Copyright in relation to this thesis*

Under the Copyright Act 1968 (several provisions of which are referred to below), this thesis must be used only under the normal conditions of scholarly fair dealing for the purposes of research, criticism or review. In particular, no results or conclusions should be extracted from it, nor should it be copied or closely paraphrased in whole or in part without the written consent of the author. Proper written acknowledgement should be made for any assistance obtained from this thesis.

Under Section 35(2) of the Copyright Act 1968 'the author of a literary, dramatic, musical or artistic work is the owner of any copyright subsisting in the work'. By virtue of Section 32(1) copyright 'subsists in an original literary, dramatic, musical or artistic work that is unpublished' and of which the author was an Australian citizen, an Australian protected person or a person resident in Australia.

The Act, by Section 36(1) provides: 'Subject to this Act, the copyright in a literary, dramatic, musical or artistic work is infringed by a person who, not being the owner of the copyright and without the licence of the owner of the copyright, does in Australia, or authorises the doing in Australia of, any act comprised in the copyright'.

Section 31(1)(a)(i) provides that copyright includes the exclusive right to 'reproduce the work in a material form'. Thus, copyright is infringed by a person who, not being the owner of the copyright, reproduces or authorises the reproduction of a work, or of more than a reasonable part of the work, in a material form, unless the reproduction is a 'fair dealing' with the work 'for the purpose of research or study' as further defined in Sections 40 and 41 of the Act.

Section 51(2) provides that "Where a manuscript, or a copy, of a thesis or other similar literary work that has not been published is kept in a library of a university or other similar institution or in an archives, the copyright in the thesis or other work is not infringed by the making of a copy of the thesis or other work by or on behalf of the officer in charge of the library or archives if the copy is supplied to a person who satisfies an authorized officer of the library or archives that he requires the copy for the purpose of research or study'.

*'Thesis' includes 'treatise', dissertation' and other similar productions.
The Dynamics of Feral Pig Populations in the Semi-arid Rangelands of Eastern Australia

by

David Choqueonot

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

University of Sydney

October, 1994
STATEMENT OF ORIGINALITY

Except where otherwise stated, the work in this thesis is my own

David Choquet
25/10/1994
SUMMARY

(1) A great deal of interest and some controversy has surrounded the role of food availability in the limitation and regulation of large herbivore populations. This study tested the applicability of two hypotheses used to understand and predict variation in the abundance of large herbivores, to populations of feral pigs inhabiting the semi-arid rangelands of inland Australia. The intrinsic food hypothesis proposes that the density of herbivores is regulated at or around some equilibrium ($K$) through density dependent variation in the rate of change in their abundance ($r$), through the effect of per capita food availability on their demographic rates. The extrinsic food hypothesis, proposes that herbivores do not affect variation in the abundance of their food resources and hence are not regulated through the effects of density dependent variation in per capita food availability on $r$.

(2) The applicability of the two hypotheses to feral pig populations was tested using a manipulative experiment, in which the abundance of pigs on six sites in the rangelands was reduced to one of three levels ($x2$ replicates) annually, and the abundance of pigs and their primary food resource (non-improved pastures), was monitored quarterly over two and a half years. Depending on the tendency of the pig/pasture grazing system toward equilibrium, the intrinsic food hypothesis predicted either a negative or non-significant relationship between rate of change in pig abundance and pig density. Regardless of this tendency, the intrinsic food hypothesis also predicted a negative relationship between pasture availability and pig density and a positive relationship between rate of change in pig abundance and pasture availability. The extrinsic food hypothesis predicted non-significant relationships for both rate of change in pig abundance and pasture biomass with pig density, and a positive relationship between rate of change in pig abundance and pasture availability.

(3) Despite large fluctuations in both pig and pasture abundance over the course of the experiment, no significant relationship between pig density and either rate of change in pig abundance (measured as the annual exponential rate of increase ($r$) for each study site) or pasture biomass could be demonstrated. However, a strong positive relationship between pasture biomass lagged three months and $r$ was detected. Collectively these results suggest that pig populations in the rangelands conformed to the extrinsic food hypothesis, their abundance being limited but not regulated by food availability.
(7) The relationship between pasture biomass and $r$ was used to predict the numerical response of feral pigs to variation in pasture biomass. The response indicated that pigs increase in abundance when pasture biomass exceeds 251 kg/ha, approaching a maximum intrinsic rate of increase ($r_m$) of 0.68 when pasture biomass exceeded about 600 kg/ha. When pasture biomass was below 251 kg/ha, pig abundance declined at an increasing rate approaching a maximum exponential rate ($a$) of -2.045.

(8) Two graze down trials were conducted in order to measure variation in pasture intake rate of pigs as they grazed pasture to progressively lower biomass (the functional response). The predicted response indicated that pigs were unable to graze pasture below a biomass of 92 kg/ha, while maximum intake rates were not approached until pasture biomass exceeded 700 kg/ha.

(9) The numerical and functional response of pigs were used to predict temporal variation in their abundance using a stochastic model which simulated the interaction of pigs, pasture and other herbivores (represented in the model by red kangaroos). The model was driven by stochastic rainfall which determined pasture growth and dieback, the prevailing biomass of which determined pasture offtake by pigs and other herbivores, and rates of change in their respective abundance. The relative contribution of offtake by pigs and other herbivores to variation in pasture biomass and consequent variation in pig abundance was assessed by alternately including or omitting their respective functional responses (i.e., their capacity to influence pasture biomass). The modelling indicated that the combination of high year-to-year variation in pasture biomass (due to stochastic variation in rainfall and pasture offtake by other herbivores) and the extreme asymmetry in their numerical response limited the average density of pigs which in turn constrained their ability to influence pasture availability. The lack of influence pigs appear to exert over the abundance of their food resources may explain why no evidence of intrinsic food shortage was found in the manipulative experiment.

(10) The absence of any apparent mechanism linking density to $r$ through per capita food availability suggests that pig populations in the rangelands are essentially unregulated. Despite this, the simulation modelling suggests that pigs persist in this highly unpredictable environment, solely by virtue of their impressive capacity for increase when seasonal conditions allow.
(11) Variation in maximum rates of decline \((\alpha)\) among the six pig populations used in the manipulative experiment was related to the availability of floodplain habitat on the six study sites. The mechanisms underlying this relationship are unknown, but may be related to foraging constraints arising from a need to remain in the vicinity of floodplain habitat in order to thermoregulate during hot, dry weather. The effect of variation in \(\alpha\) on pig density, probability of population persistence and time to population extinction was explored by extending the simulation models developed previously. This additional modelling suggested that the availability of floodplain habitat, through its effect on rates of change in pig abundance, may have important consequences for the distribution and abundance of pigs in the semi-arid rangelands.

(12) The results of this study suggest that rather than being discrete limiting mechanisms, intrinsic and extrinsic food shortages may represent either end of a continuum of interactions between herbivores and their food resources. The position of a grazing system along such a continuum depends on the intrinsic variability of the grazing systems environment and the efficiency of the reciprocal effect herbivores and vegetation exert over each others abundance through the functional and numerical responses. These competing influences determine the degree of environmental buffeting to which the grazing system is subjected and the strength of feedback mechanisms which work to overcome this buffeting. Pig populations inhabiting Australia's rangelands appear able to persist despite the extreme variability of their environment because they have a highly efficient numerical response. Where the efficiency of this response is reduced, such as in areas containing little floodplain habitat, the persistence of pig populations is compromised.
ACKNOWLEDGMENTS

The research upon which this project is based was supported financially by the Australian Wool Research & Development Corporation, the Wildlife Monitoring Unit of the Australian Nature Conservation Agency and the Wildlife Exotic Disease Preparedness Program of the Bureau of Resource Sciences. NSW Agriculture provided additional financial and logistic support. New South Wales Parks & Wildlife Service, Robert Bartlett, Barry Barraclough, Leon Zanker and Ross Bartlett permitted me access to land in their care and to the pigs which resided there. It is with pleasure that I acknowledge the assistance of the many individuals who contributed to various aspects of this study and in particular Brian Lukins for assistance with the often arduous fieldwork. My supervisors Glen Saunders and Chris Dickman provided advice and encouragement during the course of the project. Nick Dexter, Dave Mula, Barry Kay, Terry Korn, Mark Fosdick, Mark Rogers and Dave Schutt assisted in the field; Peter O'Brien, Bob Kilgour and Pat Taylor in various bars; and Bob Mould and Kings X everywhere. I thank Judy Caughley and Jim Hone for their incisive comments on an earlier draft of the thesis and whoever wrote @Risk for making the population modelling substantially less tedious. Finally I thank Sylvana Iracema and Homer for providing something of a sane environment in which to write this thesis.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Statement of originality</td>
<td>ii</td>
</tr>
<tr>
<td>Abstract</td>
<td>iii</td>
</tr>
<tr>
<td>Acknowledgments</td>
<td>vi</td>
</tr>
<tr>
<td>Table of contents</td>
<td>vii</td>
</tr>
<tr>
<td>Chapter 1. Background to the study</td>
<td>1</td>
</tr>
<tr>
<td>1.1 Regulation and limitation of animal population abundance</td>
<td>1</td>
</tr>
<tr>
<td>1.1.1 Intrinsic and extrinsic density dependent factors</td>
<td>3</td>
</tr>
<tr>
<td>1.2 Regulation and limitation of large herbivore populations</td>
<td>4</td>
</tr>
<tr>
<td>1.2.1 The intrinsic food hypothesis</td>
<td>6</td>
</tr>
<tr>
<td>1.2.1.1 Single-species models</td>
<td>7</td>
</tr>
<tr>
<td>1.2.1.2 Interactive models</td>
<td>12</td>
</tr>
<tr>
<td>1.2.1.3 Differences between single-species and interactive models</td>
<td>24</td>
</tr>
<tr>
<td>1.2.2 The extrinsic food hypothesis</td>
<td>27</td>
</tr>
<tr>
<td>1.2.2.1 Reactive grazing model</td>
<td>28</td>
</tr>
<tr>
<td>1.3 Aims of the study</td>
<td>31</td>
</tr>
<tr>
<td>1.4 Structure of the thesis</td>
<td>32</td>
</tr>
<tr>
<td>Chapter 2. The ecology of feral pigs in Australia</td>
<td>33</td>
</tr>
<tr>
<td>2.1 Distribution</td>
<td>33</td>
</tr>
<tr>
<td>2.2 General ecology</td>
<td>35</td>
</tr>
<tr>
<td>2.2.1 Size and growth</td>
<td>35</td>
</tr>
<tr>
<td>2.2.2 Reproduction</td>
<td>35</td>
</tr>
<tr>
<td>2.2.3 Social organisation, habitat preference and home range</td>
<td>36</td>
</tr>
<tr>
<td>2.3 Population dynamics</td>
<td>38</td>
</tr>
<tr>
<td>2.3.1 The semi-arid rangelands</td>
<td>38</td>
</tr>
</tbody>
</table>
2.3.2 The role of predation ........................................ 40
2.3.3 Other environments ....................................... 42
2.3.4 Summary .................................................. 44

