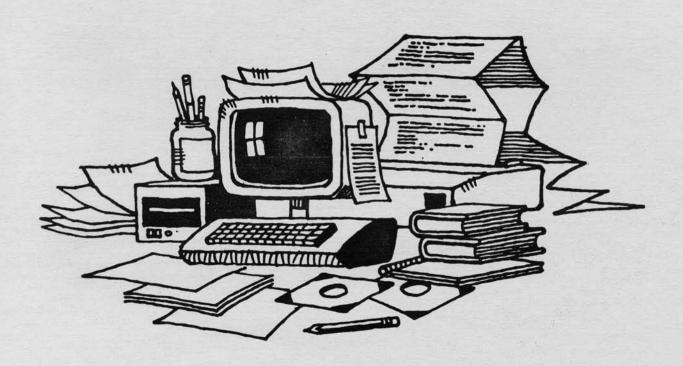
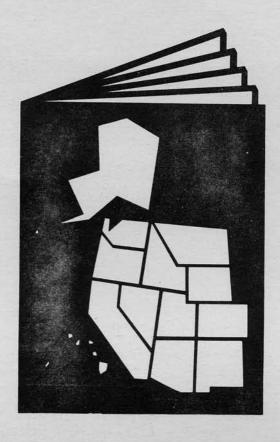
# Modeling: Three Approaches to Predicting How Herbivore Impact Is Distributed in Rangelands

A WESTERN REGIONAL RESEARCH PUBLICATION







Cooperating agencies: The Agricultural Experiment Stations of Arizona, California (Davis), Colorado, Montana, Nebraska, Nevada, New Mexico, Oregon, Texas, Utah, Washington and Wyoming; Cooperative Research, United States Department of Agriculture; and Agriculture Research, United States Department of Agriculture at locations in Colorado, Montana, New Mexico, Nevada, Oregon and Wyoming.

Under the procedure of cooperative publications, this regional research report becomes, in effect, an identical publication of each of the cooperating agencies and is mailed under the frank and indicia of each. Supplies of this publication are available at the sources listed above; distribution is according to the systems used by each agency.

New Mexico State University is an equal opportunity employer. All programs are available to everyone regardless of race, color, religion, sex, age, handicap, or national origin.

# FOREWORD

Rangelands provide basic nutrition for most ruminant livestock and substantial wildlife populations in the United States. Rangeland is important economically because over 35% of the total nutritional requirements for United States beef cattle, sheep and goat populations are derived from this resource. These facts lend credence to the need for regional research focused on optimum and sustained production from rangelands.

One method to foster regional cooperation is through regional projects such as Western Regional Project W-151 in which both state and federal research is focused on questions which not only have local but also regional importance. Regional projects normally operate within a five-year time frame. Prior to the fifth year a decision is made by the participating members as to whether the project should be revised, if a new project should be submitted or the regional research simply conducted under the guidelines of a continuing committee.

In October 1983 the research locations participating in W-151 revised the then current project for the ensuing five-year period (October 1, 1984 through September 30, 1989). The new regional project was given the title "Utilization of range forage for rangeland and domestic ruminant animal production." Two main objectives formed the basis for this project. The first focused on activities of free-ranging livestock as they relate to livestock production efficiency and its impact on the standing crop. The second objective involved assimilating current knowledge into livestock production models for evaluating management strategies and identifying research needs.

In addition to the research focus encompassed in both objectives, it was the goal of W-151 to expand the knowledge base of the research community in applied animal behavior. Many of the participants were not formally trained in ethology. One-day workshops held in conjunction with annual W-151 business meetings provided this training.

The first workshop was held 29 August 1984 in Logan, Utah. At this workshop Dr. David Balph, professor of Fisheries and Wildlife Sciences, Utah State University, Logan, Utah introduced the participants to concepts and terms used in ethology research. The second workshop was held 7 January 1986 in Las Cruces, New Mexico.

This is the first of two papers presented at the 1986 workshop to be published through W-151. This paper focuses on the use of models in describing the spatial use of rangeland by free-ranging livestock. Dr. Mark Stafford Smith was invited to present the paper on modeling. In 1986 he was research scientist in environmental ecology, Commonwealth Scientific and Industrial Research Organization, Division of Wildlife and Rangeland Research, Alice Springs, Australia.

Past Chairpersons W-151,

Dean M. Anderson and Joe D. Wallace

#### AUTHOR

DR. MARK STAFFORD SMITH is a research scientist in the Commonwealth Scientific and Industrial Research Organization (CSIRO) Division of Wildlife and Rangelands Research, P. O. Box 2111, Alice Springs, N.T. 5750, Australia.

# **ACKNOWLEDGMENTS**

The author wishes to thank the Nicolsons of Middleback and Roopena Stations, South Australia for hosting much of the work, and R. T. Lang for providing facilities at Middleback Field Centre. He also acknowledges gratefully the pioneering guidance in this work of lan Noble, whose words he may sometimes have take in vain.

Workshops require the time of many dedicated persons and substantial resources including money and expendable supplies in order to bring them to fruition. The members of W-151 especially thank the following sponsors who contributed materially to the success of this workshop:

Dr. Nolie G. Elliston

The First National Bank of Dona Ana County New Mexico

The Las Cruces Convention and Visitors Bureau

Eli Lilly and Company

The Agricultural Division of Pfizer, Inc.

Hoffmann - La Roche Inc.

Cooperative State Research Service of the U.S. Department of Agriculture

# CITATION INFORMATION

Smith, M. S. 1988. Modeling: three approaches to predicting how herbivore impact is distributed in rangelands. New Mex. Agr. Exp. Sta. Reg. Res. Rep. 628.

# CONTENTS

1.	. SUMMARY	iv		
2.	. INTRODUCTION	1		
3.	MODELS, CONCEPTUAL AND APPLIED.			
	A. Conceptual models	3		
	B. Operational models	4		
4.	. WHOLD PADDOCK MECHANISTIC MODEL	7		
	A. Conceptual approaches and resulting studies.	7		
	B. The model	12		
	C. Proving			
	D. Predictions	24		
	E. Conclusions	26		
5.	REGRESSION MODELS	28		
	A. Data and methods	28		
	B. A simple approach: data averaged over the long-term	31		
	C. Results over the long-term			
	D. Modeling changing conditions	36		
	E. Results for changing conditions	38		
	F. Discussion	41		
6.	KNOWLEDGE-BASED SYSTEM	44		
	A. An application in its infancy	45		
7.	CONCLUSIONS	50		
3.	LITERATURE CITED	51		

#### SUMMARY

Arid zone vegetation has often been mismanaged. Conceptual models of the functioning of the arid zone must take account of the unpredictable nature of climate and its failure to accord with annual cycles. Spatial heterogeneity is also fundamental to the development of patterns in animal movement and vegetation. A useful approach to understanding the arid zone is that of modelling, and the task of predicting patterns of grazing impact exemplifies both of these factors.

Operational models may vary greatly in the degree to which they include details of processes, but all models have some level which is purely descriptive. A mechanistic model of the functioning of a complete sheep paddock, driven only by climatic influences on the initial spatial design and vegetation pattern, is outlined. It predicts sheep behaviour and distributions very well under most conditions, but is inadequate in an extreme drought. This inadequacy is due to our limited understanding of learning and nighttime activities by sheep in large paddocks. Exposing these limitations is an important function of detailed models.

A simpler approach to predicting animal distribution patterns is regression modelling. Observed animal distributions can be predicted on the basis of spatial characteristics such as distance to water and vegetation type. Given statistical caution, the approach can be extended to include climatic conditions in a way which supports a simple theoretical model; this assumes that sheep distributions are mainly constrained by the distance that sheep can walk before next needing to drink, and by how this distance is modified by air temperature and wool length. The regression models predict sheep distributions reasonably under moderate conditions, but are again inadequate in an extreme drought.

Given the limitations in our understanding of the effects of extreme conditions and unusual sequences of events, a knowledge-based heuristic model can provide as much precision as is really valid. It is possible to adequately predict sheep distributions in experimental paddocks under moderate climatic conditions on the basis of eight simple rules. These are derived from the insights given by the more complex models, and the approach can include more detail as our understanding improves. In the meantime, it is a quick way of explicitly summarising the best knowledge currently available.

A spatial element in models is essential for arid zone ecosystems. Spatial models of grazing impact have great potential for integration with spatial models of erosion and other landscape processes to help management. Development of an integrated approach for cattle in central Australia is proceeding.

# Modeling: Three Approaches To Predicting How Herbivore Impact Is Distributed In Rangelands

Arid zone vegetation has been notoriously mismanaged in many parts of the world (Dixon 1892, Cloudsley-Thompson 1974, Woods 1983, Karrar & Stiles 1984). Two factors have contributed to this mismanagement. Firstly, although the vegetation has been recognised to have a low carrying capacity, it has been implicitly assumed that this is somehow evenly distributed through management units. Secondly, satisfactory policies for establishing possible carrying capacities and modifying these sensibly during periods of low productivity have rarely been developed.

The result of non-random movements by animals in the large paddocks of extensive grazing systems is that the actual use of a particular location bears little relationship to that which might be expected from "mean stocking rates" (Low 1979, Wilson & Harrington 1984). The real patterns of use have important implications for forage intake and animal production (Wilson et al. 1984), as well as for soil disturbance (Willatt & Pullar 1983) and long-term pasture productivity (e.g. Barker & Lange 1969) and patterns (Bakker et al. 1983).

To apply the results of any behavioural research in rangeland grazing systems, we need to be able to describe the spatial distribution of animal movement in ways that can be applied easily to various management purposes. Modelling is an important approach to this need, and is attractive because of its relative cheapness in a system of such low returns per unit area (Goodall 1971). The integration of any studies into a modelling framework can also provide a valuable means for assessing the importance and applicability of results.

In this paper I address four related topics. Firstly, I discuss briefly the uses of models in research and management, in order to comment on the philosophy that should underlie their use. The thoughts summarised here may be found elsewhere in the literature, especially in some of the I.B.P. volumes (e.g. Goodall 1974, Goodall et al. 1981). Underlying all work should be good conceptual models, from which may be derived operational models that span a continuum of complexity and purposes.

I then discuss three models which partly span this continuum. All three are applied to the same general system of extensive sheep or cattle grazing in the Australian arid zone; each aims, amongst other intentions, to predict the patterns of grazing impact in a large (i.e. >1000 ha) paddock (i.e. a fenced field) as a result of the animals' free use of food, water, and the landscape available to them. These models are very different in size and scope, and also in stage of development.

The first is a detailed mechanistic model of a paddock; it was conceived as a research-criented project which might be used to derive management principles. It has the most generalised structure, and I shall dwell on it longest. The second is a regression model approach,

based partly on a conceptual understanding that was derived from the first model. It is descriptive and local, but cheap to use. The third approach, which is least developed, uses concepts of knowledge-based systems, wherein the heuristic knowledge of experienced managers is structured into a decision-making framework.

#### MODELS, CONCEPTUAL AND APPLIED

Simulation models have often been seen as mathematical behemoths implemented in incomprehensible computer languages. However, there is no dividing line between these monstrosities and our everyday thought (Goodall 1981). Every time a manager makes a decision about whether to move his stock, he is basing that decision on some form of internal model; this model is his idea of how much the animals will eat in comparison to the remaining feed, the vegetation's growth rate and the likelihood of a drought-breaking rain. In summary, the question is not whether to use models, but how to make sure we use good ones.

A statement such as "an inch of rain will bring up enough feed for a month" is a model of considerable complexity, since it integrates a knowledge of soil type, infiltration, growth, season, diet selection, and animal production. Of course, it need not be arrived at from a detailed consideration of all these factors: it may be merely a description of what has happened in the past, coupled with the assumption that it will occur again in the future under the same circumstances, and that the "same" circumstances can be recognised. Whether these assumptions are satisfactory depends on how good the conceptual model underlying the description is.

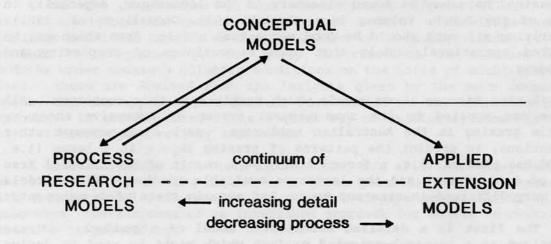


Figure 1: Types of models and their interactions.

Firstly, then, we must make a division between two types of entity that we term as "model". There are the conceptual models that we carry with us about a system, and there are operational models which are the simplified versions of the world with which we attempt to predict the behaviour of real systems (Fig. 1). The distinction is perhaps not absolute, and is ultimately based on whether or not the models contain information which is specific to a particular system, but under most circumstances we treat the two types quite differently.

# Conceptual models

We all carry mental models of the systems in which we work, or even live. In ecology, the complete functioning of a system is too complex for us to contain in our heads, so these mental models are inevitably simplifications of the system. Good science and good experimental design can only be derived when the simplifications inherent in these models reflect reality in a satisfactory way.

Two mental models are particularly important in rangeland systems. Firstly, both researchers and managers often arrive in the Australian arid zone with the assumption that everything runs on an annual cycle, superimposed on which there are occasional blips which are called "disturbances". This mental model works quite well in the higher and more reliable rainfall districts, since rainfall patterns, temperatures, fire seasons and so on are indeed highly correlated with the annual cycle, and occasional droughts, major wildfires or other oddities can be seen as disturbances.

In the arid zone, however, the climate is much less predictable, and as a result everything appears to be disturbance. For example, knowing that a year had 250mm of rain is useless, since the season and intensity of rainfall is almost totally unpredictable (not to mention temperatures and cloudiness in the days after, and frosts the following winter). Here a mental model which deals in the effect of specific combinations of events is far more valuable (Harrington et al. 1984, Griffin & Friedel 1985). In the absence of this explicit recognition, it would be easy to design experiments based around annual replicates, possibly without measuring important climatic covariates (Bender et al. 1984), and end up with hopelessly confounded data. There may be no sensible or relevant descriptors of "mean" conditions, and variance distributions may have functional forms that are non-Gaussian in important ways. Climatic variability and climatic extremes must ultimately be taken into account.

