonly available meteorological parameter. Consequently, our validations are carried out using a simplified estimator of ground temperature from the other variables and equations already used in the model.

Noble's (1975) original model followed Priestley (1957) in assuming that $T_g$, if not available, may be approximated by wooltip temperature, whilst Mount and Brown (1982) assume $T_g = T_{air}$. For high solar radiation loads, the latter approximation is severely deficient since $T_g$ may exceed $T_{air}$ by at least 30°C. Priestley's assumption results in a simplification of the longwave equation, but this hides the fact that $T_g$ has effectively become dependent on wool-length. It is also being approximated by the 'mean wooltip temperature' of the whole sheep rather than the more relevant horizontal surface temperature. We therefore decided to model $T_g$ separately, so that it is independent of zoologically-variable parameters.

Accurate modelling of ground temperature is a complex procedure which must account for the lag in heat conduction to depth (e.g. Parton & Logan 1981). This involves knowing soil specific heat and conductivity, as well as having some integrated measure of energy stored at depth. Since soil parameters are highly variable with soil type and moisture regime, such complexity was not warranted here, and we choose to generate a gross approximation based on equations we already have in use for a sheep's back. Validation results show that this approach is adequate for this temperature range, but we do not suggest that these equations accurately model all the processes involved in the ground surface heat balance.

Our approach is to model a flat surface with the conductive and reflective properties of a sheep's back. The albedo of red clay or sand surfaces is similar to that used here for sheep (i.e. 0.26). We assume surface longwave emissitivity to be the same. Taking the surface to be flat rather than cylindrical requires a small change in the convection term: this adjustment resulted in no significant improvement in the correlation, so it is not made.

The most unrealistic assumption made is that the conduction term may be considered equivalent to conduction through wool of thickness $\ell_w$ to a heat sink at sheep body temperature. A long value of 'wool length' was found to be best, and we have used $\ell_w$=0.1 m.

With this value, for a range of ground temperatures, wind speeds and solar inputs, we obtain a correlation between predicted and measured values of $r^2$=.879 in the open, $r^2$=.937 in the shade (for both, n=104, p<0.0001). Results from the sections below were very little affected by whether this predictor of $T_g$ was used, or the measured values.

### (iii) Wooltip temperatures.

Following Noble (1975), we modelled the solution to the heat balance equation for any surface in equilibrium in the sun as:

Shortwave radiative input + net longwave radiative input
- net convective losses - net conductive losses = 0,

in order to obtain the surface temperature. The sheep's torso is assumed to be a perfect cylinder with no significant end effects, and with the remarkable property of being able to orient itself with its long axis simultaneously perpendicular to both the solar azimuth and the direction of wind movement (McArthur and Monteith [1980] found that the orientation of their model sheep to wind had little effect on the bulk mean resistance of the fleece: they did, however, find differences between windward and leeward sides as would be expected). The sheep's body is taken as a perfect heat sink at a body temperature $T_b$ at the other end of the wool covering. Sheep appear to allow their body temperature to rise only slowly, until their cooling mechanisms begin to fail (e.g. Hales & Brown, 1974); although storage of heat in the body is significant in some large animals (Schmidt-Neilsen, 1964), we assume a constant body temperature here. We also assume that there is no significant storage of heat in the fleece, and no lag in heat flux down the fleece. In fact there may be a lag of up to 20 minutes for long fleeces (see Noble 1975), but this would greatly complicate any modelling and the results appear to justify ignoring these factors here (as does an hourly timestep in the overall model).

## Table 2

Correlation statistics for wooltip temperature validations: predicted vs actual temperatures at various positions on the sheep's torso, at two wool lengths, in shade or full sunlight. (All $r^2$ are significant at <.0001 level). Coefficients are from regression equation, predicted = A[1] + B * measured.

| | | A[1] | B | $r^2$ | n |
|---|---|---|---|---|---|
| SHORN (.01 m) | | | | | |
| open | B | - | .97 | .83 | 82 |
| | Q | 9.2 | .77 | .69 | 82 |
| | Z | - | 1.04 | .87 | 82 |
| | M | 6.0 | 1.02 | .76 | 82 |
| in shade | | - | 1.06 | .96 | 104 |
| overall | | 4.2 | .91 | .82 | 432 |
| WOOLLY (.07 m) | | | | | |
| open | B | 4.1 | .80 | .90 | 104 |
| | Q | 8.8 | .77 | .96 | 104 |
| | Z | -3.4 | 1.12 | .94 | 104 |
| | M | 11.3 | .71 | .92 | 104 |
| in shade | | - | 1.06 | .96 | 104 |
| overall | | 7.3 | .79 | .84 | 520 |
| ALL DATA | | 7.0 | .81 | .83 | 952 |

[1] where significantly different from 0 (p<.05).

Initially we solve the balance equation for any point at an elevation angle θ on the sheep's torso (see appendix), and test this solution against our measured values. For both the woolly and the shorn sheep, we present data from the shade and the open on clear days. In the open, we took temperatures at four locations on the sheeps' torso: on the back (B), on the vertical side in the sun (S), on the vertical side in the shade (Z), and the point of maximum locatable temperature (Q - which corresponds to the point in line with the sun's azimuth) (see Figure 1). These positions are not differentiable in the shade, nor under cloudy conditions. We also present data for clouded days, in the shade and the open for both wool lengths.

Figure 3(a,b) show one day's traces for the different points on the torso ($T_a$ is also plotted to show that we are not simply tracking it), and Fig.4 is a plot of all the predicted against

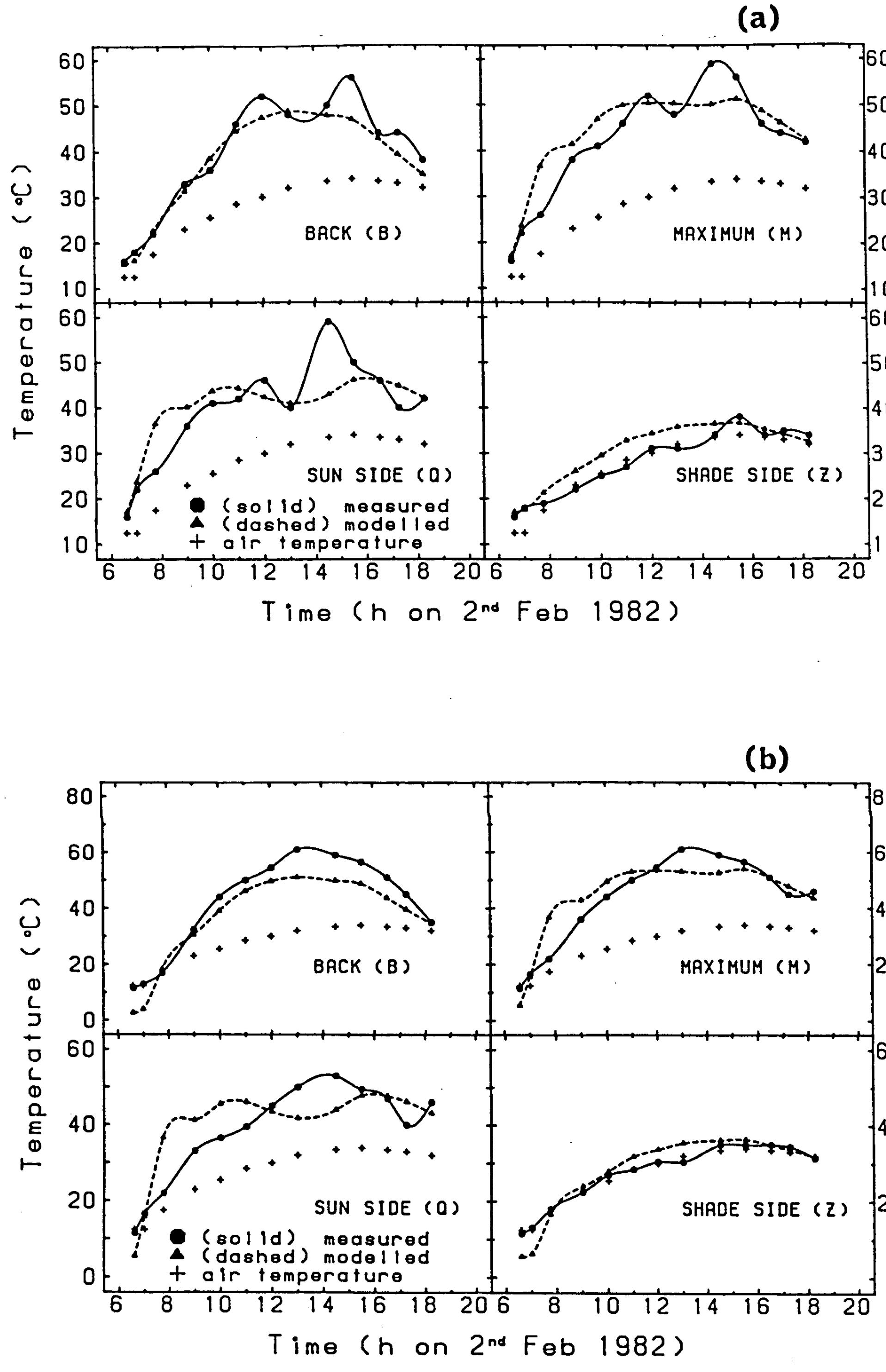


Figure 3: Wooltip temperatures at various positions on a sheep's torso (see Figure 1) during one day; predicted and observed traces for (a) shorn sheep, (b) woolly sheep. Line is spline fit; air temperature is also plotted.

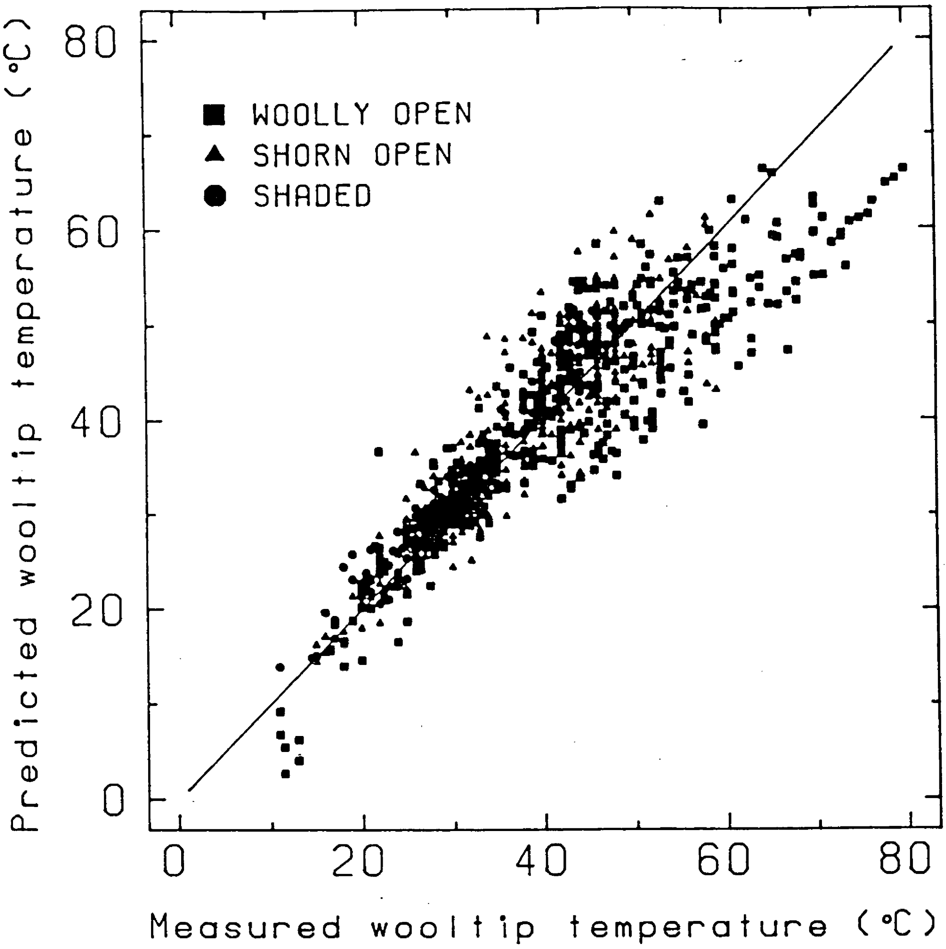


Figure 4: Summary plot of all predicted against measured wooltip temperatures used in this validation. Line is Y = X.

measured data. A summary of the results from the many combinations is given in Table 2. In general, the predictions are good. For points with high solar input, we tend to underpredict at the highest temperatures, which occur mainly on the longer fleece wooltips. Residual analysis shows that this cannot be attributed to lack of responsiveness to any one of our input variables (Q, V, $T_a$, cloud), although solar altitude does explain about 18% of the residual variation: it is unlikely to be due to wool conductivity being too low since this would affect the shorn animals more. The predictions are satisfactory for our purposes.