Chapter 3. Study sites ............................................. 45
3.1 The semi-arid rangelands .................................... 45
3.2 The Paroo River area .......................................... 46
  3.2.1 Study sites ............................................ 48
  3.2.2 Climate ................................................ 49
  3.2.3 Topography and soils .................................. 50
  3.2.4 Vegetation ............................................ 51
  3.2.5 Fauna ................................................ 52

Chapter 4. Pig density, pasture biomass and rate of population increase .......... 53
4.1 Introduction .................................................. 53
4.2 Methods ..................................................... 55
  4.2.1 Study sites and conditions during the experiment .......... 55
  4.2.2 Experimental design .................................... 58
  4.2.3 Estimating the abundance of pigs and other herbivores ... 61
  4.2.4 Estimating pasture biomass ................................ 63
  4.2.5 Analysis .............................................. 64
4.3 Results ...................................................... 65
  4.3.1 Variation in pig density .................................. 65
  4.3.2 Effect of treatment and pig density on r .................. 65
  4.3.3 Variation in grazed pasture biomass ....................... 68
  4.3.4 Effect of soil type, rainfall and flooding on pasture biomass ... 68
  4.3.5 Effect of treatment and pig density on pasture biomass .... 72
  4.3.6 Effect of pasture biomass on r .......................... 76
4.4 Discussion .................................................. 79
  4.4.1 Variation in pig density .................................. 79
  4.4.2 Variation in pasture biomass .............................. 80
  4.4.3 Pig density, food availability and the extrinsic food hypothesis .... 80
<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>The functional response and dynamics of pig populations grazing</td>
<td>5.1 Introduction</td>
<td>83</td>
</tr>
<tr>
<td></td>
<td>native pastures</td>
<td>5.2 Methods</td>
<td>85</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.2.1 Graze down trials</td>
<td>85</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.2.2 Grazing system models</td>
<td>87</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.3 Results</td>
<td>89</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.3.1 Graze down trials</td>
<td>89</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.3.2 Grazing system models</td>
<td>91</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.4 Discussion</td>
<td>97</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.4.1 The functional response</td>
<td>97</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.4.2 Comparison of grazing system models</td>
<td>99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.4.3 The intrinsic and extrinsic food hypotheses</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.4.4 Centripetality and population persistence</td>
<td>102</td>
</tr>
<tr>
<td>6</td>
<td>Habitat-related variation in the numerical response of pigs</td>
<td>6.1 Introduction</td>
<td>106</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.2 Methods</td>
<td>106</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.3 Results</td>
<td>107</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.3.1 Observed variation in $a$ and $r_m$ with the percentage of</td>
<td>107</td>
</tr>
<tr>
<td></td>
<td></td>
<td>floodplain habitat</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.3.2 Population modelling</td>
<td>108</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.4 Discussion</td>
<td>109</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.4.1 Habitat-related variation in $a$, pig density and</td>
<td>109</td>
</tr>
<tr>
<td></td>
<td></td>
<td>population persistence</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.4.2 Percent floodplain coverage and maximum rate of decrease</td>
<td>112</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.4.3 Maximum rate of decrease and the edge of a populations range</td>
<td>115</td>
</tr>
<tr>
<td>7</td>
<td>Conclusions and general discussion</td>
<td></td>
<td>118</td>
</tr>
<tr>
<td>Appendix 1</td>
<td>Estimating feral pig abundance using aerial survey and</td>
<td></td>
<td>124</td>
</tr>
<tr>
<td></td>
<td>maximum percentage bait take</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Chapter 1. Background to the Study

This thesis is about the dynamics of feral pig (Sus scrofa) populations inhabiting riverine floodplains in the semi-arid rangelands of inland eastern Australia. As such, it is largely about spatial and temporal variation in the rate at which the abundance of these populations changes and factors which influence this variation. An understanding of the dynamics of feral pig populations inhabiting the rangelands is important in order to; (1) determine appropriate strategies to manage their agricultural and environmental impacts (Tisdell 1982, Choquenot and O'Brien 1989), (2) optimise offtake for commercial harvesting and recreational hunting (O'Brien 1987), and (3) extend knowledge of the interaction of herbivores and their food resources in unpredictable environments (Caughley 1976a). This thesis emphasises the third of these points by identifying two general hypotheses developed to explain variation in herbivore population abundance and examining their relevance to the dynamics of the pig populations studied. In particular, an experiment where the abundance of six feral pig populations was manipulated to assess the applicability of two models associated with these hypotheses is described and discussed. In this first chapter some terms and concepts related to population dynamics and rates of change population abundance are introduced, and the development of hypotheses to account for variation in herbivore population abundance is reviewed.

1.1 Regulation and limitation of animal population abundance

Because many animal populations persist through time without going extinct or increasing indefinitely in abundance it seems logical that the abundance of these populations is regulated in some way. Varley et al. (1973) formally defined a regulated population as "one which tends to return to an equilibrium density following any departure from this level". Nicholson (1933) had earlier identified "density dependent" processes as being solely responsible for population regulation. Density dependent processes slow the rate at which animals are added to the population (immigration and fecundity), or accelerate the rate at which animals are lost from the population (emigration and mortality) with increasing density (Nicholson 1933). Not all additions to or removals from populations will be density dependent. Many factors,
Diagrammatic interaction of density independent productivity ($P$) with (a) density independent mortality ($mdi$), (b) density dependent mortality ($mdd$) and (c) inverse density dependent mortality ($midd$) for a population of animals. Density at stable equilibria are indicated by $K$, and at unstable boundary points by $B$ (after Sinclair 1989).
particularly abiotic processes, will be either constant or random with respect to population size (density independence), while others such as predation may accelerate additions to and/or slow removals from the population at higher densities (inverse density dependence) (Varley et al. 1973). Figs 1.1(a), (b) and (c) show the effect of density independent \((m_{dzi})\), density dependent \((m_{ddi})\) and inversely density dependent \((m_{idd})\) mortality on a population with density independent productivity (fecundity and/or immigration are constant with respect to population density).

Density independent mortality reduces the population's productivity irrespective of its prevailing density. Density dependent mortality increases with prevailing population density such that at some density the population's production and loss are balanced and its density stabilises at an equilibrium, \(K\). If the population is perturbed above or below this equilibrium, mortality alternately increases or decreases and the population moves back toward \(K\). Inverse density dependent mortality decreases with population density so that again a density exists where production and loss are balanced. However, in the case of inverse density dependence, this point is an unstable boundary \((B)\) rather than an equilibrium. Perturbation of population density above \(B\) reduces mortality which further increases density, while perturbation of density below \(B\) increases mortality which further reduces density. Hence, while all forms of mortality can act to reduce the productivity of a population and hence affect its density, only density dependent processes regulate the size of a population at this level of abundance. Sinclair (1989) termed the setting of a population's density limitation, and factors which determine this density, limiting factors. All three forms of mortality shown in Fig. 1.1 alter the density of the population and so act as limiting factors. However only density dependent processes act to regulate the population at this density.

1.1.1 Intrinsic and extrinsic density dependent factors

Density dependent processes can result from both intrinsic and/or extrinsic factors operating on a population (Krebs 1985). The exponential rate of increase in abundance \((r)\) of an intrinsically regulated population slows through the effect of some type of spacing behaviour on mortality and/or fecundity as population density increases. Such populations can be
thought of as being "self-regulated", with rate of change in their abundance at any point in
time being determined instantaneously by their prevailing density (Caughley and Krebs
1983). On the other hand, for an extrinsically regulated population \( r \) is affected by the
availability of some environmental resource (i.e. food or nesting sites), or the effect of some
limiting environmental agent (i.e. a predator, pathogen or parasite) (Andrewartha and Birch
1954). Rate of change in the abundance of these populations at any point in time is
determined instantaneously or cumulatively by the availability of the critical resource or the
effect of the environmental agent.

1.2 Regulation and limitation of large herbivore populations

The abundance of large herbivore populations is widely held to be limited by extrinsic
factors, most commonly food supply (Caughley 1970, 1987, Laws et al. 1975, Sinclair 1975,
1991), predation (Bergerud 1980, Gasaway et al. 1983, Messier and Crete 1984, 1985,
Messier 1991, 1994), or both (Caughley 1976a, 1977). Factors which limit the size of large
herbivore populations may or may not also regulate them, depending on whether they operate
in a density dependent fashion. Sinclair (1989) reviewed studies of regulation in large
terrestrial mammals and concluded that the vast majority (including all ungulates) were
regulated by density dependent mortality related to food availability. Similar conclusions
were reached by Fowler (1981a,b), using many of the same case studies. Further, Sinclair
(1989) found that while predator removal experiments have shown predation to be an
important limiting factor for large herbivore populations, there were no empirical data
implicating predation as a regulating factor. Skogland (1991a) and Boutin (1992) concurred
with Sinclair's conclusion, finding no consistent evidence for the regulation of ungulate
populations by predation. However, Messier (1994) inferred from a comparative study of the
interaction of moose (Alces alces) and wolves (Canis lupus) across North America, that
moose populations could be regulated by wolf predation. Similarly, Pech et al. (1992)
provided compelling evidence that populations of introduced European rabbits (Oryctolagus
cuniculus) in Australia could be regulated by predation from foxes (Vulpes vulpes) and cats
(Felis catus), if their abundance was first reduced by food shortage associated with drought.
In the absence of predation, processes which might limit and/or regulate large herbivore populations reduce to (1) intrinsic (socially mediated) mechanisms, (2) the debilitating effects of parasites and/or pathogens and (3) food availability.

Andrewartha and Birch (1954, 1984) suggested that food shortage for a population of animals could be absolute or relative. They considered absolute food shortages (i.e. no food) to be uncommon on all but a local scale. In contrast, they considered relative food shortages (i.e. food present but unavailable in the appropriate form, location or quantity to satisfy the needs of animals feeding on it), to be much more common and hence the more important influence on the local and regional dynamics of many animal populations. Andrewartha and Birch (1954, 1984) argued that food shortages could occur in two ways, (1) intrinsic shortages and (2) extrinsic shortages. Intrinsic shortages are an absolute or relative food shortage brought about by the actions of the animal itself acting as a "predator" on its food resources. In contrast, extrinsic shortages are a consequence of some component of the animal's environment which is independent of the interaction between the animal and its food resources. Andrewartha and Birch (1954, 1984) identified weather as an important factor leading to extrinsic food shortages for many animal populations.