A second important concept is a result of scale in the arid zone, and is especially relevant to describing the distribution of grazing impact: the sum of many point processes is not necessarily enough to explain spatial patterns (e.g. Forman 1981, Noy-Meir 1981). Ecological work has always tended to proceed by study of processes operating at a point, and rarely deals with the fact that what happens at one point can

depend greatly on what is happening at adjacent points. This is obvious in some processes such as runon/runoff, but it is often overlooked during a change of scale. For example, animal behaviour in small paddocks does not necessarily predict behaviour in large areas because the large areas can contain great environmental heterogeneity (Low 1979). Not only does the use of different areas differ because of their varying "quality", but also as a result of location relative to other resources, and because of their history.

For example, in central Australia, certain preferred landscape units tend to be "grazed out" by cattle after a rain-induced flush, following which the animals start to use other, less-preferred units (Low 1972, Low et al. 1981). The rate at which this occurs depends on how much of the unit is available to the cattle in the paddock, how far from water it is situated, how many cattle are present, and whether it is slightly or greatly preferred over alternative units. Once the preferred units have been grazed, the cattle's patterns of movement change, but the time at which this occurs at a particular location cannot be determined independently of the rest of the paddock.

# Operational models

Operational models range from the simplest statement of heuristic results through regression equations to complex mechanistic or process models of whole ecosystems (Fig. 1). The decision to choose a particular model type is often described as a balance between three criteria - realism, precision and generalism (Levins 1966); to these may be added the matter of cost-effectiveness, which applies both at the stage of creating the model, and running it.

However much they may attempt to incorporate processes, all models must become descriptive at some level of detail; it is usually sensible that all components of a model should reach this descriptive level at a comparable degree of realism and precision. An example is provided by one element of the model that I describe below; this element concerns the prediction of when sheep will move to shade on a hot day. It is possible to predict movement to shade reasonably as a regression against air temperature and wool length; this is a simple descriptive model obtained by observing many sheep groups under different conditions. However, it clearly does not take account of other climatic variables, such as cloud, wind and shortwave input from the sun.

Alternatively, it is possible to derive a heat balance model for a sheep which predicts much more accurately what the heat load on the sheep is after taking account of extra climatic variables; then the level of the heat load at which they move to shade can be determined (Stafford Smith et al. 1985). This model incorporates much more mechanism, but still contains a descriptive level. Given suitable physiological information, the heat load could probably be interpreted into blood temperature rises and a trigger in the sheep's brian; this

could include much more mechanism again, but would still depend on describing the threshold level of brain stimulation at which the sheep moved to shade.

When should such increasing incorporation of mechanism cease? Clearly this depends upon the purpose to which the model is to be put. On the whole, a model which explains more mechanism will be more readily generalised to different systems; however, it will need more information to build, probably be much more expensive to run and may contain a level of precision which is irrelevant to the task in hand. For the model of shade-seeking by sheep, the simple regression may be adequate to estimate the number of days that sheep will use shade in a year, but more realism is needed to predict behaviour on an hour-by-hour basis.

Biological models which include a large amount of mechanism have been used mainly in the research arena, rather than applied to specific management problems. Their value has lain mainly in developing a better understanding of how the system works (and hence in helping to develop better conceptual models), because they are often too large and expensive to run for extension purposes. I give an example of such development later in this paper. Because of the complexity of biological systems, the supposed realism of these models does not reliably result in increased generality or precision.

Models involving less mechanism, such as regression models, inevitably tend to be restricted to the localities or conditions in which the data used to build them was collected, but may provide precise results within this constraint. As shown below, however, they sometimes provide support for functional relationships which are more widely applicable. Data collection for development and validation is likely to be expensive, especially if it has to be repeated in different localities, but their simple form makes running the developed models both fast and cheap.

The recent evolution of knowledge-based processing techniques (e.g. Michie 1982) is permitting the development of models that are even more heuristic - that is, derived simply from experience, as is the expertise of most managers. All managers actually use models, of whatever variable quality. So-called "expert systems" using this experience may be able to describe a system as accurately as any "traditional" model can, especially where stochasticity in the system limits the precision of numerical models. Such models tend to be less realistic, although this and the generalism depends upon the data-base and scope of the system. Data collection for this approach may prove to be considerably cheaper than other methods, and validation can take place as part of the extension process since the knowledge base is usually open to ready modification.

Human experience in stochastic systems is limited to a few event sequences. In as-yet-unexperienced conditions, heuristic models based

on this knowledge are likely to be inadequate. It is important to realise, however, that all models contain this descriptive level, and the addition of what appears to be more explicit mechanistic representation may only disguise the inadequacies of the descriptions. As a consequence, the quality of any model is crucially dependent on good underlying conceptual models, which must establish what explanatory variables or processes are relevant and adequate.

The comparison of different degrees of model complexity for a given management problem can shed much light on where research priorities should be targeted, and whether different areas of research are proceeding at a comparable level of detail. It is often true that research effort is being directed at areas which are not important, either because some other area of research is lagging in detail and therefore limiting, or because there are environmental limits on the interpretation of the results which mean that additional detail is useless to management. I now turn to consider three models, which not only highlight areas of conceptual development and research that are limiting, but also show the integration of different research streams, and illustrate environmental limitations on useful output detail.

#### WHOLE PADDOCK MECHANISTIC MODEL

The first model that I wish to describe is a detailed mechanistic model of the functioning of a whole sheep paddock in the Australian arid zone. This model was originally conceived and written by Noble (1975), and updated by Stafford Smith (1984); an outline of the model may also be found in Noble (1979). These sources are not highly accessible, and I shall outline the present model structure here. A detailed description of the behavioural sub-model will be produced soon (a computer coding in BASIC or FORTRAN is also available). First, however, I discuss the development of the model.

# Conceptual approaches and resulting studies

Any modelling approach to the ecological problems of the rangelands must satisfy at least two criteria: it must model spatial patterns so that real local stocking rates can be estimated, and it must permit the testing of alternate management strategies. To these can be added the need for the model not to be restricted to supposed "average" conditions.

Prior to the model described here, there had been a number of attempts to include spatial patterns in models (as reviewed by Noble 1979), perhaps most notably by Goodall. He devised several models of hypothetical paddocks which included a spatial component (e.g. Goodall 1967, 1969), which he then used in an exemplary manner to assess different management strategies (Goodall 1969, 1971). These models usually took the approach of breaking down the landscape into irregular cells, which may have been vegetation types, or areas which were broadly at the same distance from water. The model developed by Noble (1975) took a more explicitly spatial approach, by using a regular grid array of cells, each of which had particular landscape characteristics and spatial relationships with other cells. There have, of course, been many other models dealing with ecosystem functioning (e.g. ELM, Innis 1978; BRIND, Shugart & Noble 1981; etc.), and with how production fits into this (e.g. Arnold et al. 1982; BABYBEEF, Loewer et al. 1983; SPUR, Wight et al. 1984; etc.), but these have not generally contained any spatial element.

What is the relevant underlying conceptual model of the functioning of a paddock? The model was aimed at the functioning of an arid zone sheep paddock in chenopod shrublands in the pastoral zone of South Australia. The ultimate purpose was to provide information about pastoral management and long-term productivity; as a consequence the model was restricted to the domestic animals and their major pasture food types, because native herbivores were considered to have an effect which was either negligible, or more or less constant. There was little concern about community change in the ephemeral vegetation types, so only the major perennial species were modelled in detail; the health of these long-lived plants is seen to be important to the survival of stock

during dry times. Finally, although many of the processes below apply equally well to ewes, rams and wethers (i.e. castrated males), the model was not intended to include reproduction and the effects that this might have, for example, on water turnover and group dispersion in ewes; it therefore effectively deals with a wether paddock.

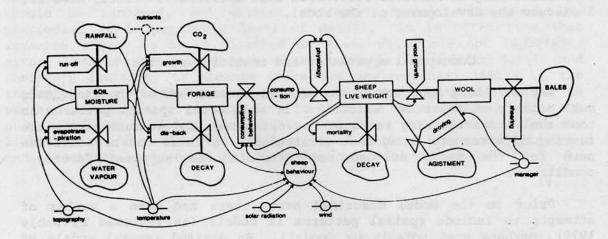


Figure 2: A simplified model of the functioning of a sheep paddock within a management scheme, using notation similar to that of Forrester (1971). The heavy lines represent the flow of water (left hand side) and carbon products (right hand side). From Noble (1975).

Given these constraining assumptions, Figure 2 shows the outline of a generalised conceptual model of the processes taking place in the paddock, except that the spatial interactions are not illustrated. Many of the interactions which are shown must be detailed much further, requiring conceptual models of the separate processes. For example, explicit behavioural submodels are required for the determination of when particular activities are undertaken and how long they are maintained; for the selection of which camp or shade site should be used under given conditions; for movement during grazing, and at other times; and for the selection of diet in areas of differing vegetation composition. Some of these were available in the literature, whilst others necessitated study in the field. Other models were needed for climate simulation, water re-distribution and soil moisture changes and vegetation germination, growth and death, but I shall concentrate on the behavioural models here.

To model the process of sheep movement around the paddock, it is necessary to discriminate location on about an hour to hour basis. As a

consequence, the choice of activity becomes fundamental to the behavioural model, since movement direction and speed depends on what activity the sheep are engaged in. Behaviours which significantly affect location at this time scale are therefore grazing, drinking, resting in the shade and night-time camping. Night-time camping is important because it is well-known that sheep spend at least part of most nights at one of very few locations in a paddock. On the other hand, ruminating, for example, is not important since it either occurs during one of the other activities or does not affect location.

To determine choice of activity, we now need a conceptual model of how activities dominate others, and whether activities can be co-dominant. Many studies have described the general daily pattern of activities of sheep (e.g. Arnold 1962, Bowns 1971, Squires 1974, Harris & O'Connor 1980, Arnold 1984), and divided those activities into a few categories which are usually assumed to be mutually exclusive. Observations of free-ranging sheep indicate that most animals in a subflock are indeed engaged in the same activity at a given time; most activities are also exclusive, except that grazing may occur both in an apparently undirected mode, and during directed movement towards a destination such as a waterpoint. This suggests a model of dominant activities capable of being modified by other needs (cf. McFarland & Sibly 1975). How do we measure the dominance of an activity?

The activities mentioned are responses to drives associated with hunger, thirst, heat load and night-time conditions. Hunger and rumen flow have been well studied for sheep, and the hunger drive seems to be a response to rumen fill. Thirst can be modelled as a balance between water gains and losses. By assuming that movement to shade is a response to heat load, and to the advantages to be gained by removing the input of direct solar energy, a heat balance model can be developed to predict this drive, and incidentally predict water use in evaporative cooling (Stafford Smith et al. 1985). Camping behaviour is poorly understood, and the best model we have for this at present is simply that sheep need to go to a campsite for whatever reason at some stage during the night, once other drives have been satisfied, and will then stay there until near dawn.

These drive submodels provide measures of physiological status. From other studies, the relative dominance of the different drives can then be assessed, so as to determine, for example, whether a thirsty and hot sheep will go to water or to shade. In reality, these factors probably interact in a continuous fashion, but too little is known about the functional forms of these interactions at present; we can therefore approximate the process by assuming some hierarchical dominance sequence. This approach also allows a sub-dominant drive status to influence the dominant drive; this is used in the model to permit grazing at various reduced intensities during movement to some destination.

Having selected an activity, what is the effect of implementing it? Grazing, for example, involves modelling total intake, diet selection and movement (cf. Arnold 1964). Although there is a substantial literature on how diets ought to be selected (optimal foraging, e.g. Emlen 1966, Schoener 1971, Pyke et al. 1977, Engen & Stenseth 1984, etc.), and on diet selection by sheep in specific environments (reviewed by Arnold & Dudzinski 1978), there have been few successful attempts to link these together for any large herbivores (but see Belovsky 1978, 1984, Owen Smith & Novellie 1982).

There are certainly real problems with large herbivores' diets (Westoby 1974), but it seems to be possible to use a simple model of preference ratings and intake rates to predict diet selection (Noble 1979, Stafford Smith 1984). This model requires a knowledge of how preference ratings may change with conditions, however, and an approach which could link these factors more directly is needed. Conceptually, it seems important to link preferences to characteristics of the vegetation which the animals can actually sense, such as intake rate, succulence, tannin content and salt content (Kenney & Black 1984, Cooper & Owen Smith 1984), and then relate these to environmental condition; although this need has been recognised for many years (see Arnold & Dudzinski 1978, p.100), the approach is still in its infancy.

There is some evidence that total intake in sheep may be related to available pasture "quality" (Blaxter et al. 1961, Allden & Whittaker 1970), although this has not always been supported (e.g. Thornton & Minson 1973, Arnold 1975). Intake is probably limited by time in some conditions, and bulk in others, so that models assuming one or other fail in extreme conditions. Inasmuch as the hunger drive is taken to be related to rumen content, bulk limitations on intake are probably reasonable, subject to a maximum time limit to allow for rumen processing.

Movement in grazing has two components - direction and speed. Movement direction in grazing by sheep is often assumed to be related to wind direction, since there is abundant evidence of the tendency for grazing to be taking place in areas of paddocks which are into the wind. The hypothesis that grazing tended to occur into the wind was not strongly supported by paddock studies, however; although there may be a small effect, the main influence of wind direction seems to be on which location is next used for a non-grazing activity. Additionally, no evidence was found during this study to indicate that the sheep were moving deliberately to preferred vegetation types (this may be partly a result of the relative homogeneity of these chenopod shrublands since some evidence was found by Squires [1976]; also regression models have since indicated that there may have been a weak effect).

Movement speed in grazing could be assumed to be constant; however, sheep do seem to move further in poor conditions, and studies found some evidence of movement speed changing with vegetation condition (probably as a result of a greater distance between food items). This

requires no assumption of learning by the sheep, and may be inadequate since they seem to have enough sense not to loiter in areas of no vegetation when there is food elsewhere.