(iv) Energy flux into the body, and a respiration index.

To calculate the internal energy balance, we solve the external equation for a mean wooltip temperature over the whole body. With this temperature, E2.17 gives the energy flux into the body, and E0.13 gives metabolic heat production.

Evaporative cooling occurs in the respiratory tract during respiration, and from the skin in sweating. Earlier reports, such as Macfarlane (1964), considered that no more than one tenth of the total evaporative losses at high temperatures were from sweating. More recent estimates have varied from 20 to 90% (Hofmeyr _et al_ 1969, Hales & Brown 1974, Hopkins _et al_ 1978). These estimates depend greatly on the breed of sheep, and on the conditions in which the animals are observed: in particular, the proportion is likely to vary with ambient temperature and humidity, and with whether forced evaporation is allowed to occur due to air movement.

Not all the latent heat is absorbed from the body during sweat evaporation, and there is an exothermic reaction of water with the fleece (Klemm 1962). Wind and orientation of the animal affect forced evaporation from bare areas such as the ears, face and legs. The efficiency of sweating is likely to be affected by temperature. The transfer of latent heat down the wool and consequent heat loss, as distinct from the water loss, is therefore difficult to calculate (e.g. Gatenby _et al_ 1983).

In this model we ultimately require an index of the heat load on the sheep for use as a behavioural indicator, and a predictor of the water usage by the sheep for cooling in hot conditions. We therefore ignore sweating, and assume that all evaporation occurs in the respiratory tract. Clearly, the respiration index derived in this fashion will numerically over-predict real respiration rates, but, inasmuch as respiration rate reflects heat loading, the two should be correlated. Since the evaporative process is similar for both sweating and respiratory cooling, the heat and water balances will show smaller errors. We expect to overpredict the respiration rate with increasing winds, as sweating becomes more effective.

E0.14 then gives the evaporative cooling for a respiration rate R ($min^{-1}$), and E2.18 is the solution for the value of R necessary to maintain a constant body temperature. Table 3 and Figure 5 show the results of comparison between this predicted respiration index and measured respiration rates.

Table 3

Correlation statistics for respiration index compared with measured respiration rates: for two wool lengths, in the shade and in the open. (All $r^2$ are significant at p<.0001 level). Coefficients are from the regression equation,

index = A + B * measured respiration rate.

| | A | B | $r^2$ | n |
|---|---|---|---|---|
| SHORN (.01m) | | | | |
| in open | 108.2 | 1.027 | .764 | 70 |
| in shade | 107.4 | 1.368 | .747 | 90 |
| WOOLLY (.07m) | | | | |
| in open | 154.7 | .883 | .707 | 101 |
| in shade | 178.1 | .768 | .548 | 101 |
| all shorn | 110.1 | 1.164 | .716 | 160 |
| all woolly | 170.8 | .780 | .609 | 202 |

Several facts are clear from Figure 5. Firstly, the sheep are capable of a basal degree of heat loss which we are not modelling: the result of this is that they do not start to use respiratory cooling until a higher energy influx level than we would predict. We expect this to be a result both of cutaneous sweating over the body, and of additional controlled heat loss after vasodilation in naked areas of the body such as ears, face and perhaps legs. The effect occurs for both wool lengths.

Secondly, once the shorn sheep do start panting, their rate does not rise as fast as our index does. Presumably there is still some temperature-dependent adjustment to the effectiveness of sweating, although one would expect a complicating compensation due both to the decreasing tidal volume as respiration rate rises (Hales & Webster 1967), and because non-evaporative heat loss from naked areas must become less significant as air temperature rises

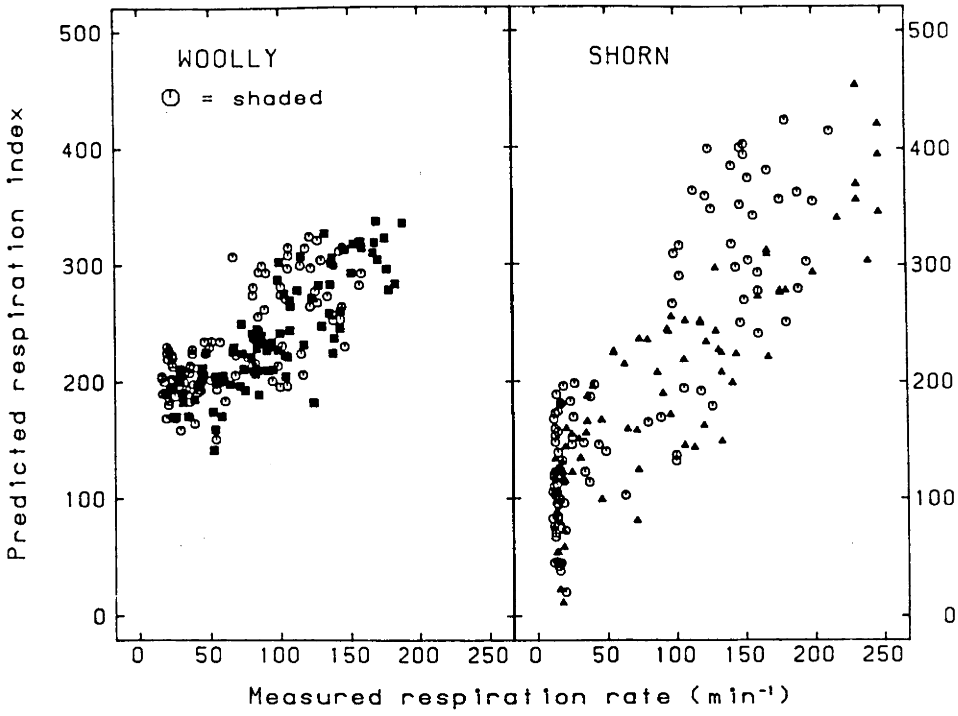


Figure 5: Plot of predicted respiration index against measured respiration rates, for woolly and shorn sheep; solid symbols are sheep in the open.

to and above body temperature.

Thirdly, there is a small significant difference in the slopes between the shorn and woolly sheep, such that the shorn sheeps' actual respiration rate rose slower relative to the index than the woolly sheeps'. This may reflect an improved effectiveness of sweating through short wool, or may relate to some physiological adjustment to being shorn in severe conditions (e.g. see Hopkins et al 1978). This difference supports our assumptions regarding the insignificance of heat storage in the wool, and time lag in conduction down it, since both effects could be expected to reverse this difference in slopes between wool lengths.

## Open paddock behaviour.

This section, including one table and two Figures, is presented and expanded upon in Chapter VI(b.i-iii); it is therefore omitted here.

## Discussion.

The most complete model of sheep heat balance in the literature is Mount & Brown (1982), for sheep under British conditions. Their model predicts net energy loss from a sheep through its fleece, but does not take this measure further to correlate it with behavioural responses. We have run their model, using our shortwave submodel, on our data, and found encouraging agreement with the predictions of our model for the net energy flux through the fleece: this is despite their very different approach to the convection and conduction terms. This may be partly because shortwave radiation is such an important component in the conditions that we are considering. Nevertheless, it seems that we can now model the physical portion of the heat balance well.

We have also demonstrated that the energy flux through the fleece can be used to calculate a respiration index that is strongly correlated with actual respiration rates. This index is also shown to predict the use of shade by sheep in large, open paddocks. Since the index is linked to shade and water use, it can perform an important predictive role in behavioural models such as that of Noble (1975, 1979). We have shown that there are subtle interactions between the influences of heat, thirst and hunger on sheep behaviour; these interactions make it difficult to predict behaviour on the basis of a single index.

Our overall model of the use of large paddocks by sheep, of which this heat balance section is but one component, allows for interactions between hunger, thirst and heat loading indices, but the detailed form of these interactions are not well known. The heat-linked respiration index described in this paper has three uses in the overall model. It is used to predict when the sheep will go to shade sites, when they may leave them, and how much water is lost in evaporative cooling. With the hourly time-step that is used in the overall behavioural model, predictions of when sheep will move to shade, that are based on the respiration index and a single trigger level, are adequate in most conditions.

A complete behavioural model can account for a large part of the variability of spatial utilisation of a paddock (c. 80% in Noble 1975, 1979), and thus provides the basis for simulating the impact zones around sites of herbivore concentration. The application of heat and water balance models will also be useful in predicting herbivore distributions in other grazing regimes, such as in game reserves and in semi-nomadic grazing systems.

-------------

## APPENDIX.

The salient heat transfer equations that are used in the model, and their modifications for validation, are listed in Table A-2. In this appendix, we briefly describe their derivation (i-iv) and their use to build these models (v-viii). Note that equation numbers prefixed with 0 are listed in Table A-2, those with 1 are general equations, and those with 2 are derived in the text below. Symbols are summarised in Tables 1 and A-1.

The external and internal heat balance equations are:

E1.1 Shortwave input + net longwave input - net convective loss - net conduction into the wool = 0,

E1.2 Net conduction from the wool + metabolic heat production - evaporative latent heat losses = 0.

One caveat must be inserted here. Because the model involves the solution of balance equations, small errors in absolute values of the various energy inputs are often be compensatorily dampened by other terms in the course of solving for temperature or respiration rate. Consequently, good final agreement of the model with reality does not imply perfect accuracy in all its components, should these be used independently.

### (i) Shortwave.

Shortwave input on a clear day is based upon equations E0.1-0.6 (Table A-2), derived from Berry (1964), McCullough & Porter (1971) and Harris (1972) (see Noble 1975 for more details). Solar declination (E0.1) and the effect of the eccentricity of the earth's orbit (E0.2) must be calculated for each day D, then the hour angle H is calculated for time t hours (E0.3), to derive the solar altitude expression (E0.4). From this the shortwave radiation $Q_{max}$ impinging on a surface perpendicular to the sun rays may be approximated (E0.5): the attenuation constant, k, was taken as 0.8. In practice there is the additional constraint that if $\alpha<0$ then $Q=0$ (this slightly under-predicts shortwave near

## Appendix to heat balance paper

### Table A-1

Parameters in the equations, and values used in this validation.

| Parameter | Symbol | Value |
|---|---|---|
| GLOBAL CONSTANTS | | |
| Solar constant | $Q_0$ | 1360 W $m^{-2}$ |
| Earth's eccentricity | - | 0.0167 |
| Stefan-Boltzmann constant | $\sigma$ | $5.67 \times 10^{-8}$ W $m^{-2}$ $K^{-4}$ |
| OTHER SYMBOLS USED IN PAPER | | |
| Conductive heat transfer | $C_d$ | W $m^{-2}$ |
| Convective heat transfer | $C_v$ | W $m^{-2}$ |
| Conduction coefficient | $c_f$ | W $m^{-2}$ $^oC^{-1}$ |
| Metabolic heat production | $E_m$ | W |
| Respiratory evaporative heat transfer | $E_R$ | W |
| Hour angle | H | radians |
| Convection coefficient | $h_c$ | W $m^{-2}$ $^oC^{-1}$ |
| Shortwave radiation: horizontal surface | $Q_h$ | W $m^{-2}$ |
| maximum at ground level | $Q_m$ | W $m^{-2}$ |
| Respiration rate | R | $min^{-1}$ |
| Total radius of animal (= $r_b$ + $\ell_w$) | r | m |
| Shade (S=1 in shade, 0 in open) | S | |
| Temperatures: ground | $T_g$ | $^oC$ |
| in Kelvin | $T_{,K}$ | K |
| mean wooltip | $T_w$ | $^oC$ |
| at angle $\theta$ | $T_\theta$ | $^oC$ |
| Sky-subtended proportion at angle $\theta$ | $U_\theta$ | |
| Solar altitude | $\alpha$ | radians |
| Solar declination | $\delta$ | radians |
| Longwave radiation | $\Lambda$ | W $m^{-2}$ |

dawn and dusk). It should be noted that the cosine functions in E0.1 and E0.2 must be phase-shifted by $\pi$ for the northern hemisphere. Shortwave radiation striking a surface of elevation $\theta$ may then be obtained as E0.6.