Because a herbivore population suffering an intrinsic food shortage has affected the availability of its food resources, any relationship between the abundance of those resources and the fate of individuals in the population will lead to density dependent population regulation. In this context, density dependence arises not through a direct causal link between current population density and $r$ (self-regulation), but through the negative effect on prevailing mortality rates of a correlation between previous population density and current food supply (Caughley 1987). Such populations can be viewed as having a negative feedback from density to $r$, the population being regulated at or around some equilibrium through food availability. In contrast, a population suffering an extrinsic shortage will display no such feedback between density and $r$ because the population has no influence on the availability of its food resources. As such, a population subject to extrinsic food shortage is limited by density independent variation in food availability and, unless some other factor operates to impose negative feedback between population density and $r$, it will be unregulated.
In the discussion of these concepts and the description of experimental work which follows, Andrewartha and Birch's (1954, 1984) "intrinsic" and "extrinsic" shortage are replaced by "intrinsic food hypothesis" and "extrinsic food hypothesis" respectively. These terms were used to (1) avoid confusion with intrinsic and extrinsic factors discussed in section 1.1.1 and (2) emphasise that applicability of these hypotheses to pig populations was evaluated by testing specific predictions from models associated with them.

1.2.1 The intrinsic food hypothesis

Hypotheses relating large herbivore abundance to food supply have been generalised to propose that density dependent mortality regulates population abundance through food shortage (Sinclair et al. 1985). This hypothesis is coincident with Andrewartha and Birch's (1984) concept of intrinsic shortage and hence represents an intrinsic food hypothesis. The hypothesis differs from the extrinsic food hypothesis in that the abundance of herbivores influences the availability of their food resources and therefore the herbivore population is regulated through negative feedback from density to $r$.

Two types of models, (single-species and interactive), have been used to conceptualise how the intrinsic food hypothesis is related to regulation of the size of herbivore populations and to interpret empirical results from tests of the application of the hypothesis to these populations. Single-species models evolved directly from the conceptual models used to develop theories of regulation and density dependence, which were in turn developed from the logistic model of population growth (May 1973). Dissatisfaction with the implicit nature of single-species models, and in particular their application to multi-trophic systems, led to the development of more complex two-species interactive models. Interactive models were used initially to represent the dynamics of systems in which predators and their prey interacted (Holling 1959, Rosenzweig and MacArthur 1963, May 1973). Noy-Meir (1975), Caughley (1976a) and Caughley and Lawton (1981) adapted these models to represent the interaction of herbivores and the vegetation on which they fed. The development of single-species and interactive models are discussed in turn.
1.2.1.1 Single-species models

Most tests of the intrinsic food hypothesis of population regulation for large herbivores have been set in a single-species context. These tests have typically involved (1) manipulating population density (or allowing a catastrophe to do so) and assessing whether the population returns to its premanipulation level (Houston 1982, Sinclair et al. 1985), or (2) testing for density dependence in the rate of population increase or some valid demographic correlate of it (i.e. growth, body condition, fecundity or mortality) (O'Roke and Hammerston 1948, Woodgerd 1963, Boyd and Jewell 1974, Sauer and Boyce 1983, Messier and Crete 1984, Clutton-Brock et al. 1985, Eberhardt 1987, Clutton-Brock et al. 1991, Choquenot 1991, Messier 1991). Both approaches interpret any decline in rate of increase (or its index) as the population approaches a hypothetical equilibrium \( K \) or is held at some density below it, as the effect of decreasing per capita food availability on herbivore demography. In order for any decline in rate of increase with density to be consistent (and hence measurable in a repeatable fashion), both approaches also assume \( K \) to be relatively constant.

Caughley (1976a) reviewed single-species models which underlie such tests of the intrinsic food hypothesis. The simplest of these models, used to predict change in the abundance of the herbivore population \( N \), is the logistic which has the form:

\[
\frac{dN}{dt} = r_N N \left(1 - \frac{N}{K}\right)
\]

(1.1)

where \( r_N \) is the population's intrinsic rate of increase and \( K \) is its abundance at ecological carrying capacity. Ecological carrying capacity is the density where food resources are sufficient only to allow replacement of each member of the population in subsequent generations. The trajectory of a population growing logistically is shown in Fig. 1.2.
Fig. 1.2  Trajectory of a population growing logistically.

Fig. 1.3  Density dependent variation in the exponential rate of increase ($r$) for a population growing logistically.
Caughley (1976a) pointed out that application of the logistic equation to a herbivore population assumes that food available to the population in the form of edible vegetation at time \( t \) is unaffected by the number of animals feeding upon it at time \( t_1 \). That is, per capita food availability is solely a function of the number of herbivores which are currently sharing the food resource, past density having no ongoing influence on current food production. This assumption means that per capita food availability can be indexed by the immediate abundance of the population itself, and that the population's exponential rate of increase, \( r \) (equivalent to the population's per capita productivity when it is growing exponentially), declines linearly with increasing density until the abundance of resources is insufficient to generate a positive rate of population growth (Fig 1.3). Density dependence in \( r \) reflects the cumulative effects of density dependent change in fecundity and/or mortality. Perturbation of herbivore density above or below \( K \) will alternatively decrease or increase per capita food availability, alternately decreasing or increasing \( r \) with the result that \( N \) will move back toward \( K \). As such, a population which grows in this way is regulated at \( K \) by the density dependent influence of intraspecific competition for food resources.

Caughley (1976a) concluded that the logistic model could not accurately represent the dynamics of large herbivore populations regulated by their food resources because the number of herbivores which have fed on these resources in the past influences current food availability (e.g. Sinclair et al. 1985). This has the effect of delaying the influence of herbivore population abundance on food supply, associating current \( r \) with density at some time in the past. Caughley (1976a) described a delayed logistic model derived originally by Hutchinson (1948, 1954), which refers the population's rate of change in abundance at time \( t \) to it's density at time \( t-T \), where \( T \) is the lag between changes in the population's density and its rate of increase. The delayed logistic model has been widely used to interpret the effect of density dependent variation in demographic rates on the regulation of large mammal populations (Fowler 1981b). The model has the form:

\[
\frac{dN(t)}{dt} = rN\left(1 - \frac{N(t-T)}{K}\right)
\]  

(1.2)
May (1973) demonstrated that depending on the size of the product $r_mT$, the delayed logistic produced population trajectories which alternatively (1) increase monotonically to $K$ in the same way as that predicted by the logistic model (Fig. 1.4a), (2) approach $K$ through a series of dampening oscillations (Fig. 1.4b), or (3) form regular stable-limit cycles (Fig. 1.4c). As with the logistic model, a herbivore population which grows according to the delayed logistic does so through the effects of density dependent intraspecific competition for food resources (May 1973, Caughley 1976a).

Although the trajectories for many large herbivore populations appear to correspond with one or another of the outcomes of the delayed logistic model, Caughley (1976a) argued that the product $r_mT$ had no general biological significance and that single-species models generally provide little insight into causal trophic relationships underlying observed population trajectories. Caughley's (1976a) criticisms stem from the fact that single-species models imply the interaction of herbivores and their food resources rather than representing them explicitly. Hence, while single-species models produce population trajectories which are qualitatively similar to those observed for herbivore populations, they may (1) overlook important insights into the interaction of herbivores and their food resources and/or (2) arrive at incorrect conclusions concerning the role of food resources in the regulation of a herbivore population (Caughley 1976a,b). Caughley (1981) went further, identifying the almost exclusive use of single-species models in the development of concepts of population regulation for what he viewed as a less than useful fixation on density dependence in studies of large herbivore population dynamics (a point returned to by Caughley and Gunn 1993). Caughley (1976a, 1977, 1981, 1987) argued that if conceptual and mathematical models are to accurately capture the processes underlying variation in herbivore abundance, they must explicitly include interaction between the herbivores and their food resources. Similar conclusions have been reached in relation to other multi-trophic systems, including predators and their prey (Taylor 1984, Hassell and Anderson 1989) and parasitoids and their hosts (Anderson 1989, Murdoch 1994).
Possible trajectories of populations growing according to the delayed logistic model. According to the product $r_m T$, trajectories can take the form of (a) monotonic increase to $K$, (b) approach to $K$ through dampening oscillations and (c) stable limit cycles.
1.2.1.2 Interactive models

Noy-Meir (1975) developed the earliest models which predicted variation in herbivore abundance by explicitly describing their interaction with the vegetation upon which they subsisted. These models were based on graphical techniques used by Rosenzweig and MacArthur (1963) to examine the stability properties of simple predator-prey systems. Using specific sets of assumptions concerning the shape of functions describing vegetation and herbivore productivity and consumption of vegetation by herbivores, Noy-Meir (1975) plotted hypothetical isoclines of vegetation and herbivore abundance in order to identify vegetation-herbivore equilibria and determine their stability. Fig. 1.5 summarises Noy-Meir's (1975) conclusions about stability properties for vegetation-herbivore systems in which the net change in herbivore density \( H \) depends solely on the availability of vegetation \( V \). The four herbivore isoclines lead to vegetation-herbivore equilibria with different stability properties. Where the equilibrium is on the ascending arm of the vegetation isocline it is unstable, leading to (a) asymptotic divergence to extinction or (b) cycles of increasing amplitude, where the slope of the vegetation isocline is alternately steep or moderate. Where the equilibrium is on the descending arm of the vegetation isocline it is stable, leading to (d) asymptotic convergence to a steady-state or (c) cycles of decreasing amplitude, where the slope of the vegetation isocline is alternately steep or moderate. Herbivore abundance at the stable equilibria of (d) and (c) correspond to \( K \) for the logistic and delayed logistic models respectively (Fig.'s 1.3 and 1.4b). However, now the occurrence and position of \( K \) are not defined directly by the mathematics of the model, but result from the shapes of functions describing plant and herbivore productivity and vegetation offtake by herbivores. These functions collectively define the interaction between the vegetation and herbivore populations, the nature of which determines if and how the vegetation-herbivore system attains stability (Noy-Meir 1975).
Stability properties of four simple plant-herbivore systems according to the position of equilibria in relation to density dependent vegetation productivity (Noy-Meir 1975).

Caughley (1976a) modified a predator-prey model described by May (1973) in order to develop a more formal version of the interaction between vegetation and herbivores that Noy-Meir (1975) represented graphically. The model Caughley (1976a) proposed consisted of three components:

1. The exponential growth rate of the ungrazed vegetation \( r_v \) which will generally be a function of the density of the vegetation itself \( V \), most plant populations growing logistically according to:

\[
r_v = r_v^{\max} \left[ 1 - \frac{V}{K_v} \right]
\]

where \( r_v^{\max} \) is the intrinsic rate of increase of the vegetation, and \( K_v \) is vegetation abundance where available groundwater, sunlight and soil nutrients are adequate only
for replacement of existing biomass. The resultant relationship between \( r_v \) and \( V \)
means that variation in the growth of ungrazed vegetation (plant productivity, \( VN \)) and
\( V \) describes a parabola (Fig. 1.6a).