The decision to fulfil the drive to drink, move into the shade or camp at night involves a choice of location and movement to it. Often there may only be one waterpoint, but shade and campsites are usually not unique. The simplest model is to assume that the closest location is chosen; as just mentioned, however, there is evidence that this choice should be modified for sheep to give preference to sites into the direction of the wind. This may be a result of the influence of smell, or the sound of other sheep, but there is no proven explanation of the causes as yet.

Learning about shade and camp sites does seem to take place, but whether this is significant depends on the spatial scale at which discrimination is needed. For shade sites, which are reasonably widespread in most paddocks in the study area, learning is apparently not significant. It is not yet clear what factors define a campsite (topographic height, openness and fencelines seem to be important, cf. Fig. 1.23, Arnold & Dudzinski [1978], and Taylor et al. [1984]); however, in the studied paddocks, there were so few regularly-used sites that all seemed to be available to the sheep, and little variation occurred in their use from year to year which could not be accounted for by other factors. Where there is more than one waterpoint, choice may be strongly influenced by the quality of water available (fresh dam water was usually preferred to moderately saline bore water in one study paddock, for example), as well as by how frequently the waterpoint is used; anecdotal tales abound of how slow sheep can be to learn the location of a second water when an ephemeral water dries up.

The discussion above has been in terms of an individual sheep, which may be taken to representative of one subflock. However, social behaviour and the response to environmental conditions is known to affect flock size (Arnold & Pahl 1967, Dudzinski et al. 1969), with greater flock scattering common in times of scarcity (Lynch 1974). This can be seen as an incidental result of patterns of search for food, which over-ride the forces of social cohesion within groups under conditions of poor forage. A model can be proposed whereby there is some stable "core subgroup" size for Merino sheep (perhaps about 10 sheep); when several groups meet up, for example at the waterpoint or shade site, they are assumed to be likely to stay together with a given probability of any one splitting off from the rest during a movement. This probability can be made dependent on the rate of movement and thus result in greater flock breakup during the more extensive movements occurring in poor conditions.

Certain processes not yet mentioned proceed at all times. These relate mainly to the conversion of feed into animal production, and the concomitant excretory losses. These processes are relatively well-understood in comparison to other components of the intake and

production chain. Excretory losses can be taken to be approximately continuous at the hourly time scale, and are important since they result in a spatial redistribution of nitrogen by the sheep, as well affecting the physiological status of hunger and thirst. A final minor factor is deaths, which can be modelled in terms of body weight.

This has been a brief review of the ideas underlying the paddock model. The remainder of this section outlines the actual structure, and describes its use.

#### The Model

The model was built and validated in chenopod shrubland paddocks on Middleback Station in South Australia (33°S, 137°E). Briefly, this vegetation is dominated by several shrub species up to about 1m tall, including saltbush (Atriplex vesicaria), bluebush (Maireana sedifolia), blackbush (M. pyramidata) and other Maireana, Chenopodium and Lycium species (nomenclature after Jessop 1981). Beneath these low shrubs, there is an understorey layer of "bassias" (Sclerolaena spp.) and other Maireana spp. A grass and herb layer is dominated by two grasses (Stipa variabilis and Danthonia caespitosa), but is very variable in extent depending on seasonal rainfall conditions. This layer is generally preferred by the major herbivore of the area, the Merino sheep, but these animals survive and grow mainly on the shrub layer in dry times. Figure 3(a) shows a map of Jervoise, a paddock around which much of the model development took place.

Figure 4 shows a simplified schematic outline of the whole paddock model. Briefly, rainfall and temperature, and hence evapotranspiration, 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 spatial information about the paddock being modelled is needed, including patterns of run-off, soil characteristics and the initial vegetation distribution over the paddock.

The vegetation is assumed to be represented by about six classes of plant material (this is readily varied given suitable growth information): these are the three major shrub species (saltbush, bluebush and blackbush), the low chenopod understorey (mainly bassias), grasses and standing dry material. Thus the main developments in the perennial vegetation can be followed, whilst also allowing for the variable availability and buffering effect of short-lived vegetation according to the vagaries of climate.

As Fig. 4 shows, the behavioural sub-model interacts with the distribution and condition of the vegetation, with feedback resulting directly from grazing impact and indirectly by nitrogen redistribution. The spatial component is included in the model by dividing the paddock into a number of adjoining cells on a regular grid system: Fig. 3(b) shows how this was done for Jervoise. Each of these cells has its own

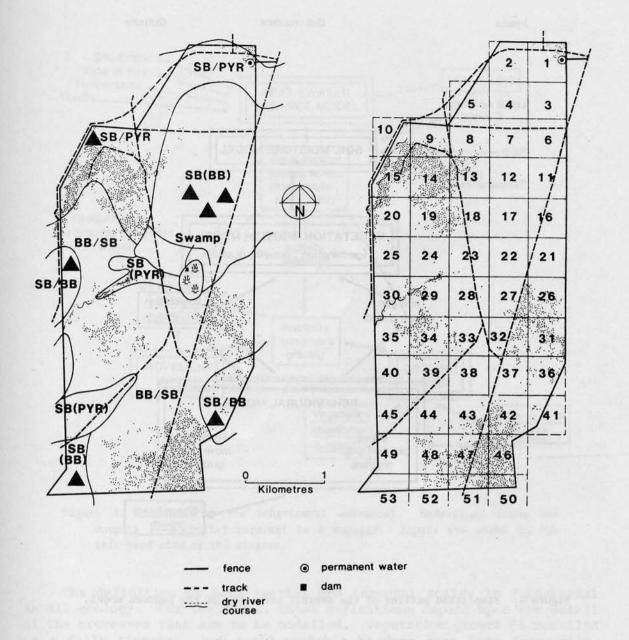


Figure 3: Jervoise paddock showing (left) general features and (right) the grid used for modelling, with numbered grid cells. Features are: fenceline (heavy lines), tracks (dashed lines), permanent water (circle in northeast), trees (dots), major night-time campsite areas (heavy triangles) and main vegetation associations (names refer to dominance of three chenopod shrub species - saltbush SB, bluebush BB, and Maireana pyramidata PYR - and a swampy area).

Inputs Sub-models Outputs

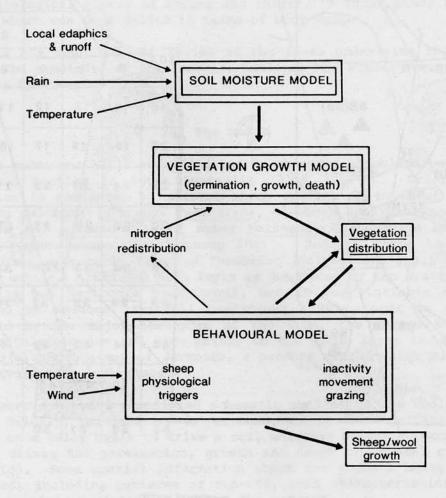


Figure 4: Simplified outline of the overall structure of the paddock model.

run-off and soil characteristics, and the growth and condition of the vegetation in each is modelled separately. In the behavioural submodel, 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 vegetation growth sub-model draws considerably on the records of the Koonamore Vegetation Reserve (Noble & Crisp 1980, Noble 1977) and it is the section which requires most information before the model can be applied to a new paddock. However, it is also the most location-specific section of the model, so I shall not dwell further on it here.

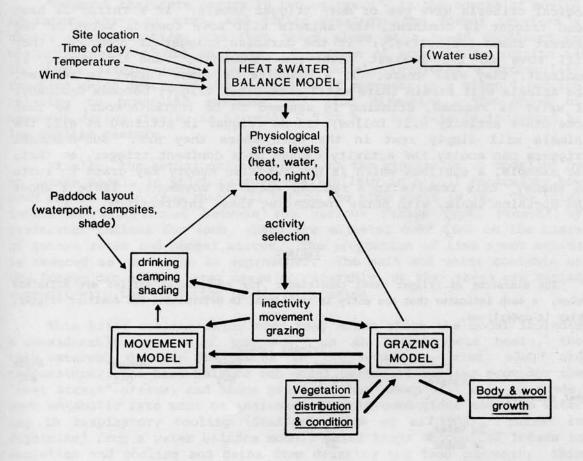


Figure 5: Outline of the behavioural sub-model. Underlined items are outputs of potential interest to a manager. Inputs are shown on the left hand side of the diagram.

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 is modelled on a daily timestep, and could probably be done even less frequently. On the other hand, animal behaviour and movement is modelled on an hourly timestep so as to be realistic in relating them to actual activities and spatial positions. The modelled paddock cells are defined as 500x500 m² for Jervoise, although larger cells of 1x1 km² have been used in other paddocks; these are comparable to the area over which sheep may graze in an hour.

The behavioural portion of the model is outlined in Fig. 5. As a result of an hourly selection of activity for each modelled subflock, that subflock may either be inactive, or moving or grazing. Activity selection is controlled by the state of four more-or-less physiological criteria; these are the evaporative load on the sheep (its "heat

stress"), its thirst, hunger, and the fall of darkness. These physiological criteria have one or more trigger levels: if a thirst or heat load trigger is dominant, the animals will move towards water or the nearest shade respectively; if the darkness trigger is dominant, they will move to the nearest night-time campsite; and if hunger is dominant, they will graze. If a campsite or shade target is reached, the animals will remain there until some other trigger becomes dominant; if water is reached, drinking is assumed to be instantaneous, so that some other activity will follow; if no trigger is attained at all, the animals will simply rest in the open where they are. Sub-dominant triggers can modify the activity caused by a dominant trigger, so that, for example, a subflock which is hot but also hungry may graze en route to shade; this results in a reduced speed of movement. Table 1 shows the decision table, with notes indicating these interactions.

#### Table 1

The hierarchy 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			
	Thirst	Heat	Hunger	Night
ranges	0-3	0-3	0-2	0-1
Next activity				
To water,	<u>3</u>	· mile	-	-
To shade	≦2	<u>3</u>		
To water	2	≦2		
To shade	<u>2</u> ≦1	2	entering his a	
Graze	≦1	≦1	2	•
(Drink) 4	<u>1</u>	≦1	≦1	
(Shade)	0	1	≦1	-
(Graze)	0	0	<u>1</u>	- I
To camp	0	0	0	1
Rest in situ	0	0	0	0

<sup>1</sup> Movement is exclusive.

3

Hunger level 2 will induce some grazing during movement.

4,5,6 These activities are conditional:

drink if near water;

Any trigger level 1 will induce some movement towards a relevant destination during grazing.

stay in shade if already there; keep grazing if already doing so,

except that, once in camp, sheep cannot leave till morning unless a trigger reaches level 3.

Movement therefore occurs in two contexts - in the course of moving to water, shade or camp, and during grazing. The former involves a choice of destination, and then takes place at a speed dependent on whether grazing occurs en route. Direction of movement in grazing is the least deterministic event in the model, involving a probability function which describes the likelihood of movement in a given direction relative to preceding movement and wind direction. The speed of movement during grazing is normally 0.5 km h , but this is increased in low quality pasture.

Finally, the actual grazing effect on the vegetation is modelled by an intake model, in which pasture availability in a cell determines how much may be eaten from that cell during the time spent in it. The total intake is apportioned between the various forage types present by preference indices for each, which are adjusted over time on the basis of intake rates and hunger status. The proportion of time spent eating is reduced as satiation is approached. The salt and water contents of the forage can affect water usage considerably, so that these are varied somewhat with the condition of the vegetation.

This brief outline skims over many areas where the model includes a considerable amount of process; on an hour-by-hour basis, the only external driving influences in the model are wind, cloud and temperature. The heat balance sub-model mentioned earlier provides the "heat stress" status, and hence predicts when sheep will move to shade, when metabolic rate must be increased in cold conditions and also water use in respiratory cooling (Stafford Smith et al 1985). Thirst is determined from a water balance model, which keeps account of losses in excretion and cooling and gains from drinking and feed contents; this is mentioned again in the next section. Hunger is assessed from rumen fill, where throughput is determined by a model based on Blaxter et al. (1956); intake is a major submodel based on time spent grazing, intake rates, and a selection model. Night-time camping is assumed to take place at such time after dark as there are no other dominant triggers, and then to continue until first light unless thirst reaches an extreme level.

# Proving

Validation of a model of this size is no easy task. Even if the overall output is sensible, it is still possible for components to be indetectably defective under normal conditions, yet crucial under extreme conditions. Validation must first involve verification that individual components and the overall model operate sensibly; sensitivity analyses can help to pick out variables which influence output more than their accuracy would justify. Then the model can be used to predict data collected from the paddock for which it was built, and other paddocks. Finally it is important that predictive runs demonstrate that it can be used to discriminate between the outcomes of alternate management strategies.

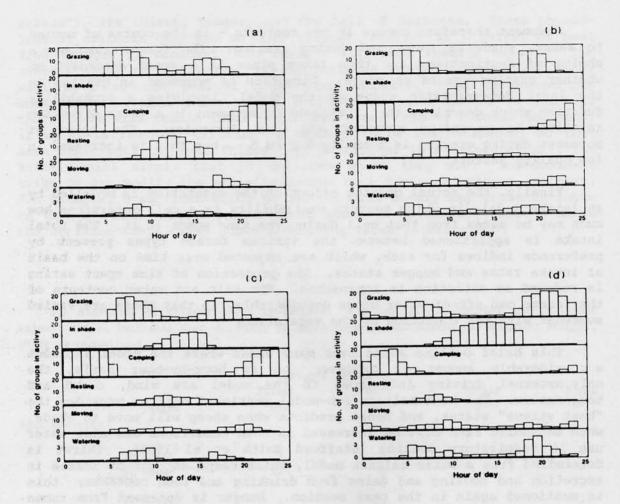


Figure 6: Predicted hourly distributions of activities through the day averaged over 60-day periods in (a) Jul-Aug 1980, (b) Dec-Feb 1980-81, (c) Apr-May 1981 and (d) Dec-Feb 1981-82. Ordinate is the number of the 20 modelled subflocks in the activity.