A point may receive shortwave from three immediate sources: direct radiation from the sun, diffuse radiation from the sky generally, and by reflection off other objects, in particular the ground. Following McCullough & Porter (1971) and Brooks (1960), about 8% of the sky shortwave input on a cloudless day is diffuse radiation, but 45% of this comes from a cone of solid angle close enough to the sun to be treated as direct. Thus about 4.4% of the sky shortwave is distributed across the sky, and 95.6% derives from the sun's primary cone: it is assumed here that this

## Table A-2

Listing of main equations used in model.

SHORTWAVE

E0.1 $\delta = 0.4102 * \cos[0.017214 * (171.3-D)]$ ...radians

E0.2 $1/r^2 = 1 + 0.0334 * \cos(0.017214 * D)$ ...

E0.3 $H = -0.2618 * (t-t_{noon})$ ...radians

E0.4 $\sin\alpha = \cos\phi * \cos\delta * \cos H + \sin\phi * \sin\delta$ ...

E0.5 $Q_m = Q_0 * (1/r^2) * k^{(1/\sin\alpha)}$ ...W $m^{-2}$

E0.6 $Q_\theta = Q_m * \cos(\alpha-\theta)$ ...W $m^{-2}$

LONGWAVE

E0.7 $\Lambda_T = \varepsilon * \sigma * T_K^4$ ...W $m^{-2}$

E0.8 $\sigma T_K^4 \approx 298.5 + 6.36 * T$ ...(T in °C)

CONVECTION

E0.9 $C_v = h_c * (T_w-T_a)$ ...W $m^{-2}$

E0.10 $h_c = 4.036 * V^{0.805} * r^{-0.195}$ ...W $m^{-2}$ $^oC^{-1}$

CONDUCTION

E0.11 $C_d = c_f * (T_w-T_b)$ ...W $m^{-2}$

E0.12 $c_f = \lambda_w / \ell_w$ ...W $m^{-2}$ $^oC^{-1}$

METABOLIC HEAT PRODUCTION

E0.13 $E_m = 5.5 * W^{0.75}$ ...W

EVAPORATIVE HEAT LOSS IN RESPIRATION

E0.14 $E_R = R * (0.58 - 0.0053 * T_a)$ ...W

distribution is even. These assumptions lose validity at low solar altitudes (e.g. see Weber & Baker, 1982), but by then the absolute quantities are small.

The ground is taken to be horizontal, so that the total radiation striking it is given by E0.6 with $\theta=\pi/2$. The proportion reflected is given by the ground albedo, $a_g$, and absorption of impinging radiation at the wooltips is similarily reduced by the wool albedo, $a_w$. In the Middleback region $a_g$ is typically about 0.25. Wool albedo may be very high for clean wool, but was found to decline rapidly to about 0.26 in the field; a similar value has been used by other workers (e.g. Mount & Brown 1982).

Cloud cover greatly affects atmospheric shortwave transmission. Studies such as Lumb (1964) or Maine (1958) were too detailed to be used here. However, Mount and Brown (1982) use Lumb's finding that about 15% of total solar radiation is transmitted through thick cloud. Alternative mean estimates may be derived from Black et al (1954) or Hounam (1963,1969) in Australia suggesting transmissions of 38 or 30%. We regularily measured values in the range 20-30% for varying densities of 8/8 cloud, so we have adopted 25% as the mean transmittance on a totally overcast day. We then assume a linear effect of increasing cloud on this figure, so that,

E2.1 $Q_{actual} = Q * (1-.75 * c)$

where c is the proportion of the sky that is covered by cloud. Additionally, as cloud increases, the mean proportion of the radiation that is diffuse as opposed to direct increases from its clear sky value to 100%. We approximate this by supposing that, with integration over time,

E2.2 $Q(c)_{diffuse} = Q(0)_{diffuse} + c * Q_{direct}$ , and,

E2.3 $Q(c)_{direct} = (1-c) * Q(0)_{direct}$

This is not realistic for instantaneous measurements. There is no net effect on reflected radiation from a rough surface.

Finally, it is the shortwave input that is most affected by shade. When the sheep move into shade, we assume that none of the direct solar radiation reaches it: this was certainly true for our artificial shade, and is approximately so for many shade trees. Our measurements suggest that c. 40% of the diffuse and reflected components still reach under a shade tree, so we assume that this proportion strikes the sheep. This is accounted for as,

E2.4 $Q_{actual} = (1-S) * Q_{direct} + (1-.6*S) * Q_{diffuse+reflected}$

where S=1 if in shade, 0 if not.

(ii) Longwave.

Net longwave input is given by longwave from the sky ($\Lambda_{sky}$) and the ground ($\Lambda_g$) less longwave emission from the wool surface. Longwave emission $\Lambda$ from a surface at temperature $T_k$ (Kelvin) is given by E0.7: $\sigma T_k^4$ may be linearly approximated to T (°C) by E0.8. This approximation has an error range of +2 to -5% for temperatures from 0 to 60°C, with a mean error of 0.5%, and an error of 8% at 80°C. The range of temperatures under consideration were $0<T_a<50$ and $0<T_w,T_g<80$, with the higher ends being exceptional.

Swinbank (1963) describes sky longwave emission as being

$$\Lambda_{sky} = -170.9 + 1.195 * \sigma T_{k,air}^4 \qquad \text{...W m}^{-2}$$

for clear skies. Using the approximation (E0.8) above, one may calculate (after Monteith, 1973) that under clear conditions the effective radiant temperature of the sky is about 20°C below air temperature, for a normal range of air temperature values. In fact our measurements showed a range of 14 to 35°C deficits, with a mean of about 22°C. Under heavily clouded conditions, similar calculations predict a deficit of about 2°C below air temperature: however, we found under less dense 8/8 cloud conditions that the range was from 0 to 13°C, with a mean around 9°C. Although Monteith's reasoning applies only to average conditions, and may be less adequate for drier skies especially, we assume that the effective radiant temperature may be approximated as linearly changing from 20 to 10°C below air temperature with increasing cloud. Thus,

$$T_{sky} = T_{air} - 20 + 10*c \qquad \text{...}^{\circ}\text{C}$$

where c is again the proportion of the sky covered by cloud.

On a clear day, sky longwave flux decreases by 20-30% from horizon to zenith (Monteith, 1973), with a mean value at about 37° elevation. Most points on a sheep's upper torso will be exposed to a substantial proportion of this variability, so that the error in assuming an even input from all over the sky will be much less than 20-30%: this assumption is therefore made.

When the animal is in shade, most of its 'sky' longwave input comes from the canopy overhead. We found, for both our artificial shade and two typical shade trees nearby, that the effective radiant temperature of the canopy was usually 0-6$^oC$ (mode 1.4$^oC$) less than $T_{air}$, with a slight tendency for the deficit to increase with increasing $T_{air}$. It was not consistently affected by cloud. In shade we therefore assume that $T_{sky} \approx T_{air}$, so that in general,

E2.5 $T_{sky} = T_{air} + (1-S)*(10*c - 20)$

where S=1 in shade, 0 in the open. We also assume that all ground longwave comes from shaded ground when the animal is in the shade. We use an emissitivity $\varepsilon$=.98 for all surfaces.

(iii) Convection.

If $T_w$ and $T_a$ are unequal, convective exchange will occur according to E0.9. We follow Noble (1975) in deriving the convection coefficient for a cylinder, $h_c$, as E0.10, where r is the external radius of the cylinder. The derivation is similar to Gates (1962), but for Reynolds number applicable to a sheep-sized cylinder: it assumes the cylinder to be oriented perpendicularily to the wind. This equation compares reasonably well with the table of convective losses given by Priestley (1957) for a 0.5 m diameter sheep, and overpredicts the low wind speed measurements obtained by Joyce et al (1966). We also assume a minimum wind speed of 0.5 m $s^{-1}$ (less than the walking speed of a sheep), so that special equations for free convection at low Reynolds numbers need not be included.

The same convective equation is used throughout the model, despite the gross approximations involved when individual points are considered. The equation derived by the same reasoning for a flat surface in moderate wind speeds differed only by a multiple of 1.17, so the simplification to a single equation is made for ground temperature.

(iv) Conduction through the wool.

Conduction will occur along the wool when $T_w$ and $T_b$ are unequal, and may be approximated as E0.11, where the conduction coefficient $c_f$ is given by E0.12 for a wool length $\ell_w$. We assume here that heat storage in the wool itself is negligible, and that the lag in transmission down the wool is insignificant. We also assume here that body temperature is constant at the base of the wool. The model as a whole has provision for severe heat stress and rising body temperature if the modelled respiration rate becomes untenable, but this was not allowed to occur in the validation readings, and would be a rare event in natural conditions when shade is available.

The conductivity of wool, $\ell_w$, is taken as 0.064 W $m^{-1}$ $^oC^{-1}$, the mean <u>in vivo</u> estimate of Blaxter <u>et al</u> (1959). This may on average be a low value, since no account is taken of wind ruffling the wool surface (Hutchinson, 1964, McArthur & Monteith, 1980), nor of the effect of rain. Rain is of rare occurrence in conditions of potential heat stress: its effect could be partially allowed for by an approach similar to that of Mount and Brown (1982), but we have no available validatory data.

### (v) Heat balance for a flat surface, and ground temperature.

The solution of the heat balance equation E1.1 for a horizontal surface involves no ground reflection or transmittance terms. Shortwave input is direct and diffuse, suitably corrected for cloud and shade (E2.1-4), and reduced by the albedo term. Longwave input is entirely from the sky with re-emittance by the surface according to E0.7, linearised by E0.8. For the convection term, we use E0.9 with $h_c$ given by E0.10, and, as stated above, we approximate by applying $h_c$ for a whole cylinder to the horizontal portion. For a sheep's back, conduction is given by E0.11-2: ground temperature is estimated using $\ell_w$=.1 m.

Total shortwave for the horizontal surface, $Q_h$, is therefore given by,

E2.6 $$Q_h = (1-a_w)(1-.75c)\{(1-S)*Q_{direct}*\sin\alpha + (1-.6S)*Q_{diffuse}\} \quad ...W\ m^{-2}$$

where,

E2.7 $Q_{direct} = (1-c)*.956 * Q_{max}$, and,

E2.8 $Q_{diffuse} = .044 * Q_{max} + c * .956 * Q_{max}$.