2. The functional response of herbivores which describes variation in their per capita rate
of vegetation offtake (\( IR \)) as a function of prevailing vegetation biomass (\( V \)).
Caughley (1976a) expressed the functional response as a Type 2 curve in Ivlev (1961)
form by:

\[
IR = c_H \left( 1 - e^{-d_I} \right)
\]

where \( c_H \) is the herbivore's maximum offtake rate, vegetation biomass being high
enough that intake is satiated, and \( d_I \) is the rate at which \( c_H \) is approached with
increasing vegetation availability. Holling (1959) described four possible functional
responses depending on (1) the efficiency of the response (Types 1 and 2), (2) the
existence of some unconsumable residual abundance of prey (Type 3), and a decline
in intake rate at high prey abundance (Type 4). A Type 2 functional response for
herbivores is shown in Fig. 1.6b. Intake rate is satiated at high vegetation availability.
However, as vegetation becomes scarce herbivores must spend increasingly more time
searching for plants or plant parts to consume and intake rate declines.

3. The numerical response of herbivores which describes variation in their exponential
rate of increase in abundance (\( r_H \)) as a function of prevailing vegetation biomass (\( V \))
(Holling 1959). Caughley (1976a) expressed the numerical response, again in Ivlev
form, by:

\[
r_H = a_H \cdot c \left( 1 - e^{-d_H} \right)
\]

where \( a_H \) is the maximum rate at which the herbivore population declines in the
absence of vegetation, \( c \) is a constant describing the difference between the
population's maximum rates of decline (\( a_H \)) and increase (\( r_{mH} \)) such that
\( r_{mH} = c - a_H \).
1.6 The 3 functions which comprise Caughley's (1976a) interactive vegetation-herbivore system; (a) parabolic vegetation productivity \((HV)\) as a function of vegetation biomass \((V)\), (b) a Type 2 functional response of herbivores relating variation in per capita rate of vegetation intake \((IR)\) to vegetation biomass \((V)\), and (c) the numerical response of herbivores relating variation in their exponential rate of population increase \((r)\) to vegetation biomass \((V)\) (Caughley 1976a, 1981).
and $d_2$ is an index of the population's demographic efficiency describing the rate at which the shift from $a_H$ to $r_{mH}$ occurs with increasing vegetation availability. The numerical response of herbivores is shown in Fig. 1.6c. The maximum rate of increase ($r_{mH}$), which occurs when food is plentiful, is the population's genetically or physiologically determined maximum capacity to increase in it's given environment. Because the capacity of a population to decrease is less genetically or physiologically limited, the numerical response will often be asymmetrical, with an incremental decrease in food availability reducing $r$ more than an equivalent increase elevates it.

The three components of the interactive vegetation-herbivore model operate collectively as two negative feedback loops governing the influence which the vegetation and herbivores comprising the system exert over each other's abundance (Fig. 1.7) (Caughley 1976a, 1981). Parabolic plant productivity forms the first feedback loop (the vegetation biomass loop), which reduces plant growth at high vegetation biomass, placing an ultimate ceiling on how much vegetation can grow. This loop keeps vegetation availability in check regardless of how good seasonal conditions are or how limited the offtake of the herbivores is. The functional and numerical responses of the herbivores form the second feedback loop (the vegetation-herbivore loop) which links vegetation to herbivore abundance by increasing the number of herbivores and the amount each eats at high vegetation biomass, which in turn exerts grazing pressure on the vegetation leading to lower availability, fewer herbivores and lower intake rates. Caughley (1976a) combined these feedback loops in 2 linked equations which predict coincident variation in the abundance of vegetation ($V$) and the herbivores which feed on it ($H$):

$$\frac{dV}{dt} = -\alpha_H \cdot V \left(1 - \frac{V}{K_r}\right) - c_H H (1 - e^{-4r})$$  \hspace{1cm} (1.3a)

$$\frac{dH}{dt} = [r_{mH} - r]\left[1 - e^{-4r}\right]$$ \hspace{1cm} (1.3b)
Fig. 1.7 A conceptual model of an interactive vegetation-herbivore system showing the two feedback loops which control the reciprocal influence of vegetation and herbivore abundance.

Fig. 1.8 Trajectory of vegetation ($V$) and herbivore ($H$) growth to a stable equilibrium according to the interactive plant-herbivore model (Caughley 1976a).
Fig. 1.8 shows an example of the model, where a population of herbivores is introduced into a new environment. The parameter values used in the model are; \( r_{mv} = 0.8, K_v = 3,000, c_H = 1.2, \, d_1 = 0.0001, \, a_H = 1.1, \, c = 1.5 \) and \( d_2 = 0.001 \). While the predicted trajectory for the herbivore population is qualitatively similar to that shown for the outcome of the delayed logistic model in Fig. 1.4b, the mechanisms underlying the pattern are resolved at a fundamentally different level. In the delayed logistic, all interaction between herbivores and their food supply is implied through the existence of an equilibrium density for the herbivores \( K \), and the lagged effect of herbivore density on the population's prevailing rate of increase, \( r \). In contrast, interaction of the herbivore population and its food supply is explicitly predicted in the interactive model through the two feedback loops which define the system.

As with the graphical approach of Noy-Meir (1975), the interactive model requires no imposed density dependence or specifically defined equilibrium for the herbivore population. Rather, interaction between the population and its food supply governs if and when density dependence and equilibrium herbivore density manifest themselves. This does not mean that a herbivore population which grows through interaction with its food supply is unregulated. Fig. 1.9 shows the plant and herbivore growth trajectories of Fig. 1.8 plotted as a phase diagram, the ratio of plant and herbivore abundance approaching equilibrium through the same series of reciprocal dampening oscillations. The herbivore population displaced to any part of this phase space moves back toward equilibrium through a series of reciprocal oscillations with vegetation biomass. While this process is essentially density dependent (the vector of the plant-herbivore system at any point in time is a direct result of past grazing activity which is a consequence of past herbivore density), the tendency toward equilibrium is of more consequence to the stability of the grazing system than is attainment of the equilibrium itself. For this reason Caughley (1987) coined the term centripetality to describe central tendency in the vector of herbivore and vegetation abundance. Centripetality de-emphasises the importance of an equilibrium in herbivore and vegetation abundance, while implying the stabilising properties that its potential existence imparts.

The stable equilibrium indicated by the phase diagram shown in Fig. 1.9 is not the only possible outcome from interactive vegetation-herbivore models. Caughley (1976a) demonstrated that depending on the parameter values used in equations (1.3a) and (1.3b), two
other potential outcomes could be realised; (1) stable limit cycles, where vegetation and herbivores occupy a cyclic equilibrium trajectory arising from regular, periodic oscillations in the ratio of herbivores to vegetation; and (2) unstable equilibria, where vegetation and herbivores occupy an equilibrium point only as long as the system is not displaced from it (Figs 1.10a and b). Stable limit cycles are centripetal in the sense that the system will return to the same stable trajectory following perturbation either inward or outward through essentially density dependent processes. However, unstable equilibria are non-centripetal, even slight perturbations giving rise to oscillations of increasing amplitude until either vegetation or herbivores go extinct.

Fig. 1.9 A phase diagram of the reciprocal abundance of vegetation ($V$) and herbivores ($H$) for the interactive vegetation-herbivore system modelled in Fig. 1.8 (Caughley 1976a).
Fig. 1.10  Phase diagrams for interactive vegetation (V)-herbivore (H) systems displaying (a) stable limit cycles and (b) oscillations of increasing amplitude to extinction.

Stable limit cycles and unstable equilibria arising solely through the interaction of herbivores with their food supply are virtually unknown in nature, although there has been considerable speculation about their existence. Examples of stable limit cycles have been sought amongst strongly cyclic herbivore populations such as lemmings and snowshoe hares (May 1973), and amongst less obvious candidates such as African elephants (Caughley 1976b). Unstable equilibria, because of their ephemeral nature, are even more difficult to identify although they have been suggested as a possible reason for many unsuccessful introductions of ungulates to oceanic and habitat islands (Caughley 1976a, Leader-Williams 1988). In contrast, any persistent population of large herbivores represents a potential example of a centripetal plant-herbivore system occurring at or around some stable equilibrium. Given this, it is surprising that so few attempts have been made to explicitly describe how large herbivores and their food resources interact (Eberhardt 1987, 1988).
Caughley (1970) tested the hypothesis that body condition and demography of Himalayan thar \((Hemitragus jemlahicus)\) introduced into New Zealand, would reflect changes in per capita food availability as they passed through a series of reciprocal oscillations with food availability on their way to achieving some more or less stable equilibrium density. Caughley (1970) found that mortality increased from low levels at the thar invasion front, through very high levels where thar populations had been established long enough that they had consumed most available vegetation, approaching intermediate levels toward their point of original liberation where a food-related die-off of thar had allowed vegetation to re-establish to some degree. Variation in mortality of thar was reflected in their rate of population increase, which was high at the invasion front, negative where thar had over-exploited available vegetation, and approaching zero where thar were moving toward some equilibrium with vegetation productivity. Caughley (1970) interpreted this pattern of variation in the demography of thar as the consequence of reciprocal oscillations in their abundance and that of the vegetation they fed upon, as the grazing system progressed toward equilibrium.

Sinclair (1977) examined the relationship between food availability, demography and rate of population increase for African buffalo \((Syncerus caffer)\) increasing in abundance following control of the livestock disease rinderpest in eastern Africa. He found that buffalo density was positively correlated with rainfall and hence food supply, implying that buffalo populations were regulated by food availability in the same manner as thar in New Zealand. Sinclair (1977) found that adult mortality increased proportionally with population density, while fecundity was relatively constant and juvenile mortality was density independent, varying with the vagaries of season. Using age-structured single-species population models, Sinclair (1977) found that trajectories of growing buffalo populations reflected variation in adult mortality, as did the equilibrium population density at which they eventually stabilised. Juvenile mortality, while it was found to have a much more profound effect on rates of population change than adult mortality, had little influence on long-term population trends because its sensitivity to stochastic environmental variation meant that its year-to-year effects were random. As such, juvenile mortality tended to produce random variation around population trajectories and ultimately around the population's equilibrium abundance (these general findings have been extrapolated to other African ungulates (Starfield and Bleloch...
1986, Van Sickle 1990). By examining the relative contribution of different herbivore species in the ecosystem to the reduction in availability of the short green grass leaves which buffalo preferentially grazed, Sinclair (1977) found that the food shortage which appeared to regulate buffalo population abundance resulted primarily from intraspecific competition (an intrinsic food shortage), but also from interspecific competition (an extrinsic food shortage). In particular, invasion of riverine grasslands (a preferred feeding habitat of buffalo) by wildebeest during the dry season had the potential to significantly affect the amount of food available to buffalo and their consequent rate of increase.