Patterns of sheep movement had been mapped in Jervoise and two other paddocks for about four days four times a year during 1980-83, resulting in a total of 291 maps in Jervoise, and fewer in the other paddocks. Dung surveys were also carried out across most cells in Jervoise on several occasions (a few small edge cells were not surveyed) to establish measures of activity which were integrated over several weeks instead of being instantaneous (cf. Lange & Willcocks 1978). These surveys avoided shade and camp sites used by sheep, as well as the immediate proximity of the waterpoint, so that they measured extensive, rather than total, activity. The period of study included one of the most severe droughts suffered by the property this century (Martin 1983).

Some patterns of daily activities predicted by the model over 60-day periods using real weather data in 1980-82 are shown in Fig. 6.

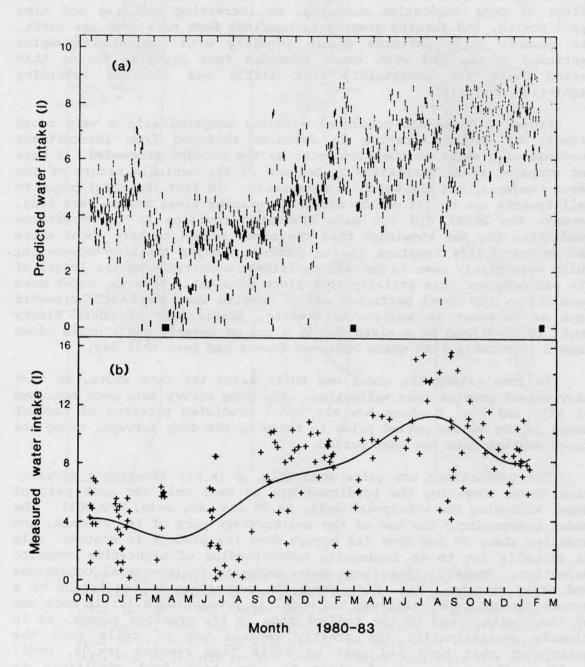


Figure 7: Mean daily water intake by sheep in Jervoise 1980-1983, (a) as predicted daily by the model (each point is one day), (b) as estimated from intermittent readings at the Jervoise water meter (each point is the daily intake since the previous reading averaged over 1 to 60 days; curve is a spline fit).

A comparison of winter and summer activity patterns (Fig. 6a,b) shows notably less use of shade and water in winter; 1981-82 was a period of increasing drought, and the comparison between Fig. 6(b,d) shows the effect of poor vegetation condition on increasing watering and time spent moving, and forcing grazing to continue much more into the night. The general daily patterns accord sensibly with published examples mentioned above, and with those recorded from Jervoise during this period (with the uncertainty that little was recorded regarding night-time activity).

Figure 7 shows how predicted watering compared with a very rough measure of actual watering in Jervoise obtained from intermittent readings of a meter on the waterpoint as the drought proceeded. I have not compared these statistically because of the variable nature of the meter readings, but the match is reasonable. In fact the model began to fail towards the height of the drought: grazing times became very long, because the model did not make adequate provision in these extreme conditions for the knowledge that the sheep seemed to have about where the better forage remained in the paddock. Major trekking movements, which were rarely seen in better conditions, occurred down the length of the paddock, and more activity took place at night. However, under most conditions, the model performed well; despite some stochastic elements such as movement in undirected grazing, predictions of where flocks ought to have been on a given day in a run of several years would often accord reasonably with where observed flocks had been that day.

To some extent the model was built using the data above, so that they cannot provide true validation. The dung survey data were not used at all, and Fig. 8 shows how the model predicted patterns of paddock usage in the 30-day period prior to three of the dung surveys, using the known weather data for that period.

The predictions are quite good (Fig. 8 [a,b]) (Pearson's correlation tests comparing the predicted use of each cell for each pair of maps, excluding the waterpoint cell, r=.76 and .80, n=46, P<0.001). The model overpredicts the use of the southeastern part of the paddock, and modelled sheep do not move far enough down the paddock in winter; this is probably due to an inadequate understanding of night-time campsite selection. However, these were under moderate environmental conditions and early drought; Fig. 8(c) shows the comparison in the height of a severe drought, and, although the model is predicting a little more use of the southern end of the paddock than in the previous summer, it is clearly overestimating the greatly reduced use of cells near the waterpoint that have had most of their feed removed (r=.02, n=46, P>.10). The responses of sheep to very poor feed conditions is inadequately understood.

Better validation comes from predicting the behaviour in another paddock altogether. Nearby Wizzo North (Fig. 9) was mapped at lesser detail than Jervoise, and modelled on a grid cell size of 1x1 km<sup>2</sup>. Wizzo North contains three waterpoints, which were variously available

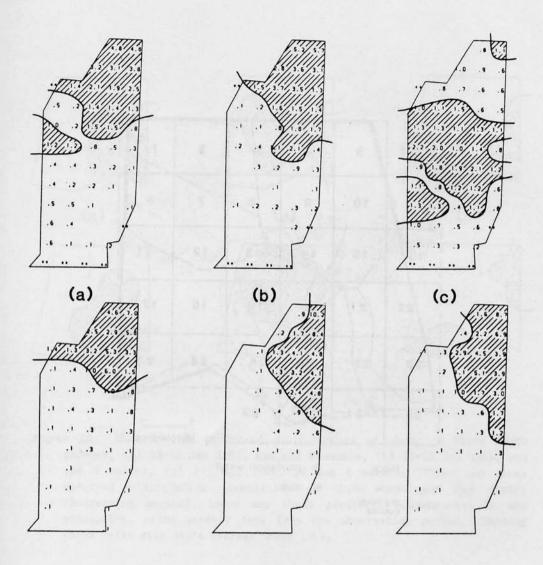


Figure 8: Dung survey data and distribution of extensive behaviour in Jervoise as forecasted by the paddock model for (a) Jul 1981, (b) Feb 1982, (c) Dec 1982. Upper map of each pair is observed dung distribution, lower map is predicted behaviour during the 30-day period prior to the date of the dung survey. \*\* marks cells not surveyed; cells with no activity are left blank. Shading shows cells with above average usage (>1).

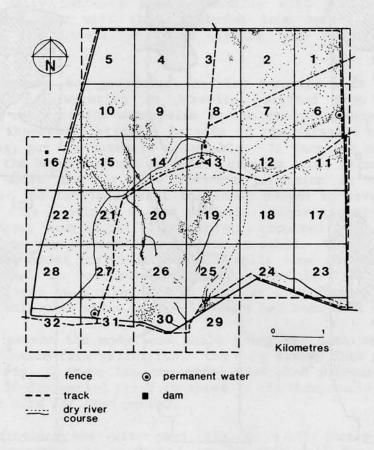


Figure 9: Gridded map of Wizzo North paddock, notation similar to Figure 3.

Note the change in scale. Eastern (E) and southwestern (SW) permanent waters and a near-permanent central dam are shown.

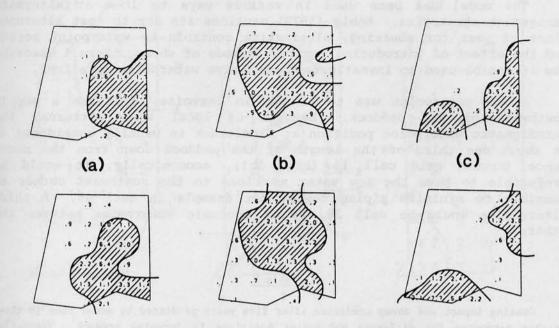


Figure 10: Observed and predicted distributions of sheep in Wizzo North paddock, (a) 23-25 Jan 1981, dam and E waters, (b) 11-13 Jul 1981, dam and E waters, (c) 7-9 Apr 1982, SW and E waters. Upper map shows observed distribution (cumulation of three maps per day during observation period), lower map shows predicted distribution in one simulation, using weather data from the observation period. Shading shows cells with above average usage (<1).

to the sheep. No dung survey data is available, so predictions are compared with the cumulated observations of sheep in each cell over a four day mapping period. A simple model of memory for different waterpoints was added to the paddock model, and Fig. 10 shows how the patterns of movement were predicted in this very different paddock when different waters were available. The patterns are reasonable (r=.51, .46 and .42, n=32, P=.003, .008, .015 respectively for Fig. 10a-c), even during the drought period; it is likely that the shape of Jervoise is more critical than that of Wizzo North, and Wizzo was in any case mapped at less detail.

#### Predictions

The model has been used in various ways to look at alternate management strategies. Noble (1979) mentions its use to test alternate times of year for shearing, alternative controls to waterpoint access and the effect of introducing improved breeds of sheep. Here I describe how it can be used to investigate alternative waterpoint locations.

A new waterpoint was to be put in Jervoise, fed from a supply southwest of the paddock. Because of 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, around grid cell 13 (Fig. 3b); economically, it would be preferable to have the new water as close to the southwest corner as possible to minimise piping costs, for example in cell 45. A third alternative would be cell 28, as an economic compromise between the others.

#### Table 2

Grazing impact and sheep condition after five years predicted by model runs in three 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 text). 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	Mean body weight	
0/0 E	<10%	<50%	(% baseline)	(% overall)
Water at cell	13	Special Spayers		
Normal	3	7	86	107
Dry	6	20	69	87
Wet	3	8	88	120
Water at cell	28			
Normal	2	12	87	109
Dry	3	23	67	88
Wet	2	7	89	120
Water at cell	<u> 45</u>			
Normal	3	10	86	105
Dry	7	21	69	87
Wet	3	6	89	120

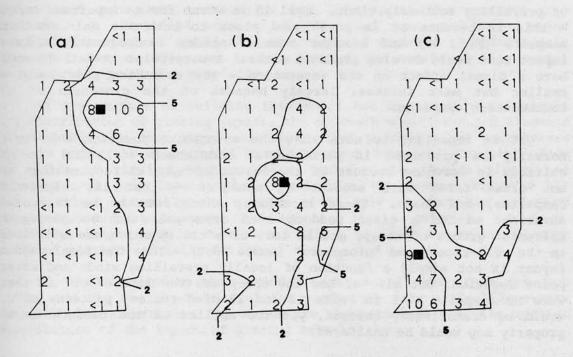


Figure 11: Predicted distribution patterns of subflocks in extensive activities during five years simulation for Jervoise using a moderate weather sequence, with a new waterpoint (heavy square) located at (a) cell 13, (b) cell 28, and (c) cell 45 (see Figure 3(b)). Numbers are mean subflock hours spent per day in each cell during the run; contours are drawn on these values.

The model was run with no sheep for 5-year periods, using simulated weather; several different sequences were selected as baseline runs, and then re-run for each waterpoint position with the normal flock of 260 sheep in the paddock in 10 subflocks. The perennial vegetation biomasses in each cell at the end of the runs were then compared with those obtained without any sheep, and the number of cells counted in which the biomass was less than 10% or 50% of the baseline run. Table 2 shows these for "normal", "wet" and "drought" sequences of years. As an index of productivity, the mean sheep body weights are also compared with the overall mean for all runs. Adopting as a management aim the desire to spread any impact as widely as possible, and minimise "sacrifice areas", the predictions show that fewest cells will be severely damaged (reduced to <10% baseline biomass) with the waterpoint at the compromise position (cell 28); this is associated with a generally wider spread of milder grazing impact (cells reduced to <50% baseline biomass).

Figure 11 shows the predicted distribution patterns for the "normal" weather sequence, where again it can be seen that the central waterpoint permits the most even use of the paddock, despite the effect

of prevailing southerly winds. Cell 13 is worse for an important reason - this is because it is positioned close to both the main northern campsite (Fig. 3a) and a major area of shade; consequently a large impact zone would develop around a water. A waterpoint in cell 45 would have a dismal effect on the vegetation - the sacrifice zone would be smaller but more intense, largely because of the closeness of the southwestern campsite.

It is important to note that the waterpoint position that would normally be preferred in paddocks at Middleback (cell 13) is not suitable in Jervoise because of the layout of spatial factors that are not often taken into account by managers - that is, night-time campsites, and shade. These locations, which seem to be reasonably invariant within a given paddock even over years of occupation by different groups of sheep, act as foci of activity which are additional to the well-recognised "piosphere" (Lange 1969). Thus the ideal paddock layout is not simply a function of locally prevailing winds and water-point location, but also of how the sheep use the landscape; if there were no campsite hill in cells 12 and 17 of Jervoise, patterns of use would be dramatically changed, yet the outline of the paddock on the property map would be unaltered.

As Noble (1975, 1979) found, the difference between runs in productivity (as measured here by body weight) is affected much more by climatic conditions than management; however, there are consistent small differences in weights which parallel the effects predicted on the vegetation. The same was found with other experimental runs of the model in Wizzo North, where I examined the effect of different degrees of active management of waterpoint access. The general result in Wizzo was that a policy of active management - controlling access to waters so that permanent waters were not usually used when ephemeral waters were available - would improve the evenness of use of the paddock in the long-term.

#### Conclusion

The model described above takes about one minute of central processor time on a large computer to run for one year with 10 subflocks. About 85% of this time is spent on the behavioural sub-model, and the remainder on soil moisture and vegetation dynamic sub-models. The theoretical and applied knowledge built into the various process submodels took a considerable time to collect in the initial building of the model. Although the model is designed to be modified for a new paddock with reasonable ease, a non-trivial amount of data about that paddock (mostly spatial, and in particular a vegetation map with initial biomass estimations) is needed.

Clearly the model is most useful as a research tool with the two main purposes of (a) clarifying the gaps in our knowledge about the ecological functioning of the paddock ecosystem, and (b) testing

generalised management strategies and principles on representative paddocks. A simplified version of the model was used in a major simulation project of arid zone properties and regional planning models (Freeman & Benyon 1983), and in this respect the model was also useful as a starting point for simplification.