Now the external balance equation, E1.1, becomes,

$$Q_h + \varepsilon(\Lambda_{sky}-\Lambda_T) - h_c(T_h-T_a) - c_f(T_h-T_b) = 0$$

After substitution for $\Lambda$ in which the constant terms cancel, and with constant values from Tables 1 and A-1, rearrangement readily yields the solution for $T_h$ as,

E2.9 $$T_h = \{Q_h + T_a(6.23+h_c) + c_f*T_b + 6.23(1-S)(10c-20)\} / \{6.23 + h_c + c_f\} \quad ...^{\circ}C$$

where $h_c$ is obtained from E0.10, and $c_f$ from E0.12.

(vi) Heat balance at other points on a cylinder.

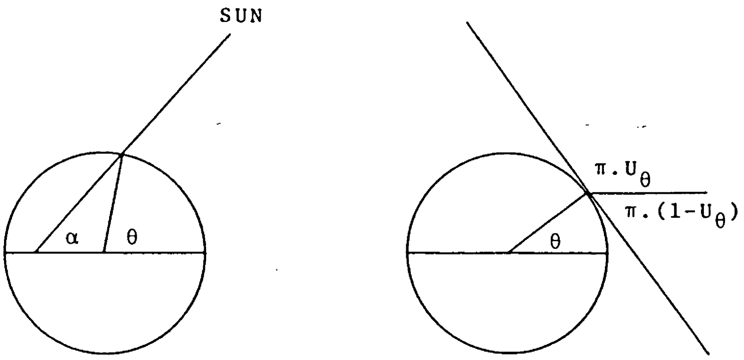
Using the equations above, it is possible to derive an equation for the temperature anywhere on the cylinder. Our validation involved measurements of temperatures on the sunny vertical side, the shaded vertical side and of the maximum locatable temperature, as well as the back temperature already derived (points Q, Z, M and B respectively in Fig.1). In general (see Fig.A-1), a point on a cylinder at angle $\theta$ ($-\pi/2<\theta<\pi/2$) receives radiative input from both the sky and ground in a ratio of $\pi/2+\theta:\pi/2-\theta$: i.e. a proportion $U_\theta = (\pi/2+\theta)/\pi$ from the sky, and $1-U_\theta$ from the ground. This general factor reduces to U=0.5 for points S and Q, and $U_\alpha = (\pi/2+\alpha)/\pi$ at M.

For direct shortwave, input to a point at elevation $\theta$ occurs according to E0.6, with correction for cloud and shade: except that point S on the sheep never receives direct shortwave by definition. Diffuse radiation is received according to the ratio $U_\theta$. Also, such a point 'sees' a proportion $1-U_\theta$ of the shortwave reflected from the ground. Hence the generalised shortwave input to any point, allowing for shade and cloud, is,

E2.10 $$Q_\theta = (1-a_w)(1-.75c)\{(1-S)*Q_{direct}*\cos(\alpha-\theta) + (1-.6S)[U_\theta*Q_{diffuse} + (1-U_\theta)*Q_{reflected}]\} \quad ...W\ m^{-2}$$

where,

## Appendix to heat balance paper



---

Figure A-1: to illustrate the proportion $U^{\theta}=(\pi+\theta)/\pi$.

E2.11 $Q_{direct} = (1-c)*.956*Q_{max}$, or 0 for shade side point Z,

E2.12 $Q_{diffuse} = .044*Q_{max} + c*.956*Q_{max}$ , and

E2.13 $Q_{reflected} = a_g*Q_{max}*\sin\alpha$

and $Q_{max}$ is given by E0.1-5.

By similar reasoning, the general net longwave input to a point at elevation θ is,

$$\Lambda_\theta = \varepsilon\{\Lambda_{sky}*U_\theta + \Lambda_{ground}*(1-U_\theta) - \Lambda_{wool}\} \qquad ...W\ m^{-2}$$

Using the approximation (E0.8), and allowing for shade and cloud, the constant terms again cancel, and this becomes,

$$\Lambda_\theta = 6.23\{U_\theta*[T_a - T_g + (1-S)(10c-20)] + T_g - T_\theta\} \ ...W\ m^{-2}$$

We assume that convection and conduction are unaffected by position (i.e. continue to use the cylindrical Reynolds number) and use E0.10-12. Substituting into the external heat balance equation, we obtain,

$$Q_\theta + \Lambda_\theta - h_c(T_\theta-T_a) - c_f(T_\theta-T_b) = 0$$

and rearrangement again yields the solution for $T_\theta$ as,

E2.14 $$T_\theta = \{Q_\theta + T_a(6.23U_\theta+h_c) + 6.23T_g(1-U_\theta) + c_fT_b + 6.23U_\theta(1-S)(10c-20)\} / \{6.23 + h_c + c_f\} \qquad ...^{o}C$$

where $Q_\theta$, $h_c$ and $c_f$ are obtained from E2.10, E0.10, and E0.12 respectively.

(vii) Net conduction into the body.

To calculate the net heat flux into the sheep's body, the surface heat balance equation E1.1 is solved for a notional 'mean wooltip temperature', $T_w$: this does not differ significantly from the result obtained by integrating all the point temperatures. This is then substituted back into the conduction term E0.11. To obtain $T_w$, the energy fluxes are estimated for the whole surface of the sheep cylinder, radius r, length l (m).

Direct shortwave is intercepted on an area equal to the projection of the sheep body, i.e. 2rl. Diffuse shortwave is received by the upper half of its surface area, i.e. πrl. Ground-reflected shortwave is assumed to strike evenly on the equal lower half, except that (see Noble, 1975) the input is reduced by one third to account approximately for the part of the source in shadow (or covered, in the case of a lying sheep). Allowing for shade and cloud, total shortwave input is then given by,

$$Q = (1-a_w)(1-.75c)\{(1-S)*Q_{direct}*2rl + (1-.6S)(Q_{diffuse}*\pi rl + .667*Q_{reflected}*\pi rl)\} \quad ...W$$

or,

$$\text{E2.15} \quad Q/rl = (1-a_w)(1-.75c)\{2(1-S)*Q_{direct} + \pi(1-.6S)(Q_{diffuse} + .667*Q_{reflected})\}$$

where $Q_{direct}$, $Q_{diffuse}$ and $Q_{reflected}$ are as given above in E2.11-13.

Longwave input is assumed to strike half the wool surface from the sky and half from the ground. Emission occurs from all over the body, so that net longwave input is,

$$\Lambda = \varepsilon\{\Lambda_{sky}*\pi rl + \Lambda_{ground}*\pi rl - \Lambda_{wool}*2\pi rl\} \quad ...W$$

which, on substitution, becomes,

$$\Lambda = 6.23\pi rl\{T_a + (1-S)(10c-20) + T_g - 2T_w\} \quad ...W$$

The convection equation E0.9 is now fully justified and is applied over the whole body area of 2πrl, as is the conduction term E0.11. With the usual values and rearrangement, the 'mean wooltip temperature' may now be calculated as,

E2.16 $$T_w = \{Q/\pi rl + T_a(6.23+2h_c) + 6.23T_g + 2c_f T_b + 6.23(1-S)(10c-20)\} \; / \; 2\{6.23 + h_c + c_f\} \quad \ldots {}^{o}C$$

This value may now be substituted back into the conduction equation E0.11, applied over the whole body, to obtain the net inward flux of energy to the torso as,

E2.17 $$E_c = 2\pi rl*\lambda_w*(T_w-T_b)/\ell_w \quad \ldots W$$

(viii) Evaporative cooling, body heat balance and the index.

The internal equation, E1.2, balances net heat conducted into the body and metabolic heat production against evaporative cooling. We assume that the term $E_c$ above represents net conducted heat (i.e. that special bare areas such as ears, face and legs do not lose significant non-evaporative heat).

We assume that under high heat loads the sheep will not be especially active: net metabolic heat production is not substantially affected by energy expended in panting, until critical levels are reached (Hales & Brown 1974), although it is increased in cold conditions. (In the full model, the index is not allowed to fall beyond a minimum value, below which extra heat is produced by raising the metabolism, with consequent effects on wool and body weight growth). Thonney et al (1976) have suggested that the .75 power approach to fasting heat production is too generalised when applied to a single species. Their re-analysis suggests that .75 is an overestimate for ewes, but they stress that any population needs to be assessed for its particular environment. We therefore estimate metabolic heat production from the maintenance requirements for sheep grazing pastures in cool weather (Young & Corbett, 1972): these results may be summarised (Vickery & Hedges, 1972) as E0.13.

Finally, we assume here that all evaporative losses may be modelled as respiratory loss (see the main text for further discussion). After Noble (1975), we take the sheep's tidal volume to be constant (in fact it initially declines with increasing respiration rate [Hales & Brown, 1974], but this may be partially offset by the animal bringing extra evaporative surfaces such as the tongue into greater play), and the water lost in each 'respiration' to be independent of external conditions. E0.14 then gives the energy exchange per respiration at an external temperature $T_{air}$: the components are latent heat of evaporation in raising the air's relative humidity to 85%, and energy transfer in changing the temperature of the air to near body temperature. With these assumptions, water loss is 0.0085g per respiration.

Combining E0.13-4 and E2.17, and solving for the respiration index, R, we obtain,

E2.18 $$R = \{2\pi rl^{*}c_f(T_w-T_b) + 5.5W^{7.5}\} / \{.58 - .0053T_a\} \quad \ldots \text{min}^{-1}$$

(ix) Summary.

To summarise, the equations needed for each prediction are:

| | | |
|---|---|---|
| | $Q_m$ | E0.1-E0.5 |
| | $T_g$ | $Q_m$, E2.6-E2.9, E0.10, E0.12 |
| | $T_\theta$ | $Q_m$, E2.10-E2.14, E0.10, E0.12 |
| | $T_w$ | $Q_m$, E2.11-E2.13, E2.15-E2.16, E0.10, E0.12 |
| and | $R$ | $T_w$ in E2.18. |

---

# Bibliography

Allden, W.G. & Scott Young, R. (1964) The summer nutrition of weaner sheep: herbage intake following periods of differential nutrition. Aust.J.Agric.Res. 15, 989-1000.

Allden, W.G. & Whittaker, I.A.McD. (1970) The determinants of herbage intake by sheep: the interrelationship of factors influencing herbage intake and availability. Aust.J.Agric.Res. 21, 755-766.

Alvey, N., Galwey, N. & Lane, P. (1982) An introduction to GENSTAT. Academic Press, London, 152pp.

Anderson, D.J. (1982) The home range: a new nonparametric estimation technique. Ecology 63, 103-112.

Anderson, T.W. & Goodman, L.A. (1957) Statistical inference about Markov chains. Ann.Math.Statist. 28, 89-100.

Andrew, M.H., Noble, I.R., & Lange, R.T. (1979) A non-destructive method for estimating the weight of forage on shrubs. Aust. Rangel.J. 1, 225-231.

Arnold, G.W. (1962) The influence of several factors in determining the grazing behaviour of Border Leicester x Merino sheep. J.Br.Grassl. 17, 41-51.

Arnold, G.W. (1964a) Some principles in the investigation of selective grazing. Proc.Aust.Soc.Anim.Prod. 5, 258-271.

Arnold, G.W. (1964b) Grazing experience in early life and subsequent performance in sheep. Field Station Rec.Div.Plant Ind.CSIRO (Aust.) 3, 13-20.

Arnold, G.W. (1964c) Factors within plant associations affecting the behaviour and performance of grazing animals. In: 'Grazing in Terrestrial and Marine Environments' (ed Crisp, D.J.) Blackwell, Oxford, pp133-154.

Arnold, G.W. (1966) The special senses in grazing animals. II. Smell, taste and touch and dietary habits in sheep. Aust.J.Agric.Res. 17, 531-542.

Arnold, G.W. (1975) Herbage intake and grazing behaviour in ewes of four breeds at different physiological states. Aust.J.Agric.Res. 26, 1017-1024.

Arnold, G.W. (1977) An analysis of spatial leadership in a small flock of sheep. Appl.Anim.Ethol. 3, 263-270.