Sinclair's (1977) analysis suggests that the vegetation-buffalo system increasing toward equilibrium would trace a phase diagram qualitatively similar to that shown in Fig. 1.9, due to systematic variation in adult mortality as it responded to per capita food availability. Random variation around the general trend and around the equilibrium point once it was attained, would result from stochastic environmental effects on year-to-year variation in juvenile mortality. That is, the population is regulated by the effects of food availability on adult mortality. In contrast, the effects of food availability on juvenile mortality represent a limiting factor. Monitoring of buffalo populations since Sinclair's (1977) original study generally confirmed that trends in buffalo abundance were as predicted by the intrinsic food hypothesis (Dublin et al. 1990).

General patterns in the interaction of large herbivores and their food resources described by Caughley (1970,1976a) and Sinclair (1977) have been elaborated for populations of roe deer (Capreolus capreolus) (Bobek 1977), white-eared kob (Kobus kob leucotis) (Fryxell 1987), reindeer (Rangifer trandus) (Skogland 1983, 1985, Leader-Williams 1988) feral donkeys (Equus asinus) (Freeland and Choquenot 1990, Choquenot 1991) and soay sheep (Ovis aries) (Clutton-Brock et al. 1991). Similarly, Starfield and Bleloch (1986) developed conceptual models of African ungulates interacting with their food resources. These studies variously estimated the direct effects of food availability or quality on demography and/or rate of population increase, emphasising the need to understand the dynamics of herbivore populations within the framework of an integrated vegetation-herbivore system. However, Caughley's (1987) summary of Bayliss (1985a,b, 1987), Robertson (1987a,b) and Short's
(1986, 1987) work on the grazing system comprising red kangaroos (*Macropus rufus*) and the pastures they graze in the semi-arid rangelands of Australia, remains the only realisation of a fully interactive model describing reciprocal variation in the abundance of a large herbivore population and its food resources.

The grazing system Caughley et al. (1987) described was driven by rainfall which had a 47% coefficient of variation in amount year-to-year but with no seasonality, leading to wide, apparently random fluctuations in the abundance of vegetation and kangaroos. These natural fluctuations were exploited to estimate the form of density dependent pasture response to stochastic rainfall (Robertson 1987a,b), and the numerical response of kangaroos to pasture availability (Bayliss 1985a,b, 1987). The functional response of intake rate by kangaroos to pasture biomass was derived experimentally (Short 1985, 1987). A phase diagram of the modelled grazing system (Caughley 1987) is shown in Fig. 1.11. While the trajectory may appear to describe something of a stable limit cycle such as that shown in Fig. 1.10a, in the absence of rainfall variation the system has a central tendency which identifies it as an equilibrium system such as that shown in Fig. 1.9. Hence, the grazing system comprising red kangaroos and pasture is centripetal and in that sense is regulated around a theoretical equilibrium by essentially density dependent processes.

In order to identify which components of the grazing system led to its centripetality and persistence, Caughley (1987) conducted a series of simulations in which elements of the grazing system were variously included or omitted. He concluded that in the absence of grazing, density dependent pasture growth was necessary for centripetality of the vegetation component of the system. However, the feedback between pasture offtake and pasture biomass when kangaroos were added was strong enough to maintain centripetality even when the vegetation biomass loop was subsequently omitted. Further, the effect of pasture offtake by kangaroo grazing, mediated by the functional response, was necessary for centripetality of the kangaroo component of the system. In its absence, the vegetation-herbivore loop linking pasture to kangaroo abundance was decoupled and kangaroo abundance increased indefinitely. This means that despite the dominant effect of rainfall variation on pasture biomass, without the less consequential influence of offtake by kangaroos, the grazing system
Fig. 1.11 Phase diagram of variation in the abundance of red kangaroos and pasture biomass according to a stochastic model derived by Caughley (1987). Points are annual averages of pasture biomass (kg/ha) and kangaroos/ha over a 100-year run of the model.

...could not maintain itself within realistic bounds. Although Caughley (1987) did not report the response of pasture biomass to the systematic manipulation of kangaroo density, by contrasting pasture biomass for the simulated grazing system with and without kangaroos, he estimated that an unculled population of kangaroos reduced pasture biomass on average by 43%. It follows that if the average density of kangaroos were constrained between that of unculled populations and zero, there would be commensurate increases in average pasture biomass up to the point where the vegetation biomass loop limited further pasture growth. The constraint of kangaroo density decouples the vegetation-herbivore loop linking pasture to kangaroo abundance by interfering with the operation of the numerical response.
1.2.1.3 Differences between single-species and interactive models

Both the single-species and interactive models represent the effects of food availability on the dynamics of herbivore populations through essentially density dependent variation in \( r \).

However, in contrast to single-species models where the degree of density dependence in \( r \) is assumed to be constant, in the interactive model herbivore density influences \( r \) only through its effect on pasture availability and hence the degree of density dependence at any point in time varies according to prevailing vegetation biomass. Therefore, in any realisation of the interactive model, increasing stochastic environmental variation will operate to increase variation in pasture biomass while the vegetation-herbivore feedback loop will operate to dampen this variation by adjusting the abundance of herbivores and their individual pasture offtake. In this sense, the intensity of density dependence implied by the interactive model shifts according to the strength of feedback between herbivore and vegetation abundance, the degree of shift depending on the intrinsic stochasticity of the environment and the relative demographic and grazing efficiency of the herbivores.

For example, Caughley (1987) found that in the absence of stochastic variation in rainfall and pasture growth, the interactive model of red kangaroo and pasture abundance moved rapidly to a stable equilibrium of 0.68 kangaroos and 230kg/ha of pasture. At this equilibrium, pasture production was sufficient only to replace kangaroos in subsequent generations \((r = 0)\), kangaroo density being equivalent to \( K \) in a single-species model. Fig 1.12 shows the effect on \( r \) of removing 41% of this stabilised kangaroo population every 10 years over a 100-year run of the model. The regular series of asymptotic declines in \( r \) as the population returns from its culled to its equilibrium density is qualitatively identical to the constant density dependence predicted by single-species models. Hence, when environmental variation is held to zero, the interactive model predicts the same constant effect of density dependent variation in \( r \) as that assumed by single-species models. In this context, the interactive model is the general case for plant-herbivore systems which conform to the intrinsic food hypothesis, single-species models representing the particular case where environmental variability is low enough and/or the grazing and demographic efficiency of the herbivores high enough, that density dependence in \( r \) can be assumed constant. It follows that as the degree of
environmental stochasticity increases, tests of the food hypothesis based on single-species models (e.g. return to equilibrium following perturbation and/or evidence of density dependence) will be progressively less able to either detect evidence of population regulation or to predict variation in $r$. These shortcomings prompted Caughley and Gunn (1993) to argue that application of such models to plant-herbivore systems "...tend to obscure rather than illuminate causal mechanisms of regulation where that regulation is powered by feedback between plant density and animal density". Krebs (1991) went further, claiming that the density dependence paradigm implied by single-species models "...does not lead to understanding because no mechanisms are specified".

Fig. 1.12 Variation in $r$ over a 100-year run of Caughley's (1987) red kangaroo-pasture model (with stochastic variation in rainfall and pasture growth removed), due to removal of 41% of the equilibrium density of kangaroos in a single operation every 10 years.
1.2.2 The extrinsic food hypothesis

The concept that animal populations are regulated at or around $K$ through density dependent variation in $r$, first articulated by Nicholson (1933), was criticised by Andrewartha and Birch (1954). They argued that the abundance of many animal populations was limited by the availability of resources over which the animals themselves exerted no influence. They termed this type of limitation an extrinsic shortage because variation in resources (usually food), was independent of any interaction between the animals and those resources. Animals which suffer extrinsic food shortage do not affect the availability of the resources which determine their rate of increase, hence their abundance may be limited but not regulated by these resources. An example of such a system was described by Nugent (1990) for introduced fallow deer (*Dama dama*) inhabiting indigenous shrub-hardwood forest on the south island of New Zealand. The deer had been established in the area for over 120 years, during which time they had removed most of the preferred ground cover species and tree seedlings, so that they subsisted on leaf fall from foliage above the browse line. Nugent (1990) argued that because deer did not influence production of foliage or leaf fall, $r$ was determined by factors extrinsic to their interaction with these food resources. As such, the prevailing rate of increase in deer was a function of density independent variation in the abundance of foliage.

Andrewartha and Birch (1954, 1984) argued that populations experiencing extrinsic shortage of resources persist in the absence of regulation because their dynamics manifest themselves through more or less independent subpopulations which give the population spatial structure. Subpopulations are generally clustered at the centre of a species range, becoming more sparse toward its edge. For each subpopulation, $r$ is independently determined over a range of densities by the influence of a few or many environmental factors which may be density dependent, density independent, inverse density dependent, or all of the above at different population densities. These factors operate collectively to influence the probability that $r$ for a given subpopulation is positive or negative at any point in time. However, they do not operate to regulate abundance at any specific equilibrium. Andrewartha and Birch (1954, 1984) acknowledged that because they lack regulatory mechanisms, subpopulations inevitably go extinct but argued that the probability of all going extinct at once is remote, particularly
where subpopulations are clustered. According to Andrewartha and Birch (1954, 1984), because regulation is not necessary to ensure population persistence, density dependence has no special role in accounting for the variation of animal abundance.

Andrewartha and Birch (1954, 1984) termed processes which operate to influence the relative probability that prevailing $r$ is positive or negative and the role of spatial structure in population persistence, a theory of environment. While regulatory mechanisms are not necessary for population persistence under this theory, a population will have notional equilibrium equivalent to the average density of its constituent subpopulations determined by $r$, also averaged across subpopulations. In this sense the theory of environment can be applied to a herbivore population by proposing that the population may have a more or less stable equilibrium, with $r$ varying largely independently of population density according to the collective influence of one or more extrinsic and/or intrinsic factors.

1.2.2.1 Reactive grazing model

The simplest population model containing no explicit or implied regulation is the random-walk model, predicting population growth ($dN/dt$) by:

$$dN/dt = rN$$

(1.4)

where $r$, varies with an average of zero and variance equal to that measured from a time series of population estimates (May 1974). Fig 1.13 shows a trajectory over 1,500 time steps for a population with a standard deviation around $r$ of 0.05. It has been demonstrated in several studies that random-walk models lead inevitably to population extinction (May 1974, Hassell et al. 1989, Murdoch 1994). The inclusion of spatial heterogeneity and ensemble dynamics of constituent subpopulations may protract the random-walk, but cannot negate the population's inevitable demise (Chesson 1981). However, Den Boer (1991) demonstrated that patterns of variation in abundance predicted by random-walk models can be identical to those measured empirically for many species, and that random-walks do not preclude the possibility of populations persisting over realistic periods (i.e. centuries). However, Den Boer (1991)
1.13 Trajectory over 1,500 time steps of a randomly walking population with a standard deviation around $r$ of 0.05.

argued that the similarity of real and modelled population trajectories did not reflect entirely random changes in population density. Rather, as proposed by Andrewartha and Birch (1954, 1984), the collective influence of a range of density dependent and independent factors on the direction and rate of change in population abundance lead to essentially random variation in population abundance.