If the purpose of building this model had been solely to predict the distribution of grazing impact, the approach would have had elements of overkill. In fact there were many other purposes, but nonetheless this is often the most useful form of output from it. Certainly from the point of view of most managers, knowing the precise biomass of vegetation at some location in a paddock to the nearest kilogram has little value; normally the manager needs only to know the order of magnitude of that biomass, and whether it is going up or down. Similarly, images such as Fig. 11 are likely to be much more useful than detailed patterns of daily activity.

So, while accepting that a model such as this has great research value, and may one day be useful for predicting very gradual long-term changes, what alternative approaches are there to modelling the spatial distribution of the impact of grazing animals?

#### REGRESSION MODELS

The model described in the previous section introduced the idea of foci of activity other than the waterpoint. It is well known that the waterpoint is the dominant focus for animal activity in the arid zone, but this raises the possibility that, after this influence has been allowed for, the mean patterns of movement around the paddock may be explained by other features, physical and otherwise. For example, preferred vegetation types, shade and campsites (where they are not too numerous) could also act as significant foci, whilst other factors such as hills and fences could modify patterns by acting as barriers. The effects of these factors would be expected to depend on climate, and perhaps distance from the most important focus, water.

Senft et al. (1983) have shown that mean cattle distributions over a suitable time period in medium-sized paddocks in Colorado could indeed be predicted reasonably on the basis of very simple pasture characteristics; these were distances from water, fences and corners (sometimes expressed as inverses), as well as elevation, aspect, slope, and cactus frequencies. They were able to separate out various activities by summer and winter, and have since examined resting sites and grazing patterns in more detail by including botanical factors (Senft et al. 1985a,b).

The regression model approach requires that the landscape be broken up into some consistent units. Once again, these do not have to be regular in shape, but an explicitly spatial element is most easily introduced by using a regular grid. It is then possible to associate with each cell in a paddock both a measure of observed animal activity and a series of characteristics which describe that cell. These may be spatial criteria such as distance to water, shade or campsites, or local characteristics such as vegetation type, slope or fence presence.

The cell characteristics that are considered for inclusion must depend mainly on our underlying conceptual model, but the process of stepwise multiple regression can then select out the best predictors for the observed data set. Importantly, the observed data set can take various different forms depending on what we wish to predict. I describe two model forms - a simple approach, and then one which is more sophisticated but statistically problematic - before mentioning some of the potential uses of the models so derived.

### Data and methods

Consider the paddock Jervoise, subdivided into 25 ha cells on a regular grid (Fig. 3b). In the course of building and testing the mechanistic model described in the first section, some 291 maps were made of the distribution of sheep subflocks in Jervoise, at various times of day, over three years and in a wide variety of different weather conditions. From these may be selected 174 maps such that any

one day is represented by at most an early morning, middle of the day and evening record.

Various measures of the long-term use of each cell may be obtained by totalling the map records in different ways; the choice of method depends on assumptions about the sheep distributions as well as on the data collection method. Although an approximately constant number of sheep were in the paddock during observations, not all of these were found on every mapping occasion. On the whole, it seemed that most groups would be seen, but not all the numbers counted reliably. However, whereas visibility was more-or-less independent of location in the paddock (with the exception of a few heavily wooded areas), group size had a tendency to decline with distance from water and to change with vegetation conditions (cf. discussion above and Arnold & Pahl [1967]). As a consequence, I use measures dependent on the number of sheep seen rather than the number of subflocks; this has the consequence of allowing for greater discrimination, since the total number of sheep in the paddock was about 250, whilst the numbers of subflocks varied from 2 to about 25. Additionally, the map records could be either converted into percentages and then totalled, or totalled as numbers; I chose the latter since this gave higher weighting to records in which more sheep were seen, and which were therefore more reliable.

Having obtained mean counts of observations in each cell, I used a Generalised Linear Model (McCullagh & Nelder 1983) regression technique in the statistical package GENSTAT (Alvey et al. 1982). Counts are normally modelled using a log-linear model (i.e. a log link function and a Poisson error distribution), but this was found inadequate for the present data, and better results were obtained with an identity link function and Normal error model. This is presumably because a large number of counts had been averaged to obtain each datum, and in any case the sample size is large compared to the probability of finding an animal in a cell, under which circumstances the Poisson distribution tends to the Normal. The results quoted are therefore derived from a "classical least squares" multiple regression.

Most of the models were run on the whole paddock, and then again with the waterpoint cell removed, since the latter usually had a very high usage which skewed the data, and which might have swamped the discrimination of variation elsewhere in the paddock. Stepwise multiple regression was ended when terms were included with coefficients which were not significantly different to zero (t-test, P>0.05).

The original observations distinguished between eight behaviours for each mapped subflock (nighttime camping, daytime resting in the open, resting in the shade, grazing with no more than 25% of the subflock moving, grazing with 25-50% moving, grazing with 50-75% moving, moving with no more than 25% of the subflock grazing, and watering). The impact of the sheep on the paddock differs between these various behaviours; for example, the effect on the vegetation occurs mainly

during grazing, whilst soil compaction occurs during all movement. I therefore use not only total activity as a dependent variable, but also grazing (weighted suitably for different proportions of time spent moving) and movement (which includes all grazing categories without weighting).

Senft et al. (1983) tested about 60 independent variables as potential predictors according to four strict criteria. The predictor had to correlate with the behavioural measure at P<0.001 and with any other predictors at a level at least one order of magnitude less; I have relaxed this criteria, since it is possible for variables correlating much more weakly by themselves to contribute usefully once major effects due to other variables have been removed. Thirdly, they allowed no interactive effects; nor have I here, although I take this up below. Fourthly, the predictors had to be interpretable in some biological sense, a sentiment I wholeheartedly endorse. Various linear and non-linear mathematical forms of the cell characteristics were tested.

Other data was collected in or near Jervoise and used in the models or in validation. This included weather information which was collected partly at a Stevenson screen in the paddock, and partly at the homestead about 20km distant. An index of vegetation condition was derived from three exclosed plots in Jervoise using the photo-comparison method developed for the Koonamore Reserve records (Noble 1977); this placed perennial vegetation condition on a scale of 1-10, and ephemeral green and dry vegetation each on scales of 1-3. These indices correlated reasonably with preceding rainfall, which could be used as a predictor for them.

Dung surveys in Jervoise and observations of sheep in Wizzo North paddock were used for validation, as mentioned in relation to the paddock mechanistic model. The dung surveys were made in most cells of Jervoise at about the same time as the observations, although they represent about one month's accumulation in comparison to several days' mappings. Observations in Wizzo occurred at the same time and under similar weather conditions to those in Jervoise, but are in a paddock of very different shape, and at a coarser scale of 1km² cells. Predictions were made for Wizzo on the basis of 25ha cells, which were then averaged to obtain the predicted use of each 1km² cell. In all cases, the predicted or observed numbers are illustrated after being transformed (after modelling) so that the average activity level in each cell is unitary; this permits the immediate comparison of different measures, but is equivalent to assuming a fixed stocking rate per area if different paddock sizes are compared.

What landscape characteristics ought to be important and in what form? Clearly distance to water should be crucially important in the arid zone, but various different models of animal movement would suggest alternative mathematical forms. For a centrally-placed waterpoint, the assumption that animals walk out approximately at a constant speed leads to a simple inverse relationship between distance from water, d, and time spent at that distance, t(d), i.e.  $t(d) \propto 1/d$ . A model assuming random walk without drift (drift being preference for movement in a particular direction) results in the relationship  $t(d) \propto \exp(d^2)$ , which the present data would be unlikely to discriminate from  $t(d) \propto 1/d^n$ ; increasing amounts of drift (which could be caused by movement into the wind with sheep) results in a functional form nearer the simple inverse. Alternatively, if the paddock is long relative to its width, or sheep walk out on only a few fixed paths, a relationship closer to linear might be expected, i.e. t(d) a a-bd. Testing the linear, inverse and inverse square would therefore seem to be adequate.

The effects of distance to shade and campsites might be expected to parallel the above, although it is less likely that it would be possible to discriminate the inverse relationships from the linear. These foci may act in a different fashion from the waterpoint in any case, since the shade or campsite in use is dependent on previous conditions. Thus, whilst the effect of wind may be to cause drift from a single waterpoint, the selection of a particular shade site may depend on wind direction; then movement out from that shade site will always be in the same direction. In other words, a shade site in the south end of the paddock may only be used in southerly winds, and may therefore always be departed from in a southerly direction. This would tend to result in a linear functional dependency of activity on distance from shade or camp sites. Distance to the nearest shade or camp site was nonetheless tested in all the above forms, and as a presence/absence variable.

Vegetation type is known to affect animal movements. However, the importance of a given vegetation type in a paddock is dependent on what else is present; in other words, what is a preferred vegetation type in one paddock may be unpreferred in another where there is something better. An alternative approach to using vegetation type, therefore, is to ascribe a relative preference rating to each vegetation type; this assumes a linear scale in rating, and is doubtful where different vegetation types occur in very different proportions over the range, but can be easily adjusted for different paddocks, and is often well-known at an approximate, ranked level.

In the following models, I tested both presence/absence variables for each vegetation type, and a preference rating, and the latter was usually included in the multiple regression at the same time as the most significant vegetation type. Consequently, only the preference rating is mentioned below.

Other potential predictors include the presence of fencelines (both north-south and east-west fences were considered) and the influence of heavy timber. The latter was included because it both reduced the available forage biomass (but often without changing the understorey vegetation type), and because it might have reduced visibility during the observations.

## Results over the long-term

The predictors which were found to be significant in various models are shown in Table 3. The actual significances of the terms are shown, as well as the linear correlation of the variable with the behavioural measure when considered by itself.

In general only a few variables were needed to explain a large proportion of the variance. Dominant amongst these is the inverse distance to water, although this is often coupled with an unexpected negative term in the inverse square. Not considered in the discussion above, regarding the effect of distance to water, was the fact that sheep may respond to the vegetation condition which develops as a result of their own grazing impact. If a paddock started off as an even stand of vegetation, any of the patterns of movement mentioned above would result in the area nearest the water being more affected than further out. If the sheep respond to this change, for example by walking faster through an area of poor vegetation, then they will begin to prefer an area a little further out from water.

This process could be expected to continue until some balance is reached between the impact at a given distance and the natural rate of recovery of the vegetation, and would result in a pattern of use which either peaks away from water before tailing off, or is sigmoidal (cf. Graetz & Ludwig 1978), with a plateau in usage close to water (in either case, a higher peak might be expected actually at the waterpoint itself). Such a process certainly occurred during the worsening drought in 1982, as the vegetation was eaten for hundreds of metres out from the waterpoint, and sheep tended to walk through these areas with ever-increasing determination (cf. dung distribution in Fig. 8c). The form of either of these functions can be approximated by a/d-b/d²; this combination occurs in all the models which include the waterpoint cell.

The residuals show no untoward trends. Fig. 12 shows the recorded and predicted patterns of total activity plotted on the paddock outline. The transform applied to the data shows that the real average stocking rate of the waterpoint cell (top right) is about nine times the supposed paddock mean in this case. As a verification, Fig. 13 shows the averaged pattern obtained from all dung surveys in Jervoise during the period of observations. Recall that the dung survey did not include the waterpoint area in the waterpoint cell, and avoided camp and shade sites; excluding the waterpoint, the predicted distributions correlate with the survey well (for total activity, r=.75, for grazing activity, r=.75, both n=46, P<0.0001).

 $\begin{tabular}{ll} \hline \textbf{Table 3} \\ \hline \textbf{Functional form of regression models for various mean activity measures.} \\ \end{tabular}$ 

Predictor	Coefficient	e e	r
TOTAL ACTIVITY: (all cells)			
variance explained: 88.5%			
Constant	-1.56	2.39*	
Inverse d to water	61.03	6.36***	.887
Linear veg pref	-28.33	3.37**	.463
Inv.sq. d to water	1.12	3.01**	.814
Linear d to shade	0.28	2.62*	.209
Fence (presence/absence)	-1.09	2.15*	.091
TOTAL ACTIVITY: (excluding waterpoint	nt)		
variance explained: 69.2%			
Constant	-1.46	2.25*	-
Inverse d to water	55.46	7.06***	.757
Linear veg pref	1.14	3.46**	.514
Linear d to shade	0.28	2.69**	.458
Fence (presence/absence)	-1.12	2.20*	.029
GRAZING: (all cells)			
variance explained: 76.1%			
Inverse d to water	43.87	7.43***	.587
Inv.sq. d to water	-35.56	6.11***	.446
Linear d to shade	-1.32	2.77**	.419
Linear veg pref	0.50	2.48*	.517
GRAZING: (excluding waterpoint)			
variance explained: 71.5%			
Constant	-1.20	3.12**	-
Inverse d to water	36.93	7.71***	.791
Linear d to shade	0.19	3.02**	.494
Linear veg pref	0.56	2.80**	.487
MOVING: (all cells)			
variance explained: 81.9%			
Constant	-1.55	3.32**	=
Inverse d to water	53.59	7.61***	.707
Inv.sq. d to water	-39.15	5.66***	.585
Linear d to shade	0.30	3.95***	.410
Linear veg pref	0.57	2.37*	.488
MOVING: (excluding waterpoint)			
variance explained: 74.3%			
Constant	-1.42	3.08**	1
Inverse d to water	46.14	8.03***	.795
Linear d to shade	0.31	4.07***	.552
Linear veg pref	0.60	2.50*	.464

<sup>\*, \*\*, \*\*\*:</sup> t-test, coefficients significantly different from 0,  $\underline{P}$ <.05, .01, .001 respectively, d.f.=51.

d is distance; inv.sq. is inverse square.

r is coefficient of linear correlation between predictor term and dependent variable (ignoring other predictors); d.f.=51.