Arnold, G.W., Ball, J., McManus, W.R. & Bush,I.G. (1966) Studies on the diet of the grazing animal. I. Seasonal changes in the diet of sheep grazing on pastures of different availability and composition. Aust.J.Agric.Res. 17, 543-556.

Arnold, G.W. & Bush, I.G. (1963) Equipment for nutritional studies on grazing animals. Field Station Rec.Div.Plant Ind.CSIRO (Aust.) 2, 59-62.

Arnold, G.W., de Boer, E.S., & Boundy, C.A.P. (1980) The influence of odour and taste on the food preferences and food intake of sheep. Aust.J.Agric.Res. 31, 571-587.

Arnold, G.W. & Dudzinski, M.L. (1967a) Studies on the diet of the grazing animal. II. The effect of physiological status in ewes and pasture availability on herbage intake. Aust.J.Agric.Res. 18, 349-359.

Arnold, G.W. & Dudzinski, M.L. (1967b) Studies on the diet of the grazing animal. III. The effect of pasture species and the pasture structure on the herbage intake of sheep. Aust.J.Agric.Res. 18, 657-666.

Arnold, G.W. & Dudzinski, M.L. (1978) 'Ethology of Free-Ranging Domestic Animals.' Elsevier, Amsterdam. 198pp.

Arnold, G.W. & Hill, J.L. (1972) Chemical factors affecting selection of food plants by ruminants. In: 'Phytochemical Ecology' (ed. Harborne, J.B.) Academic Press, London, pp71-101.

Arnold, G.W. & Maller, R.A. (1974) Some aspects of competition between sheep for supplementary feed. Anim. Prod. 19, 309-319.

Arnold, G.W. & Maller, R.A. (1977) Effects of nutritional experience in early adult life on the performance and dietary habits of sheep. Appl.Anim.Ethol. 3, 5-26.

Arnold, G.W. & Pahl, P.J. (1967) Sub-grouping in sheep flocks. Proc. Ecol.Soc.Aust. 2, 183-189.

Austin, M.P., Williams, O.B. & Belbin, L. (1981) Grassland dynamics under sheep grazing in an Australian Mediterranean type climate. Vegetatio 47, 201-211.

Barker, S. & Lange, R.T. (1969) Effects of moderate sheep stocking on plant populations of a Black Oak-Bluebush association. Aust.J.Bot. 17, 527-537.

Bateson, P.P.G. (1976) Specificity and the origins of behaviour. In: 'Advances in the study of behaviour' vol.6 (ed. Rosenblatt, J.S., Hinde, R.A., Shaw, E. & Beer, C.) Academic Press, London, pp1-20.

Batzli, G.O., Jung, H.J.G. & Gunten Spergen, G. (1981) Nutritional ecology of microtine rodents: linear foraging-rate curves for brown lemmings. Oikos 37, 112-116.

Baskin, L.M. (1974) Management of ungulate herds in relation to domestication. In: 'The behaviour of ungulates in relation to management' (ed. Geist, V. & Walther, F.) IUCN Publ.New Series 24. Morges, Switzerland. pp.530-541.

Belovsky, G.E. (1978) Diet optimisation in a generalist herbivore: the moose. Theor.Pop.Biol. 14, 105-134.

Belovsky, G.E. (1981) Optimal activity times and habitat choice of moose. Oecologia 48, 22-30.

Bennett, J.W., & Hutchinson, J.C.D. (1964) Thermal insulation of short lengths of merino fleece. Aust.J.Agric.Res. 15, 427-445.

Berger, J., Daneke, D., Johnson, J. & Berwick, S. (1983) Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. Biological Conservation 25, 193-208.

Berry, G. (1964) The evaluation of Penman's natural evaporation formula by electronic computer. Aust.J.Appl.Sci. 15, 61-64.

Bertram, B.C.R. (1976) Kin-selection in lions and evolution. In: 'Growing Points in Ethology' (ed. Bateson, P.P.G. & Hinde, R.A.) C.U.P., Cambridge, pp281-301.

Bertram, B.C.R. (1978) Living in groups: predators and prey. In: 'Behavioural Ecology: an evolutionary approach' (ed. Krebs, J.R. & Davies, N.D.) O.U.P., pp64-96.

Black, J.M. (1948) Flora of South Australia. Pts I-IV, 2nd edition, Government Printer, Adelaide.

Black, J.N., Bonython, C.W. & Prescott, J.A. (1954) Solar radiation and the duration of sunshine. Quart.J.Roy.Meteorol.Soc. 80, 231-235.

Blaxter, K.L., Graham, N.McC. & Wainman, F.W. (1956) Some observations on the digestibility of food by sheep and related problems. Brit.J.Nutr. 10, 69-91.

Blaxter, K.L., Graham, N.McC., Wainman, F.W. & Armstrong, D.G. (1959a) Environmental temperature, energy metabolism and heat regulation in sheep. 2. The partition of heat losses in closely clipped sheep. J.Agric.Sci. 52, 25-40.

Blaxter, K.L., Graham, N.McC., Wainman, F.W. & Armstrong, D.G. (1959b) Environmental temperature, energy metabolism and heat regulation in sheep. 3. The metabolism and thermal exchanges of sheep with fleeces. J.Agric.Sci. 52, 41-49.

Bobisud, L.E. & Voxman, W.L. (1979) Predator response to variation of prey density in a patchy environment: a model. Am.Nat. 114, 63-75.

Bond, A.B. (1980) Optimal foraging in a uniform habitat: the search mechanism of the green lacewing. Anim.Behav. 28, 10-19.

Bowns, J.E. (1971) Sheep behaviour under unherded conditions on mountain summer ranges. J.Range Manag. 24, 105-109.

Box, T.W. (1973) Closing comments at the Australian Water Research Foundation's Symposium on Arid Lands, Adelaide, S.A. In: Water Res.Foundation of Aust.Rpt. 40, 16.1-16.9.

Brooks, F.A. (1959) An Introduction to Physical Meteorology. Univ. of California, Davis, California.

Brown, G.D. & Lynch, J.J. (1972) Some aspects of the water balance of sheep at pasture when deprived of drinking water. Aust.J.Agric. Res. 23, 669-684.

Bueno, L. & Ruckebusch, Y. (1979) Ingestive behaviour in sheep under field conditions. Appl.Anim.Ethol. 5, 179-187.

Caughley, G. (1964) Social organisation and daily activity of the red kangaroo and the grey kangaroo. J.Mammal. 45, 429-436.

Caughley, G. & Lawton, J.H. (1981) Plant-herbivore systems. In: 'Theoretical Ecology' (ed. May, R.M.) 2nd edition, Blackwells Oxford. pp.132-166.

Chatfield, C. & Lemon, R.E. (1970) Analysing sequences of behavioural events. J.Theor.Biol. 29, 427-445.

Collias, N.E. (1956) The analysis of socialisation in sheep and goats. Ecology 37, 228-239.

Crofton, M.D. (1958) Nematode parasite populations in sheep on lowland farms: sheep behaviour and nematode infections. Parasitol. 48, 251-260.

Croker, B.H. (1959) A method of estimating the botanical composition of the diet of sheep. N.Z.J.Agric.Res. 2, 72-85.

Davidson, J. (1938) On the ecology of the growth of the sheep population in South Australia. Trans.Roy.Soc.South Aust. 62, 141-148.

Dawkins, M. (1971) Perceptual changes in chicks, another look at the 'search image' concept. Anim.Behav. 19, 566-574.

Dawson, T.J., Denny, M.J.S., Russell, E.M. & Ellis, B.A. (1975) Water use and diet preferences of free-ranging kangaroos, sheep and feral goats in the Australian arid zone during summer. J.Zool. 177, 1-23.

Dixon, D.R. & Chapman, J.A. (1980) Harmonic mean measure of animal activity areas. Ecology 61, 1040-1044.

Dixon, S. (1892) The effects of settlement and pastoral occupation in Australia upon the indigenous vegetation. Trans.Roy.Soc.South Aust. 15, 195-206.

Dudzinski, M.L. & Arnold, G.W. (1967) Aerial photography and statistical analysis for studying behaviour patterns of grazing animals. J.Range Manag. 20, 77-83.

Dudzinski, M.L. & Arnold, G.W. (1979) Factors influencing the grazing behaviour of sheep in a Mediterranean climate. Appl.Anim.Ethol. 5, 125-144.

Dudzinski, M.L., Low, W.A., Muller, W.J. & Low, B.S. (1982) Joint use of habitat by red kangaroos and shorthorn cattle in arid Central Australia. Aust.J.Ecol. 7, 69-74.

Dudzinski, M.L., Pahl, P.J. & Arnold, G.W, (1969) Quantitative assessment of grazing behaviour of sheep in arid areas. J.Range Manag. 22, 230-235.

Dudzinski, M.L., Schuh, H.J., Wilcox, D.G., Gardiner, H.G. & Morrissey, J.G. (1978) Statistical and probabilistic estimators of forage conditions from grazing behaviour of merino sheep in a semi-arid environment. Appl.Anim.Ethol. 4, 357-368.

Duncan, P. (1983) Determinants of the use of habitat by horses in a Mediterranean wetland. J.Anim.Ecol. 52, 93-109.

Eltringham, S.K. (1979) 'The Ecology and Conservation of Large African Mammals.' Macmillan Press Ltd., London, 286pp.

Ellis, J.E., Wiens, J.A., Rodell, C.F. & Anway, J.C. (1976) A conceptual model of diet selection as an ecosystem process. J.theor.Biol. 60, 93-108.

Emlen, J.M. (1966) The role of time and energy in food preference. Am.Nat. 100, 611-617.

Emlen, J.M. (1968) Optional choice in animals. Am.Nat. 102, 385-390.

Estabrook, G.F. & Dunham, A.E. (1976) Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. Am.Nat. 110, 401-413.

Estes, R.D. (1974) Social organisation of the African bovidae. In: 'The behaviour of ungulates and its relation to management' (ed. Geist, V. & Walther, F.) IUCN Publn. New Series 24, pp166-205, Morges, Switzerland.

Fontenot, J.P. & Blaser, R.E. (1965) Symposium on factors influencing voluntary intake of herbage by ruminants: selection and intake of grazing animals. J.Anim.Sci. 24, 1202-1208.

Foran, B.D. (1980) Change in range condition with distance from watering point and its implications for field survey. Aust. Rangel.J. 2, 59-66.

Fraser, A.F. & Herchen, H. (1979) The behaviour of liberated livestock. Appl.Anim.Ethol. 5, 95-101.

Freeland, W.J. & Janzen, D.H. (1974) Strategies in hervivory by mammals: the role of plant secondary compounds. Am.Nat. 108, 269-289.

Freeman, T.G. & Benyon, P.R. (1983) Pastoral and social problems in a semi-arid environment. CSIRO, Canberra and UNESCO, Paris, 575pp.

Gardiner, H.G., Wilcox, D.G. & Morrissey, J.G. (1978) The influence of liveweight on group size and mating efficiency in an ewe flock in an arid grazing environment. Aust.Rangel.J. 1, 112-116.

Gatenby, R.M., Monteith, J.L. & Clark, J.A. (1983) Temperature and humidity gradients in a sheep's fleece. I. Gradients in the steady state. Agricultural Meteorology 29, 1-10.

Gates, D.M. (1962) Energy Exchange in the Biosphere. Harper & Row, New York.

Gauthier-Pilters, H. (1974) The behaviour and ecology of camels in the Sahara, with special reference to nomadism and water management. In: 'The behaviour of ungulates in relation to management.' (ed. Geist, V & Walther, F.) IUCN Publ.New Series 24, pp.542-551, Morges, Switzerland.

Geist, V. (1971) 'Mountain Sheep. A Study in Behaviour and Evolution.' Univ. of Chicago Press, Chicago, 383pp.