For herbivore populations limited by food availability, variation in $r$ will be determined to at least some degree by variation in food abundance. The extrinsic food hypothesis proposes that variation in food available to such populations is independent of the density of the population itself. Caughley and Lawton (1981) described vegetation-herbivore systems where rate of change in vegetation biomass is independent of herbivore abundance as reactive, and considered examples to be rare in nature (although see Nugent's (1990) fallow deer study described in section 1.2.2). They considered growth of herbivore populations in such systems would be essentially logistic because the rate at which their food resources are renewed is
independent of herbivore density. Hence, the numerical response of the herbivores will dictate variation in \( r \), but there will be no reciprocal effect of offtake through the functional response. Reactive models differ from random-walk models because they include a link between food availability and rate of change in herbivore abundance through the numerical response. However, depending on the degree of variation in food availability and the effect of other environmental factors on \( r \), herbivore population trajectories predicted by reactive models may be quantitatively similar to those predicted by random-walk models with appropriate parameters (Den Boer 1991). Caughley (1987) explored the applicability of such a model to the red kangaroo-pasture grazing system, by removing the functional response from the simulation model described in section 1.2.1.2. The model has the same general form as the interactive vegetation-herbivore model with the functional response omitted:

\[
\frac{dV}{dt} - a_r V \left( \frac{V}{K_r} \right)
\]

(1.5)

\[
\frac{dH}{dt} = -a_h c \left[ 1 - e^{-a_H H} \right]
\]

(1.6)

where parameters are as defined for the interactive model. In the absence of the functional response, vegetation grows logistically and herbivores according to the numerical response. In Caughley's (1987) red kangaroo-pasture model, eliminating grazing offtake increased pasture biomass to the extent that the kangaroo population generated an indefinite tendency to increase, with \( r \) averaging 0.29. While this indicates that the extrinsic food hypothesis is inappropriate for the red kangaroo-pasture grazing system, the approach suggests how the interactive model may be generalised to grazing systems where variation in vegetation biomass is independent of the density of herbivores feeding on it. Similar approaches have been used to model non-equilibrium host-parasite systems where rate of parasitism limits host abundance (Nicholson and Bailey 1935, Murdoch 1994).
1.3 Aims of the study

In this study I sought to determine whether feral pig populations inhabiting the semi-arid rangelands were limited by intrinsic or extrinsic food shortage and hence whether or not they were regulated. Giles (1980) demonstrated that although pigs in the rangelands were omnivorous, variation in their rates of population increase were closely associated with the availability of green forage (see section 2.3.1). This suggests that pig populations represent an appropriate system upon which to test the applicability of the extrinsic and intrinsic food hypotheses. For example, pig populations in the rangelands are subject to wide environmental variation in the form of unpredictable rainfall, implying an important role for extrinsic food shortage in determining prevailing rates of population increase. However, pig populations have persisted under rangelands conditions for over 150 years (see Chapter 2), suggesting that their abundance is regulated to at least some degree by density dependent processes associated with intrinsic food shortage. In order to investigate these alternatives, predictions of two models representing the intrinsic and extrinsic food hypotheses were tested using a manipulative experiment. The experiment involved reduction of pig density on six sites in the rangelands to one of three levels (treatments), with pasture biomass and rate of change in pig abundance (r) measured quarterly over two and a half years. Outcomes predicted by the two models for three relationships estimated from the results of the experiment are shown in Table 1.1.

<table>
<thead>
<tr>
<th>Food hypothesis</th>
<th>Model</th>
<th>Relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>r with pig</td>
</tr>
<tr>
<td></td>
<td></td>
<td>density,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pasture</td>
</tr>
<tr>
<td></td>
<td></td>
<td>biomass</td>
</tr>
<tr>
<td></td>
<td></td>
<td>r with</td>
</tr>
<tr>
<td></td>
<td></td>
<td>pasture</td>
</tr>
<tr>
<td>Intrinsic</td>
<td>Interactive</td>
<td>- / 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Extrinsic</td>
<td>Reactive</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+</td>
</tr>
</tbody>
</table>

Table 1.1 Predictions of two models for three relationships measured using a manipulative experiment on feral pig populations. Relationships are predicted to be positive, negative or non-significant according to each model are indicated as +, - and 0 respectively.
If the intrinsic food hypothesis is applicable to pig populations inhabiting the rangelands, the effect of pig density on $r$ will be (1) negative if the grazing system has a strong tendency toward equilibrium (constant density dependence), or (2) non-significant if this tendency is weak (shifting density dependence). However, given the high variability of the rangelands environment (see section 3.2.2), it was considered unlikely that pig populations inhabiting them would have stable $K$ or constant density dependence. Hence, the interactive form of the intrinsic food hypothesis was tested rather than the single-species form. In either case higher densities of pigs will be associated with reduced pasture biomass and there will be a positive numerical response by pigs to increasing pasture availability.

In contrast, if the extrinsic food hypothesis is applicable to pig populations inhabiting the rangelands, there would be no significant change in either $r$ or pasture biomass with increasing pig density. However, it was decided \textit{a priori} from a review of pig population dynamics (see section 2.3) that pig populations would likely be limited by food availability, regardless of whether or not they were regulated by it. Hence the modified reactive model described by Caughley (1987) was tested rather than the alternative random walk model. The former predicts a positive numerical response by pigs to increasing pasture availability.

1.4 Structure of the thesis

The next chapter provides a brief review of the ecology of feral pigs in the rangelands and elsewhere in Australia, with emphasis on what is known of the dynamics of their populations. Chapter 3 gives an overview of the general region where the manipulative experiment mentioned above was undertaken and provides detailed descriptions of the six study sites used in the experiment. Chapter 4 summarises the manipulative experiment and its outcomes, while chapter 5 describes an additional experiment and some population modelling conducted to help interpret the results of the manipulative experiment. Chapter 6 explores an interesting observation on the spatial dynamics of pig populations made during the course of the experiment described in Chapter 4, and some subsequent population modelling. Finally, Chapter 7 provides a summary of the main conclusions of the study and attempts a brief synthesis of the general results obtained.
Chapter 2. The Ecology of Feral Pigs in Australia

Detailed studies of the ecology of feral pigs in Australia have been conducted at Yantabulla and Warren in the southeastern semi-arid rangelands (Giles 1980, Woodall 1983, Dexter 1994), at Kosciusko in the southeastern subalpine region (Saunders 1988, 1993a), and at the Douglas-Daly River and Kapalga in the tropical woodland/floodplain habitat of northern Australia (Caley 1993, Corbett 1994 respectively). Hone (1987) also studied aspects of the population dynamics of feral pigs while evaluating strategies for management of pig impacts at Willandra in the rangelands, at Namadgi National Park in a highland forest area adjacent to Kosciusko on the Mary River floodplain adjacent to Kapalga in northern Australia. The locations of some of these studies are shown in Fig. 2.1. In this Chapter the results of these studies are used to provide a general overview of the ecology of feral pigs in Australia, and in the semi-arid rangelands particularly. The rangelands environment is described in detail in Chapter 3. Emphasis is placed on the dynamics of feral pig populations in order to set a context for the current study.

2.1 Distribution

Pigs were first introduced to Australia at the time of European settlement in 1788 (Pullar 1953). Pigs spread into new areas with the movement of settlers throughout the continent, feral populations establishing from the habit of running free-ranging pigs around settlements and out-stations (Rolls 1969). Hone and Waithman (1979) attributed more recent introductions of pigs to locations along the Great Dividing Range and the east coast to deliberate release of captured animals by hunters. Feral pigs are now widely distributed throughout eastern and northern Australia, with the highest densities occurring along the inland river systems of the semi-arid rangelands and on the floodplains of tropical northern Australia (Fig. 2.2) (Wilson et al. 1992).

Feral pigs were introduced to inland Australia by graziers who settled the semi-arid rangelands during the 1830's and 1840's (Pullar 1950, 1953). Colonies of feral pigs existed on the floodplains of the Paroo, Warrego and Upper Darling rivers, in the Macquarie Marshes,
Fig. 2.1 Location of studies described in this chapter.

Fig. 2.2 Relative density distribution of feral pigs in Australia (after Wilson et al. 1992). Solid, stippled and hatched areas represent areas of relatively high moderate and low pig density respectively, as assessed by a subjective index of occurrence.
and in the Great Cumbungi Swamp at the confluence of the Lachlan and Murrumbidgee Rivers prior to the 1870's (Pullar 1950). Newspaper reports describe the shooting of 14,000 pigs in this latter area during 1882 (Rolls 1969).

2.2  General ecology

2.2.1  Size and growth

In the rangelands, growth is sexually dimorphic beyond approximately 15 months of age, males normally attaining mature weights of 70-100kg and females 40-70kg (Giles 1980). In subalpine and tablelands habitats, pigs reach higher average body weights (Saunders 1988, 1993a), while in tropical woodland habitats pigs attain similar sizes to those in the rangelands (Caley 1993).

2.2.2  Reproduction

In the rangelands, females reach sexual maturity at about 8 months of age if liveweight is above 30kg, average litter size is 6.24 and breeding occurs year-round under good seasonal conditions, 1.93 litters per female being produced on average each year (Giles 1980). Under progressively poorer seasonal conditions, both litter size and the number of litters produced per female decline. Year-round breeding also occurs in the tropics, however a strong seasonal peak in conception is evident during the early wet-season (January and February) (Caley 1993). Fewer litters are produced per year (1.11) than in the rangelands, probably because cyclic variation in food supply coupled with the nutritional stress of late-stage lactation suppresses conception during the late dry-season (Caley 1993). In contrast, while litter size for pigs in subalpine habitats (6.58) is similar to that reported for the rangelands, breeding occurs over a discrete season (conception in late spring, birth in late summer), with females consequently producing only 0.84 litters per year (Saunders 1993a).

Seasonal reproduction has been found in feral pig populations on Santa Catalina Island off California (Baber and Coblentz 1987), in South Carolina in the southeastern United States
(Wood and Brenneman 1977, Sweeney et al. 1979), in Hawaii (Giffin 1978) and in Europe (Mauget 1981, 1982). Continuous reproduction has been reported for mainland populations in California (Barrett 1978) and on the Galapagos Islands (Coblentz and Baber 1987). Mauget (1982) and Baber and Coblentz (1987) attributed seasonality in reproduction for populations in Europe and on Santa Catalina Island to spring/summer anoestrus coinciding with rapidly increasing daylength. In Australia, any effect of photoperiod on reproduction appears to be overridden by the influence of food availability. For example, Saunders (1993a) found that in contrast to pig populations in Europe and on Santa Catalina Island, reproduction in subalpine populations ceases over winter as daylength declines, and commences as daylength increases into spring. Similarly, Caley (1993) found that in tropical populations breeding has a seasonal peak despite the lack of any appreciable variation in daylength, and Giles (1980) found that breeding in the rangelands is aseasonal despite their relatively high latitude. Pine and Gerdes (1973), Conley (1977) and Barrett (1978) all identified seasonal availability of oak or beech mast as the cue for reproduction in northern hemisphere populations of pigs which display seasonal breeding.