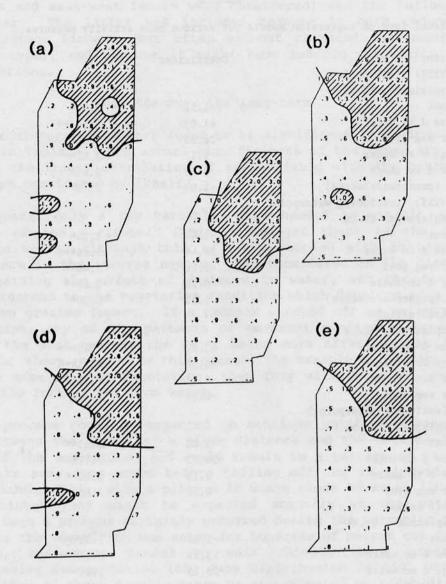


Figure 12: Observed and predicted mean distributions of sheep in Jervoise during 1980-1983; (a) overall cumulated records per cell for all observation days, (b) all activities predicted using all cells, (c) all activities predicted excluding waterpoint cell (NE corner) from model, (d) grazing activity predicted using all cells, (e) moving activity predicted using all cells. Shaded areas show cells with above average usage (>1).

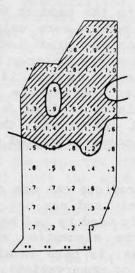


Figure 13: Overall observed distribution of dung in extensive behaviour in Jervoise, averaged from five surveys (1981-1983). \*\* marks cells which were not surveyed, and shading shows cells with above average usage (>1).

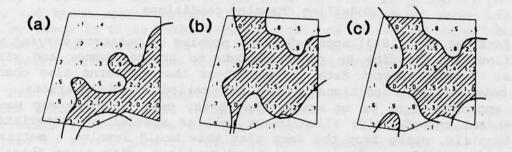


Figure 14: Overall mean observed and predicted sheep distributions in Wizzo North. (a) Cumulated records per cell for all observation days. Predictions are (b) from model using all cells and (c) from model excluding the waterpoint, and one weighted for the availability of different waters in Wizzo (cf. Figure 9). Shaded area shows cells with above-average usage (>1); blank cells had negligible use.

The models were applied to the paddock Wizzo North for validation (Figure 14). For this, the models were calculated independently for each waterpoint in Wizzo, then the predicted maps were totalled with weighting for the period during the observations in which each waterpoint was available to the sheep. In Fig. 14, these numbers have then again been transformed so that the measure averages 1 in each cell. Predictions derived from models created in Jervoise both including and excluding the waterpoint cell are shown: the predicted distributions correlate reasonably with the observed mapped activity (r=.47 and r=.52, n=32, P<0.01).

Notably, the model overpredicts the use of the north-west of Wizzo paddock, which is an open plain and was not much used by sheep; this area was, however, very heavily used by red kangaroos during most of the study and it may be that the assumption mentioned earlier, of the insignificance of native fauna, is here invalidated. When predictions were made of shorter periods of observations, in which only one or two waters were available, the quality of the results is comparable; this suggests that inadequacies are not associated with the weighting procedure. Alternative validation paddocks are being investigated.

Thus this simple approach provides reasonable results, although the reduced accuracy in Wizzo suggests that the model does contain some information specific to Jervoise. However, it was quite obvious during the period that the observations were collected that the sheep's patterns of movement were not constant; they varied both with season and increasing drought. There are certain times such as dry summers and droughts when the most important impact is likely to occur. Can this be accounted for?

# Modelling changing conditions

Senft et al. (1983) approached the problem of patterns varying with conditions by dividing up their records to create summer and winter models. In the present data, it was clear that patterns also changed with between-year conditions during the period of observations. The ideal approach might be to assume that every cell in every map was an independent record, with climatic as well as spatial characteristics. Unfortunately, aside from the fact that this would involve a matrix of over half a million numbers, statistical problems arise since there are clearly different spatial and temporal error functions.

The approach I have taken here seems biologically reasonable, but is doubtful statistically; for this reason I do not suggest that any great weight be given to statistics describing the quality of the models. I have cumulated the observations in a fashion similar to that described above, but separately for the ten field trips on which observations were made. These were separated sufficiently in time to be independent sets of observations; independence in space was assumed above and is biologically reasonable at this scale.

Each trip was then characterised for various environmental variables, including temperatures, season (as a sinuisoidal index varying from +2 in mid-summer to 0 in mid-winter, where "mid-summer" was defined as the hottest time of year - in mid-January - rather than by daylength in December), rainfall in the preceding 90 and 30 days, and the indices of vegetation conditions already mentioned. The approximate wool-length of the sheep was also included, as estimated from a constant growth rate between successive shearings in late February.

The inclusion of climatic and physiological variables allows for a more sophisticated model of the expected effect of the waterpoint, based on the water balance model from the mechanistic model of a paddock. Assuming water to be the over-riding control on movement in the paddock, which the simple model above suggests is the case, the distance that animals are able to move out from water is primarily constrained by the time that it takes them to use up the water obtained in a drink. From this it is possible to derive a model of how this distance might vary, on average, as conditions change; I emphasise that this model involves many assumptions and approximations, but it was developed prior to the regression calculations that follow.

Noble (1975) observed that water obtained from drinking by a sheep is used in salt and other excretions, and evaporative cooling, and is supplemented by water in the vegetation. Assuming that the quality of the water supply is constant, any variable salt intake comes from the diet intake; about 30ml of water is needed by sheep to excrete 1g of salt (Wilson 1966). During the period of observations, perennial water content at Middleback correlated well with the index of perennial vegetation condition; work such as Sharma et al. (1972) indicates that the salt content of some chenopods is reasonably negatively correlated with leaf water content. Thus the perennial index should correlate roughly with water and salt intake when the diet is primarily perennials, and hence approximately linearly with the rate of water use and gain by sheep in these paths between waterings (perennial water content increases with increases in the index, whilst salt content decreases). Other water losses in urine and faeces are reasonably constant.

From the data we collected to validate the heat balance model used in the mechanistic model (Stafford Smith et al. 1985), reasonable regressions (ignoring the subtler effects of wind and cloud) can be obtained to relate panting rates to air temperature for two specific wool lengths ( $r^2>0.7$ , n=76). Evaporative losses in panting can be estimated, and from these, assuming linear interpolation, an approximate relationship (for Middleback conditions and sheep) between evaporative losses (E), air temperature (T) and wool length (L) is,

$$E = 1.6L - 0.07 + T (0.006 - 0.06L) (litre h-1)$$

Now we can write the water balance of a drink of volume W litres as being,

$$W = t (E + u - cV),$$

where u is the constant rate of water losses not associated with salt excretion, V is the vegetation condition index, and c is some roughly constant factor accounting for rate of intake and the relationship of V with necessary salt excretion; then t is proportional to the time for which the sheep can walk out from the water before needing to return for another drink.

If d represents the greatest distance that can be ranged over, then the total sheep time S spent within that distance is proportional to the stocking rate, say N/d2, where N is the total number of sheep (d really varies and S is a probability function rather than a constant as implied this is only a first approximation). Now if sheep walk approximately steadily, d is proportional to t, so t is proportional to N/Sd. Substituting this into the balance equation above, we obtain,

 $W \propto N/Sd (E + u - cV)$ 

or, taking N and W as constants,

 $S \propto (E + u - cV)/d$ 

and substituting for E and adjusting constants,

 $S \propto (L + aT - bTL - cV + k)/d$ .

The various independent variable forms used for the simpler model were included in this multiple regression, as well as the climatic variables. However, interaction terms were also included; these were the products of each of the distance variables with the mean maximum temperature, with wool-length, with the perennial vegetation index, with the index of season, and with the product of wool-length and mean maximum temperature.

# Results for changing conditions

The resulting model is shown in Table 4. Rather remarkably, the terms predicted by the very approximate theoretical model above were the first to fall out; the only exception was that the T/d term was marginally less significant than and replaced by the season/d term. This may be because the seasonal index tracks long-term mean temperatures more accurately than the actual temperatures at the period of observation. In any case all these terms, including even the interaction between wool length and temperature, entered the model with the expected sign of the coefficient. The remaining terms reflect similar factors to the earlier model, with apparently greater discrimination resulting from the inclusion of some time-variable information.

Figure 15 shows the predicted distributions for the weather conditions associated with the dung surveys shown in Fig. 8. The first two are reasonably good (July 1981, r=.79, Feb. 1982, r=.87, n=46, p<.0001), but in the height of the drought in Nov. 1982 the match is valueless (r=0.10, n=46, n.s.). This parallels the inadequacy of the mechanistic paddock model to cope with these extreme conditions (Fig. 8), and again indicates that the assumption that the sheep do not qualitatively modify their behaviour in these conditions is wrong.

 $\frac{{\tt Table}\ 4}{{\tt Functional}\ {\tt form}\ {\tt of}\ {\tt regression}\ {\tt model}\ {\tt for}\ {\tt varying}\ {\tt external}\ {\tt conditions}.$ 

Predictor	Coefficient	t	r
TOTAL ACTIVITY: (all cells)			
variance explained: 71.8%			
Constant	-3.58	5.58***	
Vegn index / d	-15.17	16.14***	.430
Season index / d	55.49	10.00***	.695
Wool length / d	35.47	6.52***	.718
1 / d	200.00	5.36***	.624
Rainfall in preceding 90 days	0.05	5.12***	024
Air temp x wool length / d	-0.92	5.02***	.703
Veg pref	1.14	4.38***	.303
Air temp / d	-4.50	3.33***	.664
Distance to shade x vegn index	0.03	3.16**	.103
1 / d <sup>2</sup>	-22.36	3.05**	.582
Presence of fenceline	-1.00	2.50*	.071

<sup>\*, \*\*, \*\*\*,</sup> r: as Table 3, but d.f.=528, and note comment on statistical reliability in text.

Some predictions were made in Wizzo North paddock (Fig. 16) for the mean weather conditions of one period of mapping (i.e. four days), with suitable weighting for waterpoint availability as in the previous section. Because these models have not included daily wind conditions, there is a considerable variance inherent in these observations which relates to climatic factors not available to the model. However, five out of the seven observation periods are predicted reasonably (r=.50 to .90, n=32, P<.005), two of which are shown; the remaining two are poor, the poorest also being shown (Fig. 16c; r=.09, n=32, n.s.), partly because of unbalanced wind conditions during the observation days.

However, there is a general tendency for the models to over-predict the dispersion of the flock in Wizzo (in comparison to under-predicting this in Jervoise), which again implies that the models are not entirely independent of the spatial layout of Jervoise. One of the Wizzo waterpoint supplies is notably more saline than the water in Jervoise, which may restrict the sheep's movements somewhat as discussed below, but this does not apply to other waters.

d is distance to water; other terms described in text.

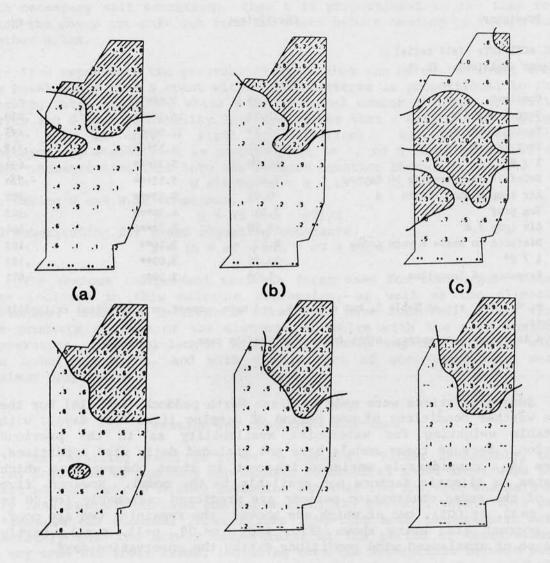


Figure 15: Observed dung and predicted distribution of total activity in Jervoise in (a) Jul 1981, (b) Feb 1982 and (c) Nov 1982. Upper map of each pair is the result of a dung survey of extensive activity (\*\* shows cells not surveyed); lower map shows predicted distribution from the model in Table 4 ("--" shows cells with a small negative predicted activity). Cells with negligible activity are left blank, and shading shows cells with above average activity (>1).

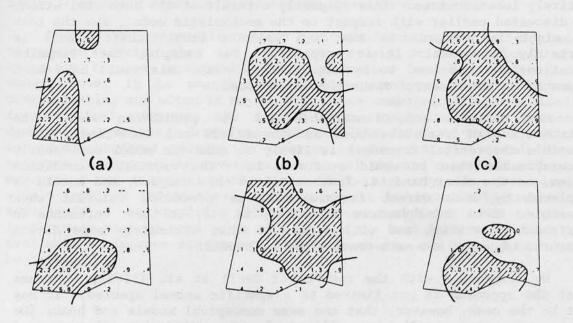


Figure 16: Observed and predicted sheep distribution in Wizzo North during (a) Feb 1982, SW water only, (b) Jul 1981, dam and E waters and (c) Apr 1981, dam and SW water. Upper map of each pair is the cumulated observations per cell over three days at each time; lower map is predicted distribution using the model of Table 4, weighted for waterpoint availability, but not corrected for special environmental conditions (e.g. wind direction) during the observation period. Cells with negligible activity are left blank; shading shows cells with above average activity (>1).

### Discussion

In reality, of course, d in the theoretical model above is not constant, but varies through time, and should really be thought of as a probability distribution. The same applies to most of the other "constants" in the equation, but it appears that the approach does provide a good first approximation to reality. Not only does the derivation suggest the use of predictive terms that are not intuitively obvious, but it can also provide useful insights. For example, the effective drink size, W, that sheep can take on one occasion is affected by water salinity (dissolved salts must be excreted, thus using up part of the drink), so that we may expect t, and hence the effective d, to be increased proportionally around waters of lower salinity than that in Jervoise. This may have been occurring in Wizzo North.

The model still fails in extreme conditions, and is evidently not entirely location-free. This is partly a result of the same limitations as discussed earlier with respect to the mechanistic model, and the lack of night-time records in the data used to create these models is certainly important. It is surprising, for example, that campsite locations never seemed to be significant, since this would have been expected on the basis of the mechanistic model.