Gibbs, W.J. (1969) Meteorology and Climatology. In: 'Arid Lands of Australia' (ed. Slatyer, R.O. & Perry, R.A.) A.N.U. Press, Canberra, pp33-54.

Gill, F.B. & Wolf, L.L. (1977) Non random foraging by sunbirds in a patchy environment. Ecology 58, 1284-1296.

Gluesing, E.A. & Balph, D.F. (1980) An aspect of feeding behaviour and its importance to grazing systems. J.Range.Manag. 33, 426-427.

Goodall, D.W. (1967) Computer simulation of changes in vegetation subject to grazing. J.Indian Bot.Soc. 46, 356-362.

Goodall, D.W. (1969) Simulating the grazing situation. In: 'Biomathematics.' (ed. Heinmets, F.) Marcel Dekker, New York, pp211-236.

Goudie, A. & Wilkinson, J. (1977) The Warm Desert Environment. C.U.P., Cambridge, 88pp.

Graetz, R.D, & Ludwig, J.A. (1978) A method for the analysis of piosphere data applicable to range assessment. Aust.Range.J. 1, 126-136.

Graham, N.McC. (1980) Variation in energy and nitrogen utilization by sheep between weaning and maturity. Aust.J.Agric.Res. 31, 335-346.

Green, R.E. (1980) Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. Theor.Popul.Biol. 18, 244-256.

Greenwood, P.J., Harvey, P.H., & Perrins, C.M. (1978) Inbreeding and dispersal in the Great Tit. Nature 271, 52-54.

Grubb, P. & Jewell, P.A. (1966) Social grouping and home range in feral Soay sheep. Symp.zool.Soc.Lond. 18, 179-210.

Grubb, P. & Jewell, P.A. (1974) Movement, daily activity and home range of Soay sheep. In: 'Island survivors: The ecology of Soay sheep of St. Kilda' (ed. Jewell, P.A., Milnes, C. & Morton Boyd, J.) Athlone Press, London, pp160-194.

Hainsworth, F.R. & Wolf, L.L. (1979) Feeding: an ecological approach. In: 'Advances in the Study of Behaviour' (ed. Rosenblatt, J.S., Hinde, R.A., Beer, C. & Busnel, M.C.) Vol. 9. Academic Press, London, pp53-96.

Hales, J.R.S. & Brown, G.D. (1974) Net energetic and thermo-regulatory efficiency during panting in the sheep. Comp.Biochem.Physiol. 49, 413-422.

Hales, J.R.S. & Webster, M.E.D. (1967) Respiratory function during thermal tachypnoea in sheep. J.Physiol. 190, 241-260.

Hamilton, B.A., Hutchinson, K.J., Annis, P.C. & Donnelly, J.B. (1973) Relationships between the diet selected by grazing sheep and the herbage on offer. Aust.J.Agric.Res. 24, 271-277.

Hamilton, W.D. (1971) Geometry for the selfish herd. J.theor.Biol. 31, 295-311.

Hamilton, W.J.III & Watt, K.E.F. (1970) Refuging. Ann.Rev.Ecol.Syst. 1, 263-286.

Harrington, G.N. & Pratchett, D. (1973) Cattle diet on Ankole rangeland at different seasons. Trop.Agric. 50, 211-219.

Harris, G.P. (1972) The ecology of corticolous lichens. 3. A simulation model of productivity as a function of light intensity and water availability. J.Ecol. 60, 19-40.

Harris, P.S. & O'Connor, K.F. (1980) The grazing behaviour of sheep (Ovis aries) on a high-country summer range in Canterbury, New Zealand. N.Z.J.Ecology 3, 85-96.

Heady, H.F. (1964) Palatability of herbage and animal preference. J.Range.Manag. 17, 76-82.

Hills, E.S. (1969) History of the world's arid lands. In: 'Arid Lands of Australia' (ed. Slatyer, R.O. & Perry, R.A.) A.N.U. Press, Canberra, pp1-10.

Hodder, R.M. & Low, W.A. (1978) Grazing distribution of free-ranging cattle at three sites in the Alice Springs district, Central Australia. Aust.Rangel.J. 1, 95-105.

Hodge, R.W. & Doyle, J.J. (1967) Diet selected by lambs and yearling sheep grazing on annual and perennial pastures in southern Victoria. Aust.J.Exp.Agric.Anim.Husb. 7, 141-143.

Hofmeyr, H.S., Guidry, A.J. & Waltz, F.A. (1969) Effects of temperature and wool length on surface and respiratory evaporative losses of sheep. J.Appl.Physiol. 26, 517-523.

Holdgate, M.W. (1984) Information needs for the decision-making process. In: 'Ecology in Practice' Part II (ed. di Castri, F., Baker, F.W.G. & Hadley, M.) UNESCO, Paris, pp249-263.

Holling, C.S. (1959) Some characteristics of simple types of predation and parasitism. Canad.Entomol. 91, 385-398.

Hopkins, P.S., Knights, G.I. & Le Feuvre, A.S. (1978) Studies of the environmental physiology of tropical merinos. Aust.J.Agric.Res. 29, 161-171.

Hounam, C.E. (1963) Estimates of solar radiation over Australia. Aust.Meteorol.Mag. 11, 1-14.

Hounam, C.E. (1969) Revised regression equations for estimation of solar radiation over Australia. Aust.Meteorol.Mag. 17, 91-94.

Houston, A. & McNamara, J. (1982) A sequential approach to risk-taking. Anim.Behav. 30, 1260-1261.

Hrdy, S.B. (1976) Male-male competition and infanticide among the langurs (Presbytis entellus) of Abu, Rajastan. Folia primat. 22, 19-58.

Hunter, R.F. (1962) Hill sheep and their pasture: a study of sheep grazing in S.E. Scotland. J.Ecol. 50, 651-680.

Hunter, R.F. (1964) Home range behaviour in hill sheep. In: 'Grazing in Terrestrial and Marine Environments' Proc.4th Symp.Brit.Ecol.Soc. (ed. Crisp, D.J.) Blackwell, Oxford, pp155-171.

Hutchinson, K.J. (1960) Measurements of wool production and its physiological components in a group of South Australian merino sheep. Aust.J.Agric.Res. 12, 696-714.

Janetos, A.C. & Cole, B.J. (1981) Imperfectly optimal animals. Behav.Ecol.Sociobiol. 9, 203-209.

Jarman, J.P. (1974) The social organisation of antelope in relation to their ecology. Behaviour 48, 215-267.

Jarman, M.V. & Jarman, P.J. (1973) Daily activity of impala. E.Afr. Wildl.J. 11, 75-92.

Jessop, J. (ed.) (1981) 'Flora of Central Australia'. (Australian Systematic Botany Society) Reed, Sydney, 537pp.

Jewell, P.A., Milnes, C. & Morton Boyd, J. (eds.) (1974) 'Island Survivors: the Ecology of Soay Sheep of St. Kilda' Athlone Press, London, 386pp.

Joyce, J.P., Blaxter, K.L. & Park, C. (1966) The effect of natural outdoor environments on the energy requirements of sheep. Res.vet.Sci. 7, 342-359.

Kenney, P.A. & Black, J.L. (1983) Identification and measurement of factors affecting diet selection by sheep. In: 'Feed Information and Animal Production', Proc.2nd Symp.Int.Network of Feed Information Centres (ed. Robards, G.E. & Packham, R.G.) Commonwealth Agric.Bureau, Canberra, pp249-253.

Kilgour, R. (1974) Potential value of animal behaviour studies in animal production. Proc.Aust.Soc.Anim.Prod. 10, 286-292.

Kilgour, R., Pearson, A.J. & de Langer, H. (1975) Sheep dispersal patterns on hill country: techniques for study and analysis. Proc.N.Z.Soc.Anim.Prod. 35, 191-197.

Klein, D.R. (1970) Food selection by North American deer and their response to overutilization of preferred plant species. In: 'Animal populations in relation to food resources' (ed. Watson, A.) Blackwells, Oxford, pp25-46.

Klemm, G.H. (1962) The reactions of unshorn and shorn sheep to hot wet and hot dry atmospheres. Aust.J.Agric.Res. 13, 472-478.

Krebs, J.R. (1978) Optional foraging: decision rules for predators. In: 'Behavioural Ecology: an evolutionary approach' (ed. Krebs, J.R. & Davies, N.B.) Blackwell, Oxford, pp23-63.

Krueger, W.C., Laycock, W.A. & Price, D.A. (1974) Relationships of taste, smell, sight and touch to forage selection. J.Range.Manage. 27, 258-262.

Lange, R.T. (1967) Nitrogen, sodium and potassium in foliage from some arid- and temperate-zone plants. Aust.J.Biol.Sci. 20, 1029-1032.

Lange, R.T. (1969) The piosphere: sheep track and dung patterns. J.Range.Manag. 22, 396-400.

Lange, R.T. (1973) New attitudes to land use in our arid zone. Water Res.Foundation of Aust.Rpt. 40, 5.1-5.7.

Lange, R.T. & Willcocks, M.C. (1978) The relation between sheep-time spent and egesta accumulated within an arid zone paddock. Aust.J. Exp.Agric.Anim.Hus. 18, 764-767.

Lange, R.T. & Willcocks, M.C. (1980) Experiments on the capacity of present sheep flocks to extinguish some tree populations of the South Australian arid zone. J.Arid Envir. 3, 223-230.

Langlands, J.P. (1968) The feed intake of grazing sheep differing in age, breed, previous nutrition and live weight. J.agric.Sci. 71, 167-172.

Laut, P., Heyligers, P.C., Keig, G., Loffler, E., Margules, C., Scott, R.M. & Sullivan, M.E. (1977) 'Environments of South Australia. Province 4: Eyre and Yorke Peninsulas'. CSIRO Div. of Land Use Research, Canberra, 289pp.

le Boeuf, B.J. (1974) Male-male competition and reproductive success in elephant seals. Amer.Zool. 14, 163-176.

Lee, D.H.K. (1950) Studies of heat regulation in the sheep with special reference to the merino. Aust.J.Agric.Res. 1, 200-216.

Lee, D.H.K. (1972) Large mammals in the desert. In 'Physiological Adaptations: Desert and Mountains', (ed. Yousef, M.K., Horvath, S.M. & Bullard, R.W.) Academic Press, New York.

Leigh, J.L. & Mulham, W.E. (1966a,b) Selection of diet by sheep grazing semi-arid pasture on the Riverine Plain. I & II. Aust.J. Exp.Agric.Anim.Husb. 6, 460-467; 468-474.

Leuthold, W. 'African ungulates. A comparative review of their ethology and behavioural ecology.' Springer Verlag, Berlin, 307pp.

Lobato, J.F.P., Pearce, G.R. & Beilharz, R.G. (1980) Effect of early familiarisation with dietary supplements on the subsequent ingestion of molasses-urea blocks by sheep. Appl.Anim.Ethol. 6, 149-161.

Lott, D.F. & Hart, B.L. (1979) Applied ethology in a nomadic cattle culture. Appl.Anim.Ethol. 5, 309-319.

Lott, D.F. & Minta, S.C. (1983) Random individual association and social group instability in American Bison (Bison bison). Z.Tierpsychol. 16, 153-172.

Low, W.A. (1972) Community preference by free-ranging shorthorns in the Alice Springs district. Proc.Aust.Soc.Anim.Prod. 9, 381-386.

Low, W.A., Muller, W.J. & Dudzinski, M.L. (1980) Grazing intensity of cattle on a complex of rangeland communities in central Australia. Aust.Rangel.J. 2, 76-82.

Low, W.A., Tweedie, R.L., Edwards, C.B.H., Hodder, R.M., Malafant, K.W.J. & Cunningham, R.B. (1981a,b,c,) The influence of environment on daily maintenance behaviour of free-ranging Shorthorn cows in Central Australia. I, II & III. Appl.Anim.Ethol. 7, 11-26; 27-38; 39-56.