2.2.3 Social organisation, habitat preference and home range

While little research has been conducted on the social organisation of feral pig populations in Australia, incidental observations suggest that it differs little from that reported for wild populations in Europe and North America (Giles 1980, Saunders 1988). Pigs are gregarious, the basic unit of organisation comprising one or more females with their offspring. Interaction between juveniles from different litters begins early and persists into adulthood (Graves 1984). Males leave family groups at about 12 months of age and only rejoin female groups to look for mating opportunities or to feed on localised food resources. Females may leave female groups for short periods during parturition (farrowing) (Barrett 1978, Saunders 1988). Males maintain larger home ranges than females (see below), presumably to contact as many female groups as often as possible (Graves 1984). Neither males nor females display territoriality or resource monopolisation (Barrett 1978, Saunders 1988, Spitz 1991, Caley 1993), although males may defend access to oestrus females once they are detected (Barrett 1978, Graves 1984).
In Australia's semi-arid rangelands Giles (1980) and Dexter (1994) found that pigs exhibited a strong preference for floodplains habitat, which contained reliable sources of permanent water and dense vegetation cover (see section 3.2.4). Pigs in the rangelands maintained relatively permanent home ranges (average size 24.0km$^2$ for males and 7.0km$^2$ for females) which expand when food availability declines and contract during hot dry weather (Dexter 1994). The home ranges of most pigs were centred on patches of floodplain habitat, although occasionally individuals established home ranges centred on permanent watering points away from floodplains (Giles 1980). The degree to which males gravitate to floodplains habitat or to the females which occur there is unknown. However, in an experiment where oestrus-induced sows were artificially distributed throughout a floodplain habitat, radio-tracked boars showed no significant movement toward the location of sows (Dexter 1994).

Pigs in wet-dry tropics, tablelands and subalpine environments, all of which have a much broader distribution of permanent water than do the semi-arid rangelands, display a preference for dense vegetation cover rather than for floodplain habitat per se (Saunders 1988, Caley 1993). Saunders and Kay (1991) estimated average home ranges of 10.7km$^2$ for males and 4.9km$^2$ for females in tablelands environments. As in the rangelands, home ranges tended to be centred on patches of thick vegetation cover and expanded when food availability was low (autumn and winter in the tablelands). Saunders (1988) estimated home ranges to be much larger in subalpine environments (34.6km$^2$ for males and 10.2km$^2$ for females), as did Caley (1993) for tropical woodlands (31.2km$^2$ for males, 19.0km$^2$ for females). Larger home ranges in subalpine and tropical woodlands probably reflect the greater spatial distribution of adequate cover in these environments rather than any direct influence of the availability of water (Saunders 1988, Caley 1993).

Pigs in all habitats are generally sedentary, long distance movements being exceptional (Saunders 1988, Saunders and Kay 1991, Caley 1993, Dexter 1994). Where such movements do occur, they are more commonly undertaken by males than females (Saunders 1988, Dexter 1994).
2.3 Population dynamics

2.3.1 The semi-arid rangelands

Giles (1980) conducted a broad study of feral pig population dynamics in the semi-arid rangelands, based on extensive mark-recapture studies and autopsy of large shot samples. Giles' (1980) study represents the only detailed assessment of feral pig ecology in Australia's rangelands. Although Giles (1980) used four study sites, most of his information on population dynamics came from two locations: Warren on the Macquarie Marshes and Yantabulla in the Cuttaburra Basin (Fig. 2.1). Both sites were within the wild-dog exclusion fence which separates the sheep rangelands of western New South Wales from the more extensive rangelands of southwestern Queensland and northeastern South Australia (see section 3.2). Hence, pigs at neither site were subject to predation by dingoes (Canis familiaris).

Giles (1980) reported population densities which varied between 8.01 and 17.47 pigs/km² over 3 years for the Warren study site, and between 0.24 and 0.77 pigs/km² over 2 years for the Yantabulla study site. Giles (1980) concluded that the variability in pig density at both sites was due to stochastic variation in prevailing seasonal conditions, rate of change in pig abundance being determined largely by the influence of dietary protein on demographic rates. Dietary studies demonstrated that protein was ingested most commonly in the form of fresh green legumes, grasses and forbs. Animal matter (mostly carrion, frogs and earthworms), when it was available, represented a secondary source of protein. Stomach contents (Fig. 2.3) indicated that variation in protein intake primarily reflected variation in the ratio of above ground vegetation (grasses and forbs) to below ground vegetation (roots and tubers) ingested. Giles (1980) linked availability of fresh green vegetation to the occurrence of flooding and/or heavy rain. Fig. 2.4 relates changes in an index of the protein content of food consumed by pigs at Yantabulla to the incidence of rainfall and flooding over six years. When adequate green feed was not available, pigs consumed mostly roots and tubers which were rich in digestible carbohydrate but contained little protein.
Fig. 2.3  Estimated volumetric composition of forestomach contents for pigs over six months of age at Yantabulla in northwestern New South Wales, 1971-75 (after Giles 1980).

Fig. 2.4  Variation in protein content of food consumed by pigs (line) in relation to rainfall (histogram) and flooding (bars at the top of the figure) at Yantabulla in northwestern New South Wales (after Giles 1980).
Giles (1980) found that the flush of green vegetation which followed heavy rains and/or flooding led to increasing body condition in pigs from both sites. If availability of green feed persisted with continuing favourable seasonal conditions, improved body condition led to decreased juvenile and adult mortality. When available green feed was inadequate for maintenance of condition, adult survival fell and juvenile survival declined dramatically. Using a combination of mark-recapture data and reconstructed age-distributions Giles (1980) demonstrated that juvenile survival increased from 0% when little or no green feed was available, to 60% when rains and/or floods prompted rapid vegetation growth. Mark-recapture studies indicated adult survival varied from 50% to 85% over a similar range of seasonal conditions. Giles (1980) suggested that a lack of protein rich green feed reduced juvenile survival by affecting the quality and/or quantity of milk produced by lactating females, and/or by providing inadequate food resources for recently weaned piglets. In either case, maximum juvenile mortality occurred at or close to weaning. A series of sensitivity analyses indicated that variation in juvenile mortality was the key factor influencing prevailing rate of population increase, suggesting that food represented a proximal limiting factor and rainfall and/or flooding an indirect limiting factor for these populations.

Giles (1980) estimated that under seasonal conditions leading to high survival of adults and juveniles, populations attained an annual exponential rate of increase \( r \) of 0.6-0.7 equivalent to a finite rate of 1.8-2.0, and that this represented a probable maximum \( r_m \). Hone (1983) estimated \( r \) for a pig population at Yantabulla in western New South Wales (Fig 2.1) which was recovering following a poisoning program to be 0.57, a finite rate of 1.77. Although not specifically estimated, data presented by Giles (1980) suggest that under poor seasonal conditions, pig populations decreased at an annual exponential rate of -0.62. Whether this represents a maximum rate of decline \( a \) for the populations studied by Giles is unknown.

### 2.3.2 The role of predation

In contrast to Giles' (1980) study, Woodall (1983) analysed data on the dynamics of feral pig populations from central and western Queensland where pigs and dingoes co-exist. Woodall (1983) used annual trends in bounty payments for dingoes and pigs to index their relative...
abundance ($N$) between 1949 and 1973. Total mortality rate ($M$) was estimated as the difference in successive $\log_{10}$ transformed abundance indices ($M$ is used for total mortality rather than the usual $K$ to avoid confusion with equilibrium density, $K$) (Varley and Gradwell 1968):

$$M_t = \log_{10} N_t - \log_{10} N_{t+1}$$

(2.1)

Woodall (1983) found (1) a significant positive relationship between pig density and $M$ suggesting density-dependent mortality consistent with population regulation, (2) some evidence of delay in density dependence in the chronological sequence of changes in $M$ which might indicate delayed density dependence, (3) a significant positive relationship between dingo density and $M$ for pigs suggesting predation by dingoes was a limiting and potentially regulating factor for pig populations, and (4) a significant negative relationship between rainfall and $M$ for pigs suggesting food availability was also a limiting and potentially regulating factor for pig populations. Unfortunately, Woodall (1983) overlooked the existence of a significant negative relationship between his measure of dingo abundance (bounty payments) and rainfall over the previous 12 months ($F=9.220$, $df=1,16$, $P<0.01$). This relationship suggests that high rainfall in the preceding year led to either (1) lower dingo density (Woodall's assumption), or (2) less dingoes caught or shot for bounty payment. Because there is no significant relationship between $M$ and density for dingoes ($F=2.257$, $df=1,15$, NS), it appears that dingo mortality is not density dependent and the latter is probably true. When the annual number of bounties paid on dingoes is corrected for the effects of rainfall, the apparent relationship between dingo density and $M$ for pigs disappears (Fig 2.5) ($F=0.097$, $df=1,16$, NS). Hence, Woodall's (1983) study suggests a negative relationship between pig mortality rate and antecedent rainfall which may show delayed density dependence, concurring with likely food limitation, but suggesting no effect of predation.
Fig. 2.5 The relationship between total mortality rate (M) for pigs and the number of dingo bounties paid, corrected for rainfall effects (data from Woodall 1983).

2.3.3 Other environments

Saunders (1993a) described the demography of a pig population in a subalpine environment over the course of a 3 year mark-recapture study at Kosciusco National Park in southeastern Australia (Fig. 2.1). Saunders (1993a) concluded that the population was relatively stable at a density of 1.6 pigs/km². Two studies of pig abundance in a highland forest area adjacent to Saunders' (1993) subalpine study site (Hone 1987, McIlroy et al. 1989) gave similar estimates of density (0.9-2.4 pigs/km²). Seasonal variation in body condition indicated that the subalpine population was limited by food availability and/or quality over autumn and winter. A life-table for the population, estimated from the standing age distribution, indicated that mortality was very high for juveniles (0.85 over the first year of life), declining through middle ages. Saunders (1993a) presented indirect evidence that at least some piglet mortality was due to predation by dingoes. He suggested that this, along with over-winter food
shortage, meant that populations in subalpine areas probably had lower rates of increase than populations in the semi-arid rangelands.

Saunders et al. (1990) estimated \( r \) of 0.25 for a population of feral pigs near Bathurst in the central tablelands recovering from a poisoning program. This estimate encompassed a period of 12 months only, and the increase appeared to have occurred more through recolonisation of the area than by intrinsic increases in the resident population.