How relevant and transferable are the predictors used? The introduction of variables such as temperature and wool-length in a sensible theoretical framework is likely to make the model more easily generalisable than it would otherwise be. The vegetation condition index, on the other hand, is less useful in this respect, and should be replaced by more direct factors such as preceding rainfall when possible. Even these factors are likely to vary in their influence in different vegetation and soil types, so that ultimately some direct measures of water and salt content may be needed.

By comparison with the results of Senft et al. (1983), it seems that the approach is not limited to a specific animal species. It may not be the case, however, that the same conceptual models and hence the same regression predictors will apply for different systems and different scales. Aspect and slope were not important in the gentle landscape of Middleback, for example, whilst these were components of the models from Colorado (also, Mueggler 1965). Work is proceeding on modelling cattle distributions in central Australia (from the data of Low 1972, Muller et al. 1976, Low et al. 1981), where the scale of paddocks is much larger than the sheep paddocks of South Australia, and where differences in vegetation communities are known to be much more important.

I have shown that this model form can predict patterns when conditions are not too extreme, and that it can be valuable in assessing the quality of theoretical models. Because the approach is so explicitly spatial, it has a number of potentially exciting applications, in conjunction with models of other spatial processes. One example is the development of spatial models based on Landsat data which describe erosion patterns and susceptibility to erosion of different parts of the landscape (Pickup & Nelson 1984, Pickup & Chewings 1985); there is scope for these models to be superimposed on grazing pattern models to rapidly assess which areas of an extensive landscape are most likely to be damaged by grazing and, therefore, need to be managed for. This integrative approach will be important in helping select locations for assessment sites in rangeland monitoring, as well as determining how amenable degraded areas may be to expensive rehabilitation work.

Other processes in the landscape also vary spatially in predictable ways; for example, patterns of fire in central Australia are being described from satellite data and related to models of fuel recovery. In the long-run, there are many forms of spatially-oriented data that could be integrated into management plans, to permit the interactive and

cheap testing of different waterpoint or fence locations, and other factors including stocking rates and management intervention.

Despite the reasonable quality and considerable potential of these regression models, they are likely to remain relatively local and certainly require considerable data collection to build. Often, as shown above, it is possible to derive prototypes which are more generalisable, and often it may be that, once combined with other models for practical purposes, the result is no longer sensitive to some doubtful parameters. Sometimes, however, the level of discrimination supposedly produced exceeds the accuracy of the prediction; individual managers (as opposed to government services) who are concerned with the management and integration of many paddocks may only use a relatively simple level of information. Furthermore, it is unavoidably true that some areas of our knowledge will not advance enough for years to come; in the mean time we need to be able to use the best information that is available to improve management. In these cases, another approach may be useful.

### KNOWLEDGE-BASED SYSTEMS

I remarked earlier that all managers use models (usually simplified) of their systems. These may be a result of good or poor understanding, but in either case form the basis for management decisions. These models are rarely explicitly mathematical, and are usually constituted of simple rules based on previous personal experience, and sometimes the experience of others. These rules evolve through a thinking person's lifetime to take account of new experiences, especially in relation to exceptions to previous rules. It is a fact, however, that experiences which are relatively recent tend to overcontribute to the weighting of different rules, especially if these rules are in conflict.

In recent years, "expert systems" structures have been developed in the field of artificial intelligence (e.g. Hayes-Roth et al. 1983). These systems have entered into the common parlance in ways which are not always correct, but basically take the knowledge of an expert in some field and distill a set of rules which permit the application of this knowledge to a particular situation. Initially they were used for problems such as medical diagnoses, but are rapidly finding applications in many other fields.

The first use in ecology seems to have been for a simple model of timing of burning (Starfield & Bleloch 1983), although several applications are under development in Australia (e.g. Noble 1985), and Starfield et al. (1985) have described the beginnings of a model incorporating population dynamics. Systems which specifically aim at the problems of handling spatial processes have also been developed, based on the geographic information system approach of establishing landscape units which function in a similar fashion (Davis & Nanninga 1985). These approaches have not yet incorporated "spatial inferencing", that is, explicit interpretation of actual spatial neighbourhood relations in the sense that the regression models described above do.

The rules that are used in knowledge-based systems neither have to be numeric, nor have to be absolute (Bonissone 1983). Most implementations of these systems permit easy evolution of the knowledge base, and many permit interfacing with sub-models which can use numeric or absolute information. In a general sense, this is precisely how models operate in the manager's head, using non-absolute rules most of the time but occasionally accessing stricter models (especially in the economic field).

Given the unpredictable nature of the arid environment, data needs to be collected over a long period, and to cope with unusual events. In the meantime, as Starfield et al. (1985) remark, managers must still make decisions, so that a working model is needed which both incorporates the best information available, and can readily evolve in the light of new understandings. In most management systems, there are some

managers who are notably better at the task than others (e.g. Lange et al. 1984), so that it should be possible to distill their knowledge into a framework which others may use to increase the mean quality of management.

# An application in its infancy

Concepts such as those of foci of activity other than the water-point could evidently form the basis of a descriptive model of patterns of activity in a paddock. At the simplest level, a reasonable descriptive model could use rules related simply to the location of water, shade and camp sites in relation to fencelines and the accessibility of the paddock. Certain long-term climatic influences can be easily incorporated, such as the influence of prevailing wind directions in relation to paddock orientation.

On the basis of information mentioned earlier in this paper, and from the comments of local managers (e.g. Lange et al. 1984), a first order model of sheep distribution patterns at Middleback could loosely be stated as the following six relationships:

- activity level decreases with distance from water
- local camp or shade sites increase activity
- areas of heavy timber decrease activity
- activity is increased in areas into the prevailing wind direction relative to the waterpoint in use
- summer conditions usually concentrate activity closer to water
- poor vegetation conditions disperse activity from water.

These relationships already contain some information that most managers would not explicitly use in considering animal distributions, and some information that was not incorporated in the models previously described. They can be stated in an explicit model form given the definitions in Table 5 and the rules in Table 6. The clarifications in Table 5 illustrate how additional defining information can be made available about a keyword that the user may not understand. Most of the operators used in the rules ("if", "not", "then", etc.) are self-explanatory, although I have used the operator "order of" to mean the numeric position in an ordered list of possible values to simplify the rules; "activity level" and "distance to water" are then specifically defined as variables with lists of allowable values which are ordered. With a little re-organisation, this model can readily be re-written in a language such as PROLOG.

When run on each grid cell, this model results in the predicted patterns of use in Jervoise and Wizzo North paddocks that are shown in Fig. 17. These may be compared with Figs. 13, 15 and 16, from which it may be seen that the patterns are reasonable. In Jervoise the use of the south-east is greatly overpredicted, because of the presence of shade and a campsite in the area which were relatively under-utilised by the sheep in reality. In both paddocks, the predicted use seems to be

#### Table 5

Definitions and clarifications for model.

Variable	Allowed values	Source
Activity level: (ordered)	very low, low, low-med, med-high, high, very high	infer
Distance to water: (ordered)	very far (>4.5km), far (>2.5km), medium (1-2.5km), near (<1km)	query
Distance to shade:	near (<500m), not near	query
Distance to camp:	near (<500m), not near	query
Distance to fence:	near (<500m), not near	query
Season:	summer, not summer	query
Vegetation condition:	poor, normal	query
Location:	into prevailing wind, opposite prevailing wind, other	query
Timber:	densely wooded, not densely wooded	query

#### Clarifications.

- Campsite: if not otherwise known, is an area up hill, or on a rise to a fence, or in a corner of a paddock.
- Shadesite: is an area with at least 1 tree per ha that is used for shade by sheep, when less than half of the paddock contains such densities.
- Poor vegetation condition: is vegetation conditions after at least 1 year of less than 75% "mean" rainfall, when the paddock has continued to be stocked during this time.
- Location into (or opposite) prevailing wind: is location in paddock such that the direction from (or to) the waterpoint in use is within 45° of the prevailing wind direction over period concerned.
- Densely wooded: is trees with more-or-less intersecting canopies, so that understorey vegetation is significantly thinned.

### Table 6

### Decision rules for model.

1. Activity level

is same order as (water effect + camp/shade effect + season effect + vegn condition effect + fenceline effect + timber effect)

2. Water effect

is order of distance to water

3. Camp/shade effect

is 1 if distance to shade is near or if distance to camp is near

4. Season effect

is 1 if season is summer and distance to water is near,

is -1 if season is summer and distance to water is far or very far

5. Vegn condition effect

is -1 if vegetation condition is poor and distance to water is near,

is 1 if vegetation condition is poor and distance to water is medium or far

6. Location effect

is 1 if location is into prevailing wind and distance to water is far or very far,

and

is -1 if location is opposite prevailing wind and distance to water is far or very far

7. Fenceline effect

is 1 if distance to fence is near and distance to water is near

8. Timber effect

is -1 if timber is heavily wooded

"same order as i" means the i'th element of an ordered set of N elements, where i is restricted to values inclusively between 1 and N.

"order of" means the numeric position in an ordered set of allowed values.

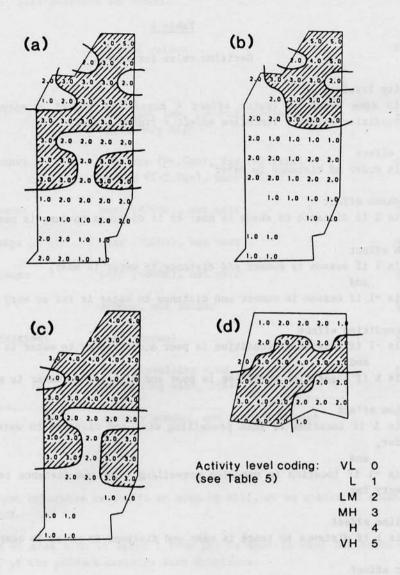


Figure 17: Predicted activity levels in Jervoise (a,b,c) and Wizzo North (d) according to knowledge-based model (Tables 5 & 6). (a) Season not summer, vegetation normal, prevailing wind from south (overall mean conditions at Middleback, cf. Fig. 13), (b) season summer (normal Middleback summer, cf. Fig. 15 (b)), (c) season summer and vegetation poor (moderately-droughted summer at Middleback cf. Fig. 15 (c) in extreme drought), (d) as (a) but in Wizzo using dam and SW waters (cf. Fig. 16 (c)). Shading shows cells with greater than medium activity level.

over-dispersed, which is a result of not weighting proximity to water more heavily than other factors. Where the reasons are understood, and the accuracy warrants it, these types of limitations can be corrected in a more sophisticated version.

This is a very simple model with a single goal (activity level). However, it can evolve to account for more factors at a given site, such as greatly preferred or avoided vegetation types or the effects of wool length on within year variation; some factors such as locally prevailing wind direction could be set as a default, or obtained from a data file; and, for the purposes of repetitive goals such as checking every cell in a paddock, certain spatial units can be equivalenced to one another for characteristics such as vegetation type, so that deductions relating to these characteristics need only be made once for each type rather than for each cell (such approaches are described admirably in the context of the expert system shell EMYCIN by Davis & Nanninga [1985]).

As multiple alternative goals are included - such as testing the effect of different waterpoint position, and testing movement impact independently of grazing impact, many of the same rules will apply to each, so that the system gains some compactness with increasing application. To complete the spatial approach, the next stage is to integrate this system into a simple description of a paddock provided by the user (e.g. using screen graphics and cursor keys), so that predicted patterns of use can rapidly be provided using a mixture of regression models and the knowledge-base about a specific region.

This approach is being developed for cattle paddocks in central Australia. With spatial scales which are even larger than the sheep paddocks of South Australia, management is tied more complicatedly to factors which change their relative importance through time. Cattle movement patterns certainly depend on vegetation conditions and time since rain in ways that are now broadly understood but which are not yet modelled in detail (Low et al. 1981). It may be that a knowledge-based approach will be the best that is possible in this less trivial system.

Finally, although these models may not be very complex, it is worth noting two of their features. Firstly they can take the best ideas in current management, as combined with such scientific understanding as exists, and as a consequence the average quality of management should improve even if the best management cannot. Secondly, the approach causes a manager to at least consider all the factors that appear to be important; he may then ignore them if he wishes, but this must be done in a conscious fashion.

#### CONCLUSTONS

Most scientific studies in rangelands are undertaken (or at least funded) with the ultimate aim of useful application to some form of land management. This paper has discussed how models can be used both in assessing and developing the scientific studies, and in applying the results of these studies to management. In considering the application of knowledge which is derived from the ivory tower of science, or even from the experience of better managers, it is important not to lose sight of the fact that managers are constrained by many factors which are unrelated to good ecological management.

Not only does the application of good ecology face conceptual blocks, such as the tendency to manage by animal productivity rather than by the condition of the soil or vegetation resource on which this productivity depends; but also there are many social and societal factors which limit this application, including tax structures, government priorities and economic exigencies (Young et al. 1984). The Northern Territory of Australia, for example, retains antiquated pastoral legislation which was oriented towards encouraging settlement last century, and which enforces a minimum stocking covenant instead of a maximum stocking rate. Similarly, economic structures rarely encourage managers to sell stock in a widespread drought, and drought subsidies often support those who have managed their land least well.

The challenge to those who try to make good ecological management strategies available is to demonstrate that these are compatible with, if not essential for, long term economic productivity. Economic assessment of existing systems tends to examine minor changes and optimise current management procedures; rarely does it concern itself with radical alterations to overall management strategies and philosophy. Predictive models offer an important way of testing out and assessing major changes to management strategies, which may result in better long term productivity, but are too expensive to make on a trial and error approach in the real world.

The scale of arid regions demands that allowance be made for heterogeneity within, rather than between, management units. A single point process cannot usually be extrapolated to do this, since spatial interactions between neighbouring point processes become fundamentally important. The distribution of grazing impact in rangelands is an excellent example of this, since the distribution is neither even across a management unit, nor necessarily determinable at one point independently of others.