Lumb, F.E. (1964) The influence of cloud on hourly amounts of total solar radiation at the sea surface. Quart.J.Roy.Meteorol.Soc. 90, 43-56.

Lynch, J.J. (1967) Ranging behaviour of sheep in large areas. Proc.Ecol.Soc.Aust. 2, 167-169.

Lynch, J.J. (1974) Merino sheep: some factors affecting their distribution in very large paddocks. In: 'The Behaviour of Ungulates and its Relation to Management' (ed. Geist, V. & Walther, F.) IUCN Publ. New Series 24, pp697-707, Morges, Switzerland.

Lynch, J.J. & Alexander, G. (1973) Animal behaviour and the pastoral industries. In: 'The Pastoral Industries of Australia' (ed. Alexander, G. & Williams, O.B.) Sydney University Press, Sydney, pp371-400.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. Am.Nat. 100, 603-609.

Macfarlane, W.V. (1964) Water distribution and turnover in desert ruminants. CSIRO Arid Zone Res. 24, 259-262.

Macfarlane, W.V. (1968) Protein from the wasteland: water and physiological ecology of ruminants. Aust.J.Sci. 31, 20-30.

Macfarlane, W.V., Howard, B. & Morris, R.J.H. (1966) Water metabolism of merino sheep shorn during summer. Aust.J.Agric.Res. 17, 217-225.

Macfarlane, W.V., Howard, B. & Siebert, B.D. (1967) Water metabolism of Merino and Border Leicester sheep grazing saltbush. Aust.J.Ag.Res. 18, 947-958.

Macfarlane, W.V., Morris, R.J.H. & Howard, B. (1956) Water economy of tropical merino sheep. Nature 178, 304.

Macfarlane, W.V., Morris, R.J.H. & Howard, B. (1958) Heat and water in tropical merino sheep. Aust.J.Agric.Res. 9, 217-228.

Macfarlane, W.V., Morris, R.J.H., Howard, B., McDonald, J. & Budtz-Olsen, O.E. (1961) Water and electrolyte changes in tropical merino sheep exposed to dehydration during summer. Aust.J.Agric. Res. 12, 889-912.

Macrae, A.W. (1971) On calculating unbiased information measures. Psychological Bull. 75, 270-277.

Maine, R. (1958) Maximum temperature prediction. Aust.Meteorol.Mag. 22, 50-63.

McArthur, A.J. & Monteith, J.L. (1980) Air movement and heat loss from sheep. II. Thermal insulation of fleece in wind. Proc.R.Soc. Lond.(B) 209, 209-217.

McBride, G., Arnold, G.W., Alexander, G. & Lynch, J.J. (1967) Ecological aspects of the behaviour of domestic animals. Proc.Ecol.Soc.Aust. 2, 133-165.

McCullough, E.M. & Porter, W.P. (1971) Computing clear day solar radiation spectra for the terrestrial ecological environment. Ecology 52, 1008-1015.

McNair, J.N. (1979) A generalised model of optimal diets. Theor.Pop. Biol. 15, 159-170.

Milinski, M. (1982) Optimal foraging: the influence of intraspecfic competition on diet selection. Behav.Ecol.Sociobiol. 11, 109-115.

Mitchell, A.S. (1979) Poisonous plants in Northern Territory rangelands. Aust.Rangel.J. 1, 239-243.

Monro, R.H. (1982) An appraisal of some techniques used to investigate the feeding ecology of large herbivores with reference to a study on impala in the northern Transvaal. Afr.J.Ecol. 20, 71-80.

Monteith, J.L. (1973) Principles of Environmental Physics. Edward Arnold, London, 241pp.

Mount, L.E. & Brown, D. (1982) The use of meteorological records in estimating the effects of weather on sensible heat loss from sheep. Agricultural Meteorology 27, 241-255.

Morse, D.H. & Fritz, R.S. (1982) Experimental and observational studies of patch choice at different scales by the crab spider Misumena vatia. Ecology 63, 172-182.

Mueggler, W.F. (1965) Cattle distribution on steep slopes. J.Range. Manag. 18, 255-227.

Murdoch, W.W. (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39, 335-354.

Newman, J.C. & Condon, R.W. (1969) Land use and present condition. In: 'Arid Lands of Australia' (ed. Slatyer, R.O. & Perry, R.A.) A.N.U. Press, Canberra, pp105-132.

Newsome, A.E. (1975) An ecological comparison of the two arid-zone kangaroos of Australia, and their anomalous prosperity since the introduction of ruminant stock to their environment. Quart.Rev. Biol. 50, 389-424,

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K & Bent, D.H. (1975) Statistical package for the social sciences. McGraw-Hill, New York, 675pp.

Noble, I.R. (1975) Computer simulations of sheep grazing in the arid zone. Unpubl. Ph.D. thesis, University of Adelaide, 308pp.

Noble, I.R. (1977) Long term biomass dynamics in an arid chenopod shrub community at Koonamore, South Australia. Aust.J.Bot. 25, 639-653.

Noble, I.R. (1979) Computer simulation models of extensive chenopod shrubland grazing systems. In 'Studies of the Australian Arid Zone IV. Chenopod Shrublands' (ed. Graetz,R.D. & Howes, K.M.W.) CSIRO, Canberra, pp125-143.

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

Noy-Meir, I. (1975) Stability of grazing systems; an application of predator-prey graphs. J.Ecol. 63, 459-481.

Noy-Meir, I. (1981) Spatial effects in modelling of ecosystem dynamics. In: 'Arid land ecosystems: structure, functioning and management', vol II (ed. Perry, R.A. & Goodall, D.W.) C.U.P., Cambridge, pp411-432.

Owen-Smith, N. & Novellie, P. (1982) What should a clever ungulate eat? Am.Nat. 119, 151-178.

Parton, W.J. & Logan, J.A. (1981) A model for diurnal variation in soil and air temperature. Agricultural Meteorology 23, 205-216.

Peden, D.G., Hansen, R.M., Rice, R.W. & van Dyne, G.M. (1974) A double sampling technique for estimating dietary composition. J.Range Manag. 27, 323-325.

Peel, L.J. (1973) History of the Australian Pastoral Industries to 1960. In: 'The Pastoral Industries of Australia' (eds Alexander, G. & Williams, O.B.) Sydney University Press, Sydney, pp41-75.

Perry, R.A. The arid ecosystem. Water Res.Foundation of Aust.Rpt. No.40, 2.2-2.17.

Pitcher, T.J., Magurran, A.E. & Winfield, I.J. (1982) Fish in larger shoals find food faster. Behav.Ecol.Sociobiol. 10, 149-151.

Porter, W.P. & Gates, D.M. (1969) Thermodynamic equilibria of animals with environment. Ecol.Monog. 39, 227-244.

Priestley, C.H.B. (1957) The heat balance of sheep standing in the sun. Aust.J.Agric.Res. 8, 271-280.

Pulliam, H.R. (1974) On the theory of optimal diets. Am.Nat. 108, 59-74.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. Quart.Rev.Biol. 52, 137-154.

Rapport, D.J. (1980) Optimal foraging for complementary resources. Am.Nat. 116, 324-346.

Reeves, G.W. (1973) The pastoral industry in Australia's arid regions: some facts and figures. Water Res.Foundation of Aust.Rpt.No.40, 15.1-15.11.

Revusky, S. & Garcia, J. (1967) Learned association over long delays. In: 'The psychology of learning and motivation' Vol. 4 (ed. Bowers, G.H.) Academic Press, New York, pp1-84.

Richards, L.J. (1983) Hunger and the optimal diet. Am.Nat. 122, 326-334.

Riney, T. (1957) The use of faeces counts in studies of several free-ranging mammals in New Zealand. N.Z.J.Sci.and Techn. 38, 507-532.

Romer, A.S. (1959) 'The Vertebrate Story.' Univ. of Chicago Press, Chicago, 437pp.

Santos Ltd. (1981) Final report on the Stony Point Summer Investigation (Oil Spill Trajectory Study). Natural Systems Research, Vic, 30pp.

Schaller, G.B. (1977) 'Mountain Monarchs: Wild Sheep and Goats of the Himalaya.' Univ. of Chicago Press, Chicago, 425pp.

Schmidt-Neilsen, K. (1964) Desert Animals: Physiological Problems of Heat and Water. Clarendon Press, Oxford, 277pp.

Schoener, T.W. (1971) Theory of feeding strategies. Ann.Rev.Ecol.Syst. 2, 369-404.

Sharma, M.L., Tunny, J. & Tongway, D.J. (1972) Seasonal changes in sodium and chloride concentration of saltbush (Atriplex spp.) leaves as related to soil and plant water potential. Aust.J.Agric. Res. 23, 1007-1019.

Shechter, M. & Lucas, R.C. (1978) 'Simulation of Recreational Use for Park and Wilderness Management'. John Hopkins Univ. Press, Baltimore, 220pp.

Shreffler, C. & Hohenbroken, W. (1980) Circadian behaviour, including thermoregulatory activities, in feedlot lambs. Appl.Anim.Ethol. 6, 241-246.

Sih, A. (1980) Optimal foraging: partial consumption of prey. Am.Nat. 116, 281-290.

Simpson, G.G. (1951) 'Horses: the story of the horse family in the modern world and through sixty million years of history.' Oxford Univ.Press, New York, 247pp.

Sinclair, A.R.E. (1977) 'The African Buffalo: a Study of Resource Limitation of Populations.' Univ. Chicago Press, Chicago, 358pp.

Specht, R.L. (1972) 'The Vegetation of South Australia.' Govt.Printer, Adelaide, 328pp.

Squires, V.R. (1970) Grazing behaviour of sheep in relation to watering points in semi-arid rangelands. Proc. XIth Int. Grassland Congr., Surfers Paradise, 880-884.

Squires, V.R. (1974a) Role of livestock behavior in the utilization of rangelands. Unpubl. Ph.D.Thesis, Utah State Univ., 203pp.

Squires, V.R. (1974b) Grazing distribution and activity patterns of merino sheep on a saltbush community in S.E. Australia. Appl.Anim. Ethol. 1, 17-30.

Squires, V.R. (1975) Environmental heterogeneity as a factor in group size determination among grazing sheep. Proc.N.Z.Soc.Anim.Prod. 35, 184-190.

Squires, V.R. (1976a) Walking, watering and grazing behaviour of merino sheep on two semi-arid rangelands in S.W. New South Wales. Aust. Rangel.J. 1, 13-23.

Squires, V.R. (1976b) The sheep and wool industry of Australia - a brief overview. In: Proc.Intl.Sheep Breed.Congr., Muresk (ed. Tomes, G.J., Robertson, D.E. & Lightfoot, R.J.) W.A.Inst.Technol. Press, Perth, pp1-12.

Squires, V.R. (1978) Effects of management and the environment on animal dispersion under free range conditions. Proc. 1st World Congr.Ethol.Appl.Zootech, pp323-334.

Squires, V.R. & Daws, G.T. (1975) Leadership and dominance relationships in Merino and Border Leicester sheep. Appl.Anim.Ethol. 1, 263-274.

Squires, V.R., Wilson, A.D. & Daws, G.T. (1972) Comparisons of the walking activity of some Australian sheep. Proc.Aust.Soc.Anim. Prod. 9, 376-380.

Stephens, D.W. & Charnov, E.L. (1982) Optimal foraging: some simple stochastic models. Behav.Ecol.Sociobiol. 10, 251-263.

Taylor, C.R., Schmidt-Neilsen, K. & Raab, J.L. (1970) Scaling of energy cost of running to body size in mammals. Am.J.Physiol. 219, 1104-1107.

Taylor, J.A. (1980) Merino sheep and the intrapaddock patterning of herbaceous species on the Northern Tablelands of New South Wales, Australia. Unpubl. Ph.D. thesis. Univ. of New England, Armidale, N.S.W., 240pp.

Taylor, J.A., Hedges, D.A. & Robinson, G.G. (1981) On animal numbers and observation intervals for characterising sheep activity. Aust.Rangel.J. 3, 161-165.

Thomas, M.U. & Barr, D.R. (1977) An approximate test of Markov chain lumpability. J.Amer.Statistical Assoc. 72, 175-179.

Thonney, M.L., Touchberry, R.W., Goodrich, R.D. & Meiske, J.C. (1976) Intraspecies relationship between fasting heat production and body weight: a reevaluation of $W^{.75}$. J.Anim.Sci. 43, 692-703.

Thornton, R.F. & Minson, D.J. (1973) The relationship between apparent retention time in the rumen, voluntary intake, and apparent digestibility of legume and grass diets in sheep. Aust.J.Agric. Res. 24, 889-898.

Tribe, D.E. (1950) The behaviour of the grazing animal: a critical review of present knowledge. J.Br.Grassld.Soc. 5, 209-224.

Vickery, P.J. & Hedges, D.A. (1972) Mathematical relationships and computer routines for a productivity model of improved pasture grazed by merino sheep. CSIRO, Anim.Res.Lab.Tech.Paper 4.

Waddington, K.D. (1982) Optimal diet theory: sequential and simultaneous encounter models. Oikos 39, 278-280.

Warner, A.C.I. & Stacy, B.D. (1972) Water, sodium and potassium movements across the rumen wall of the sheep. Quart.J.Expr. Physiol. 57, 103-119.

Weber, M.R. & Baker, C.B. (1982) Comments on 'The ratio of diffuse to direct solar irradiance (perpendicular to the sun's rays) with clear skies - a conserved quantity throughout the day'. J.Appl. Met. 21, 883-885.

Welch, D. (1982) Dung properties and defecation characteristics in some Scottish hervivores, with an evaluation of the dung-volume method of assessing occupance. Acta Theriol. 27, 191-212.

Werner, E.E. & Mittelbach, G.G. (1981) Optimal foraging: field tests of diet choice and habitat switching. Amer.Zool. 21, 813-829.

Werner, E.E., Mittelbach, G.G.., Hall, D.J. & Gilliam, J.F. (1983) Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology 64, 1525-1539.

Westoby, M. (1974) An analysis of diet selection by large herbivores. Am.Nat. 108, 290-304.

Westoby, M. (1978) What are the biological bases of varied diets? Am.Nat. 112, 627-631.

Westoby, M. (1980) Elements of a theory of vegetation dynamics in arid rangelands. Israel J.Bot. 28, 169-194.

Williams, O.B. (1979) Australia. In: 'Arid land ecosystems: structure, functioning and management', vol I (ed. Perry, R.A. & Goodall, D.W.) I.B.P. publ.16, C.U.P., Cambridge, pp145-212.

Wilson, A.D. (1966) The intake and excretion of sodium by sheep fed on species of Atriplex (saltbush) and Kochia (bluebush). Aust.J. Agric.Res. 17, 155-164.

Wilson, A.D. (1974) Water consumption and water turnover of sheep grazing semi-arid pasture communities in New South Wales. Aust.J. Agric.Res. 25, 339-347.

Wilson, A.D. & Hindley, N.L. (1968) Effect of restricted access to water on the intake of salty foods by merino and border leicester sheep. Aust.J.Agric.Res. 19, 597-604.

Wirtz, P. & Lorscher, J. (1983) Group sizes of antelopes in an East African National Park. Behaviour 84, 135-157.

Wood, J.G. (1937) 'The Vegetation of South Australia.' Govt.Printer, Adelaide.

Woods, L. (1983) 'Land degradation in Australia.' A.G.P.S., Canberra, 105pp.

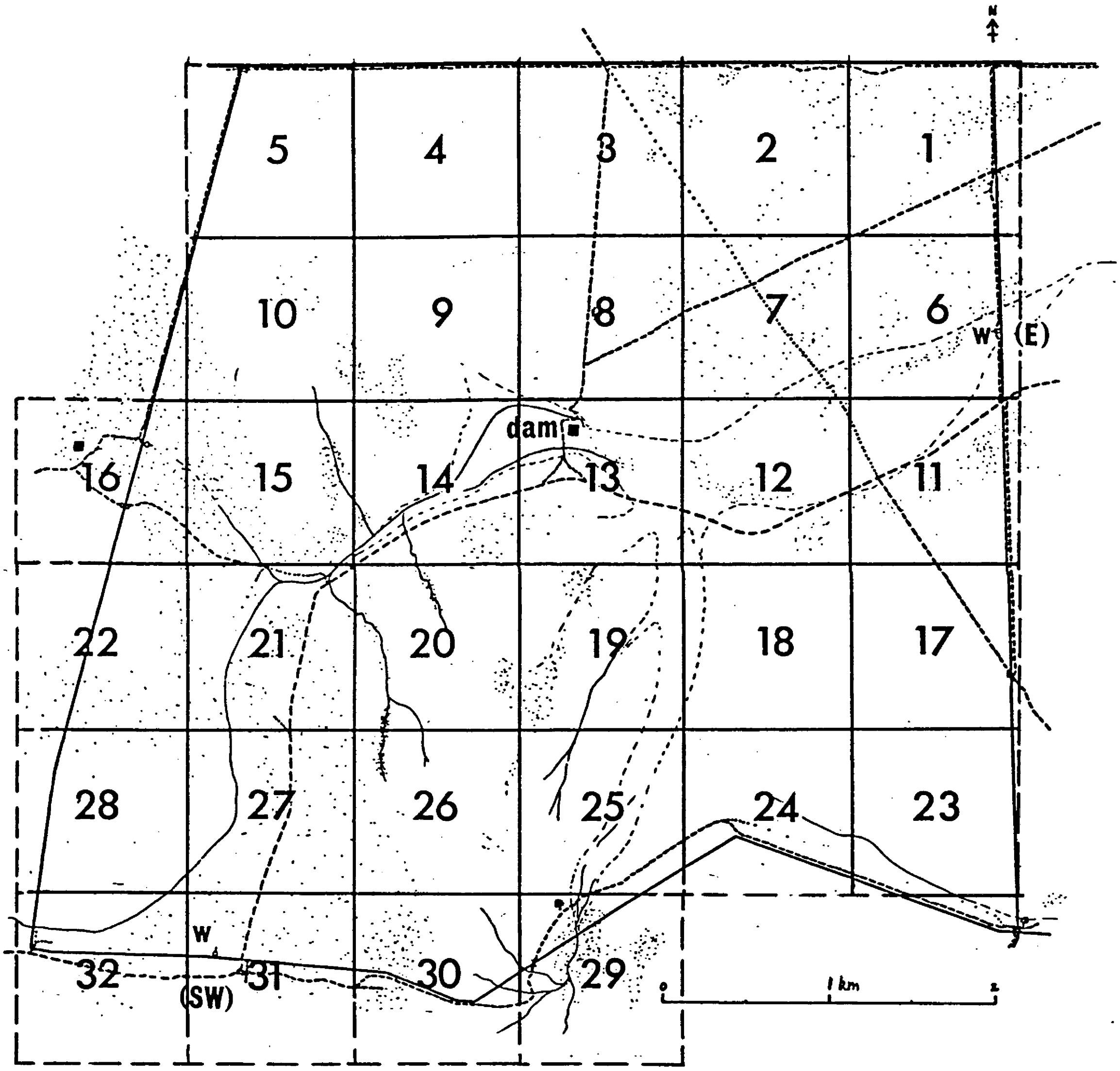
Yeates, N.T.M., & Schmidt, P.J. (1975) 'Beef Cattle Production.' Butterworths, Sydney.

Young, B.A. & Corbett, J.L. (1972) Maintenance energy requirement of grazing sheep in relation to herbage availability. 1. Calorimetric estimates. Aust.J.Agric.Res. 23, 57-76.

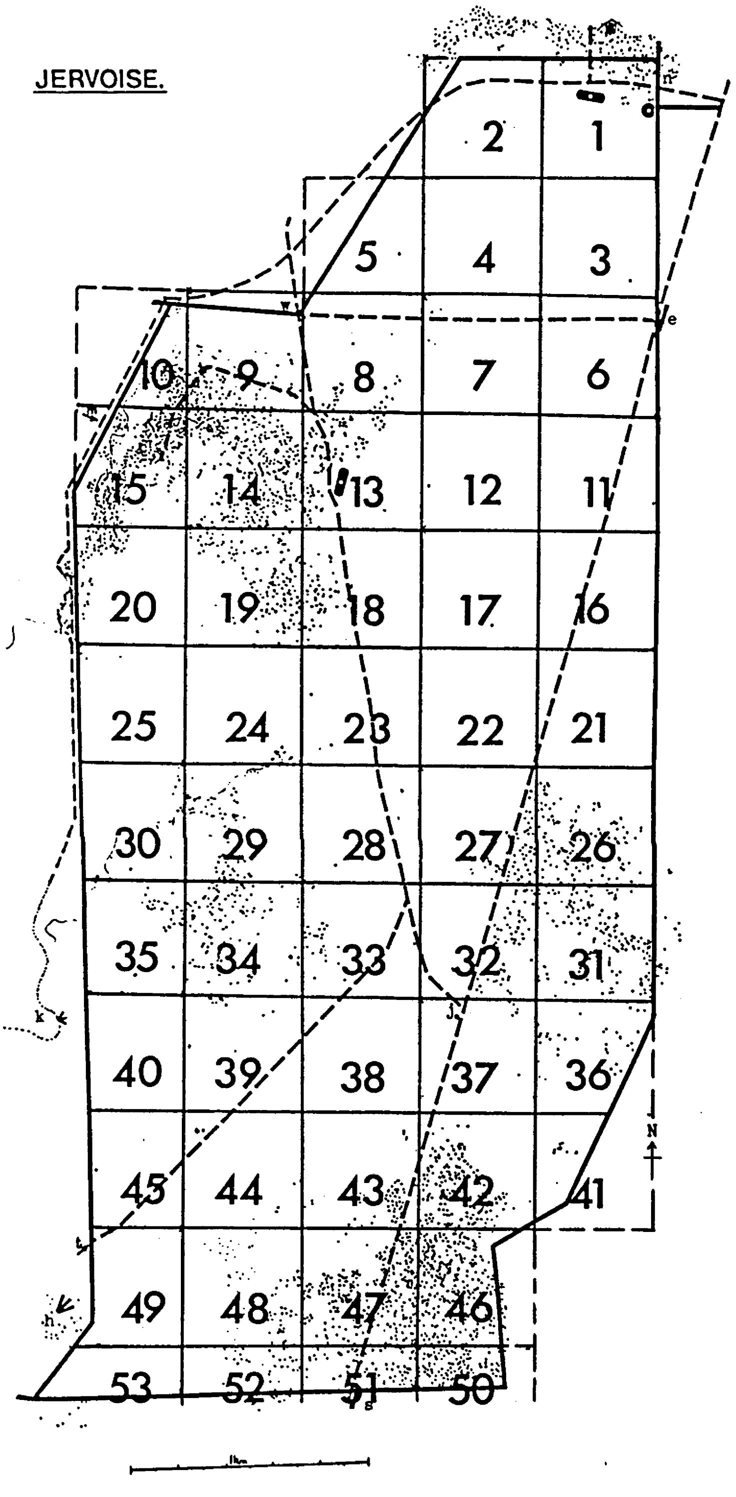
Zach, R. & Falls, J.B. (1976) Ovenbird (Aves:Parulidae) hunting behaviour in a patchy environment: an experimental study. Can.J.Zool. 54, 1863-1879.

---

## Wizzo North



Gridded map of Wizzo North, reproduced for convenience.



Gridded map of Jervoise paddock, reproduced for convenience.