Most arid zones cannot be conceptually modelled as a regular cyclic system with occasional disturbances, but are usually in a unique condition as a result of specific sequences of events (unique at least within one manager's working lifetime). The need to account for these irregular interactions in testing different management strategies, at the same time as including spatial processes, can be approached valuable

with models. In this, extreme and unusual conditions are often more important than "average" conditions; the models described in this paper go some way to coping with "non-average" conditions, but the more detailed a model is, the less adequate it seems to be under extreme conditions.

From the research point of view, detailed mechanistic models encourage the formalisation of our understanding of a system, and point up the inadequacies in our knowledge. They also provide a useful starting point for simplification into more descriptive models, which are, nonetheless, then based upon a sounder understanding of the underlying processes (cf. the call for more sensible "direct environmental gradients", which are derived from simpler indirect gradients by the application of known non-linear functions, by Austin [1971]). The mechanistic model of a sheep paddock described herein provided an example of this development; from this, sensible, but non-intuitive, predictors were selected for a regression model of sheep distributions on the basis of the understanding of water balance required for the paddock behaviour model.

Application models can vary greatly in the degree of incorporated detail. Aside from being expensive to run, detailed models are inclined to lead the scientist to the conclusion that "more study is needed"; in the meantime, however, management of the rangelands must go on. From the point of view of that management, therefore, the best information that we currently have must be made available in a form which can evolve as our understanding improves in the future. A knowledge-based model approach may be important in this effort, especially since it can link heuristic, uncertain rules with an understanding of mechanism where this is available. Management strategies derived from this approach may never be better than the best currently known, but the average quality of management must rise if they are implemented.

### References

- Allden, W.G. & Whittaker, I.A.McD. (1970). The determinants of herbage intake by sheep: the interrelationship of factors influencing herbage and availability. Aust. J. Agric. Res. 21, 755-766.
- Alvey, N., Galwey, N. & Lane, P. (1982). An introduction to GENSTAT. Academic Press, London, 152pp.
- 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. (1964). Some principles in the investigation of selective grazing. Proc. Aust. Soc. Anim. Prod. 5, 258-271.
- 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. (1984). Comparison of the time budgets and circadian rhythms of maintenance activities in sheep, cattle and horses grouped together. Appl. Anim. Behav. Sci. 13, 19-30.
- Arnold, G.W., Noy-Meir, I., & Galbraith, K.A. (1982). A process-based model of herbage consumption by grazing sheep. CSIRO Div. Land Res. Manag. Tech. Memo. 82/10. 27pp.
- Arnold, G.W. & Dudzinski, M.L. (1978). Ethology of Free-Ranging Domestic Animals. Elsevier, Amsterdam. 198pp.
- Arnold, G.W. & Pahl, P.J. (1967). Sub-grouping in sheep flocks. Proc. Ecol. Soc. Aust. 2, 183-189.
- Austin, M.P. (1971). Role of regression analysis in plant ecology. Proc. Ecol. Soc. Austr. 6, 63-75.
- Bakker, J.P., de Leeuw, J. & van Weiren, S.E. (1983). Micro-patterns in grassland vegetation created and maintained by sheep-grazing. Vegetatio 55, 153-161.
- 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.
- Belovsky, G.E. (1978). Diet optimisation in a generalist herbivore: the moose. Theor. Pop. Biol. 14, 105-134.
- Belovsky, G.E. (1984). Herbivore optimal foraging: a comparative test of three models. Am. Nat. 124, 97-115.
- Bender, E.A., Case, T.J. & Gilpin, M.E. (1984). Perturbation experiments in community ecology: theory and practice. Ecology 65, 1-13.
- 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., Wainman, F.W. & Wilson, R.S. (1961). The regulation of food intake by sheep. Anim. Prod. 3, 51-61.
- Bonissone, P.P. (1983). Coping with uncertainty in expert systems: a comparative study. Proc. Am. Control. Conf., San Fransisco. pp. 1230-1232.
- Bowns, J.E. (1971). Sheep behaviour under unherded conditions on mountain summer ranges. J. Range Manag. 24, 105-109.
- Cloudsley-Thompson, J.L. (1974). The expanding Sahara. Envir. Conserv. 1, 5-14.
- Cooper, S.M. & Owen-Smith, N. (1984). Chemical factors influencing food selection by browsing ungulates in a South African savanna. Working paper, 2nd Int. Rangel. Congr., Adelaide, Australia.
- Davis, J.R. & Nanninga, P.M. (1985). GEOMYCIN: towards a geographic expert system for resource management. J. Envir. Manag. 20, 333-347.
- 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., Pahl, P.J. & Arnold, G.W. (1969). Quantitative assessment of grazing behaviour of sheep in arid areas. J. Range Manag. 22, 230-235.

- Emlen, J.M. (1966). The role of time and energy in food preference. Am. Nat. 100, 611-617.
- Engen, S. & Stenseth, N.C. (1984). A general version of optimal
  foraging theory: the effect of simultaneous encounters. Theor.
  Pop. Biol. 26, 192-204.
- Forrester, J.W. (1971). World dynamics. Wright-Allen Press, Cambridge, Mass.
- Forman, R.T.T. (1981). Interaction among landscape elements: a core of landscape ecology. Proc. Int. Congr. Neth. Soc. Landscape Ecol., Veldhoven. Pudoc, Wageningen. pp. 35-48.
- Freeman, T.G. & Benyon, P.R. (1983). Pastoral and social problems in a semi-arid environment. CSIRO, Canberra and UNESCO, Paris, 575pp.
- 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, pp. 211-236.
- Goodall, D.W. (1971). Extensive grazing systems. In: "Systems analysis in agricultural management." (ed. J.B. Dent & J.R. Anderson). John Wiley & Sons, Sydney. pp. 173-187.
- Anderson). John Wiley & Sons, Sydney. pp. 173-187.

  Goodall, D.W. (1974). Problems of scale and detail in ecological modelling. J. Envir. Manag. 2, 149-157.
- Goodall, D.W. (1981). The modelling of arid ecosystem dynamics. In: Goodall & Perry, op. cit. pp. 385-409.
- Goodall, D.W. & Perry, R.A. (eds.) (1981). Arid land ecosystems: structure, functioning and management. Vol. 2. C.U.P., Cambridge.
- Graetz, R.D. & Ludwig, J.A. (1978). A method for the analysis of piosphere data applicable to range assessment. Aust. Rangel. J. 1, 126-136.
- Griffin, G.F. & Friedel, M.H. (1985). Discontinuous change in central Australia: some implications of major ecological events for land management. J. Arid Envir. 9, 63-80.
- Harper, J.L. (1982). After description. In: "The plant community as a
  working mechanism." (ed. E.I. Newman) British Ecological Soc.,
  London. pp. 11-25.
- Harrington, G.N., Friedel, M.H., Hodgkinson, K.C. & Noble, J.C. (1984).
  Vegetation ecology and management. In: Harrington, Wilson &
  Young, op. cit. pp. 41-62.
- Harrington, G.N., Wilson, A.D. & Young, M.D. (eds.) (1984). Management of Australia's Rangelands. CSIRO, Melbourne, Australia. 354pp.
- 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.
- Hayes-Roth, F., Waterman, D.A. & Lenat, D.B. (eds.) (1983). Building Expert Systems. Teknowledge series in knowledge engineering. Addison-Wesley, Reading, Massachusetts.
- 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.
- Innis, G.S. (ed.) (1978). Grassland simulation model. Ecological Studies, 26. Springer-Verlag, New York. 298pp.

- Jessop, J. (ed.) (1981). "Flora of Central Australia." (Australian Systematic Botany Society) Reed, Sydney, 537pp.
- Karrar, G. & Stiles, D. (1984). The global status and trend of desertification. J. Arid Envir. 7, 309-312.
- Kenney, P.A. & Black, J.L. (1984). Factors affecting diet selection by sheep. I Potential intake rate and acceptability of feed. Austr. J. Agric. Res. 35, 551-563.
- Lange, R.T. (1969). The piosphere: sheep track and dung patterns. J. Range. Manag. 22, 396-400.
- Lange, R.T., Nicolson, A.D. & Nicolson, D.A. (1984). Vegetation management of chenopod rangelands in South Australia. Aust. Rangel. J. 6, 46-54.
- 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.
- Levins, R. (1966). Strategy of model building in population biology.

  American Sci. 54, 421-431.
- Loewer, O.J., Smith, E.M., Gay, N. & Fehr, R. (1983). Incorporation of environment and feed quality into a net energy model for beef cattle. Agricultural Systems 11, 67-94.
- 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. (1979). Spatial and temporal distribution and behaviour. In:
  "Arid land ecosystems: structure, functioning and management Vol.
  1." (ed. D.W. Goodall & R.A. Perry), CUP, Cambridge. pp. 769-795.
- Low, W.A., Dudzinski, M.L. & Muller, W.J. (1981). The influence of forage and climatic conditions on range community preference of shorthorn cattle in central Australia. J. Appl. Ecol. 18, 11-26.
- 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, pp. 697-707, Morges, Switzerland.
- McFarland, D.J. & Silby, R.M. (1975). The behavioural final common path. Phil. Trans. Roy. Soc. Lond (B). 270, 265-293.
- Martin, B. (1983). The 1982 drought in Australia. Desertification Control Bull. 9, 23-30.
- McCullagh, P. & Nelder, J.A. (1983). Generalized Linear Models. Chapman & Hall, London. 261pp.
- Michie, D. (ed.) (1982). Introductory readings in expert systems. Gordon & Breach, New York.
- Mueggler, W.F. (1965). Cattle distribution on steep slopes. J. Range.
  Manag. 18, 255-227.
- Muller, W.J., Low, W.A., Lendon, C. & Dudzinski, M.L. (1976). Variation in grazing patterns of free-ranging cattle in a semi-arid area. Proc. Aust. Soc. Anim. Prod. 11, 461-464.
- 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, pp. 125-143.
- Noble, I.R. (1985). Fire effects, vital attributes and expert systems. In: "Towards an expert system for fire management at Kakadu National Park." (ed. J. Walker, J.R. Davis & A.M. Gill) CSIRO Div. of Water & Land Res., Tech. Memo. 85/2, Canberra. pp. 96-103.
- Noble, I.R. & Crisp, M.D. (1980). Germination and growth models of short-lived grass and forb populations based on long term photopoint data at Koonamore, South Australia. Israel J. Bot. 28, 195-210.
- Noy-Meir, I. (1981). Spatial effects in modelling of ecosystem dynamics. In: Goodall & Perry, op. cit. pp. 411-432.
- Owen-Smith, N. & Novellie, P. (1982). What should a clever ungulate eat? Am. Nat. 119, 151-178.
- Pickup, G. & Chewings, V.H. (1985). Random field modelling of spatial variations in flat alluvial landscapes in arid Central Australia. Ecol. Modelling, in press.
- Pickup, G. & Nelson, D.J. (1984). Use of Landsat radiance parameters to distinguish soil erosion, stability and deposition in arid central Australia. Remote Sensing of Envir. 16, 195-209.
- 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.
- Schoener, T.W. (1971). Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2, 369-404.
- Senft, R.L., Rittenhouse, L.R. & Woodmansee, R.G. (1983). The use of regression models to predict spatial patterns of cattle behaviour. J. Range Manag. 36, 553-557.
- Senft, R.L., Rittenhouse, L.R. & Woodmansee, R.G. (1985a). Factors influencing patterns of cattle grazing behaviour on shortgrass steppe. J. Range Manag. 38, 82-87.
- Senft, R.L., Rittenhouse, L.R. & Woodmansee, R.G. (1985b). Factors influencing selection of resting sites by cattle on shortgrass steppe. J. Range Manag. 38, 295-299.
- 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.
- Shugart, H.H. & Noble, I.R. (1981). A computer model of succession and fire response of the high altitude eucalyptus forests of the Brindabella Range, Australian Capital Territory. Aust. J. Ecol. 6, 149-164.
- Squires, V.R. (1974). 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. (1976). 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.

- Stafford Smith, D.M. (1984). Behavioural Ecology of sheep in the Australian Arid zone. Unpubl. Ph.D. thesis, Australian National University, Canberra. 345pp.
- Stafford Smith, D.M., Noble, I.R. & Jones, G.K. (1985). A heat balance model for sheep and its use to predict shade-seeking behaviour in hot conditions. J. Appl. Ecol., in press.
- Starfield, A.M. & Bleloch, A.L. (1983). Expert systems: an approach to problems in ecological management that are difficult to quantify. J. environ. Manag. 16, 261-268.
- Starfield, A.M., Owen-Smith, N. & Bleloch, A.L. (1985). A rule-based population model for adaptive management. S. Afr. J. Wildl. Res. 15, 59-62.
- Taylor, J.A., Hedges, D.A. & Whalley, R.D.B. (1984). The occurrence, distribution and characteristics of sheep camps on the Northern Tablelands of New South Wales. Austr. Rangel. J. 6, 10-16.
- 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.
- Westoby, M. (1974). An analysis of diet selection by large herbivores. Am. Nat. 108, 290-304.
- Wight, J.R., Hanson, C.L. & Springer, E.P. (1984). SPUR: a model for simulation of production and utilisation of rangelands. Working paper, 2nd Int. Rangel. Congr., Adelaide, Australia.
- Willatt, S.T. & Pullar, D.M. (1983). Changes in soil physical properties under grazed pastures. Austr. J. Soil Res. 22, 343-348.
- 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. & Harrington, G.N. (1984). Grazing ecology and animal production. In: Harrington, Wilson & Young, op. cit. pp. 63-78.
- Wilson, A.D. & Harrington, G.N. & Beale, J.F. (1984). Grazing Management. In: Harrington, Wilson & Young, op. cit. pp. 129-140.
- Woods, L. (1983). "Land degradation in Australia." A.G.P.S., Camberra, 105pp.
- Young, M.D., Gibbs, M., Holmes, W.E. & Mills, D.M.D. (1984). Socioeconomic influences on pastoral management. In: Harrington, Wilson & Young, op. cit. pp. 79-94.