Caley (1993), using mark-recapture methods on five occasions over two years, estimated pig density of 2.2-3.5 pigs/km\(^2\) for a tropical woodland habitat on the Douglas-Daly River in northern Australia (Fig. 2.1). These population estimates were used to derive estimates of \( r \). Using rainfall as an index of food availability because the abundance of food resources was not measured, Caley (1993) related \( r \) to rainfall over the six months prior to and including the interval between successive estimates of population abundance to derive a numerical response. The numerical response indicated a maximum rate of population increase \( (r_m) \) of 0.78 when rainfall in the six months prior to the interval of population growth exceeded 600mm. Rainfall variation (and hence food availability) in the wet-dry tropics has a very predictable temporal pattern relative to that in rangelands habitats, and Caley (1993) found that this had important consequences for variation in pig abundance. The population he studied moved from phases of population growth to population decline over the regular annual cycle of wet and dry seasons. This is in distinct contrast to the unpredictable variation in rates of population change in rangelands habitats (Giles 1980).

Corbett (1994) used natural variation in the abundance of primary prey for dingoes and an experimental manipulation of the abundance of feral water buffalo \( (Bubalis bubalis) \) to test the effects of predation by dingoes and competition from buffalo on pig abundance in an area of mixed tropical woodland/floodplain at Kapalga in northern Australia (Fig. 2.1). The total response of dingoes to pigs, derived from an estimate of the number of pigs eaten per dingo multiplied by the number of dingoes present, was negatively related to pig density suggesting an inverse density dependent relationship. Corbett (1994) concluded that dingo predation could not regulate the abundance of pigs although it could limit the size of the population.
Corbett (1994) also found that buffalo density had a significant negative effect on pig density and that pigs increased in abundance following buffalo removal. Buffalo and pigs congregate in the ecotone which moves across the floodplain with the drying of inundated areas as the dry season progresses. Corbett (1994) suggested that where buffalo are present they limit access by pigs to underground vegetation in the late dry-season through compaction of the saturated soil in this ecotone. In the late dry-season, protein-rich food is scarce and limited access to underground vegetation will reduce the ability of pigs to successfully wean their offspring. Hence, Corbett (1994) suggested that such interference competition where buffalo occurred may limit pig populations in tropical floodplain environments.

2.3.4 Summary

The population dynamics of pigs have been studied in a variety of habitats in Australia, although in detail only in the semi-arid rangelands and the wet-dry tropics. In both of these habitats, rate of change in population abundance is driven by food availability. In the wet-dry tropics food availability varies in a reasonably consistent pattern with the annual cycle of wet and dry seasons, but may be reduced in some areas by interference competition from buffalo. In the rangelands food availability varies in a stochastic fashion with rainfall and flooding. Predation does not appear to regulate pig populations in the semi-arid rangelands or in the wet-dry tropics although it may limit populations in both habitats. The effect of predation on pig populations in tableland and subalpine environments is unknown, but may be more important than for populations in rangelands or tropical environments. The dog-fence precludes dingoes from the semi-arid rangelands of western New South Wales, thus restricting factors potentially limiting pig abundance to food availability and/or socially mediated spacing behaviour. Giles (1980) demonstrated a link between rainfall, food availability, and rates of increase through variation in mortality and fecundity for pig populations in western New South Wales. These populations attain their highest densities on the floodplains of inland river systems, where they appear to persist despite often dramatic fluctuations in density in response to unpredictable seasonal conditions. The environment of eastern Australia's rangelands, where the present study was conducted is described in detail in Chapter 3.
Chapter 3. Study sites

3.1 The semi-arid rangelands

All sites used in the present study were situated in the semi-arid rangelands which cover approximately 1.7 million km$^2$ or 22% of the area of Australia (Fig. 3.1). In eastern Australia the semi-arid rangelands are generally considered to occur between the 500 and 150mm rainfall isohyets, or between the arable cropping lands to the east and the true deserts of the interior. The climate of the rangelands is characterised by temperatures which are high in the summer and mild in the winter, rainfall which ranges from moderately winter dominant in the south to summer dominant in northern areas influenced by the annual monsoon, and average evaporation which greatly exceeds average rainfall in all months.

Vegetation in the rangelands comprises open forest, woodlands, shrublands and grasslands. (Fig 3.2). Robertson et al. (1987) provided a detailed description of the various vegetation types. Open forest, dominated throughout the eastern rangelands by river red gum (*Eucalyptus camaldulensis*), occurs only along major rivers and around their more permanent billabongs. Woodlands occur on floodplains where they are dominated by black box (*E. largiflorens*), coolibah (*E. microtheca*) or yapunyah (*E. ochropholia*), with a shrub understorey typically dominated by lignum (*Muehlenbeckia cunninghamii*); or on sand plains and ridges where they are dominated by poplar box (*E. populnea*) or cypress pine (*Callitris* spp.) with a shrub understorey of woody species such as hopbush (*Dodonaea* spp.) or emubush (*Eremophila* spp.). Lower woodlands, dominated by belah (*Casuarina cristata*) and rosewood (*Heterodendrum olefolium*) or cypress pine over a shrub understorey of woody species, bluebush (*Marieana* spp.) or *Acacia* spp., also occur in these drier areas. Low shrubland, dominated by saltbush (*Atriplex* spp.) and bluebush (*Marieana* spp.), occurs in often dense stands over about 10% of the rangelands. Tall and open shrublands cover much larger areas (>50% of the rangelands) predominantly on sandplains and dune fields. These taller shrublands are dominated by mulga (*Acacia aneura*), gidgee (*A. cambagei*), western myall (*A. sowdenii*), yarran (*A. homalophylla*) or witchetty bush (*A. kemphaena*), often with a shrub understorey comprising various woody species. Mallee scrub is a characteristic
association formed by often extensive stands of low, multi-stemmed eucalypts such as *Eucalyptus socialis*, *E. dumosa* and *E. oleosa*, often with an understorey of woody shrubs or hummock grasses (*Triodia* spp.).

Grazing by domestic and introduced herbivores and a reduction in the frequency of fire coinciding with the advent of pastoralism have modified large areas of rangelands vegetation. Palatable perennial grasses such as kangaroo grass (*Themeda australis*), sub-shrubs such as old man saltbush (*Atriplex nummalaria*) and trees such as myall (*Acacia pendula*) have declined in abundance, while there have been concomitant increases in unpalatable grasses such as copper burr (*Sclerolaena* spp.) and various weeds and woody shrubs such as hopbush and turpentine (Robertson et al. 1987).

### 3.2 The Paroo River area

The bulk of research described in this thesis was conducted on five study sites along the Paroo River in northwestern New South Wales, and a sixth site on the Cuttaburra Creek, an important tributary of the Paroo (Fig. 3.3). The Paroo River area was selected for the study for three reasons: (1) it has contained significant densities of feral pigs since the region was settled in the 1840s (Giles 1980), (2) it is remote enough that harvesting and recreational hunting rarely if ever occur and (3) it is within the dog-proof fence, thus precluding the potential effects of predation by dingoes. The Paroo drains an area of approximately 73,910 km² of southwestern Queensland and northwestern New South Wales. The river crosses the Queensland/New South Wales border as a relatively well defined stream before opening into a broad floodplain comprising multiple braided channels, permanent billabongs, ephemeral waterholes and extensive semi-permanent swamps. Waters from the Paroo eventually drain into the Darling River in the region of the village of Tilpa, although no single drainage can be identified, so extensive is the Paroo floodplain at that point.
Fig. 3.1  Area of the semi-arid rangelands in Australia (Robertson et al. 1987).

Fig. 3.2  Habitat composition of the semi-arid rangelands in Australia (Robertson et al. 1987).
3.2.1 Study sites

The two most northern sites used in the study were located on Nocoleche Nature Reserve which is bisected by the Paroo. Domestic stock have been largely excluded from the reserve since sheep grazing ceased in 1975. Two study sites were established on the eastern half of the reserve, one (NP) encompassing the floodplain of the Paroo, the other (NC) encompassing the floodplain of Cuttaburra Creek, a tributary of the Paroo. While the two sites were adjacent, they were believed to contain largely distinct feral pig populations because the floodplain encompassed by each site was unconnected and separated by an area of red soil, unfavourable for pigs, 12-21km wide. Supporting the perception that the two sites contained substantially separate feral pig populations is the observation that none of 38 pigs radio-tracked on the Paroo site over a period of three years moved to the Cuttaburra site (N. Dexter, pers. comm.). All other sites used in the study were separated by at least 25km.
The NP site was 27,000ha in area, with the Paroo running north-south through its centre. The NC site was established immediately to the east of NP, and was 21,000ha in area with Cuttaburra Creek running from its north eastern corner to its southern boundary. While the Cuttaburra is a tributary of the Paroo, its floodplain is more commonly inundated by water moving back up its channels when the Paroo floods than by waters moving down from its own much smaller catchment. A 20,000ha study site (TO), encompassing the confluence of the Paroo and the Cuttaburra, was established on Toonborough, a large grazing property 30km south of Nocoleche. TO had the most extensive areas of black soil floodplains of any of the sites used in the study. A 16,500ha study site (GO), taking in the broad floodplain of the now fully integrated channels of the Paroo and Cuttaburra, was established on Goorimpa, a grazing property 25km to the south of Toonborough. A 16,000ha site (LA) was located on Laurelvale, a grazing property 30km to the southwest of Goorimpa. The most southern site (NA) was 14,000ha in area, established across three large channels and their associated floodplain on Napunyah, a grazing property 25km to the south of Laurelvale.

3.2.2 Climate

Wanaaring, a village on the Paroo to the north of the study sites, receives a mean annual rainfall of 193mm with slight summer dominance. The reliability of rainfall in a given year and season is low (Table 3.1). Maximum summer temperatures in the region often exceed 40°C while minimum winter temperatures can fall below 0°C. Evaporation exceeds rainfall in all seasons (Gentilli 1971).

The Paroo floods irregularly in response to high rainfall anywhere in its Queensland catchment. Floodwaters move down into the region of the study sites, filling the braided networks of channels as they spread across the broad floodplain. Waterholes and billabongs become connected, and the extensive black soil floodplains become submerged, creating shallow swamps which may persist for considerable periods after the peak of flooding passes. The extensive nature of the rivers floodplain means that both the frequency and intensity of rainfall in the catchment of the river affect the frequency of flooding through the area of the study sites. While less intense rainfall events may lead to widespread flooding on the more
### Table 3.1
Annual and seasonal rainfall at Wanaaring on the Paroo River, and its reliability. Seasonal rainfall is the mean for three months for the period 1926-1991.

<table>
<thead>
<tr>
<th>Season</th>
<th>Summer (Dec-Feb)</th>
<th>Autumn (Mar-May)</th>
<th>Winter (June-Aug)</th>
<th>Spring (Sept-Nov)</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall</td>
<td>63</td>
<td>52</td>
<td>53</td>
<td>57</td>
<td>193</td>
</tr>
<tr>
<td>SD</td>
<td>55</td>
<td>55</td>
<td>24</td>
<td>44</td>
<td>94</td>
</tr>
<tr>
<td>CV%</td>
<td>87</td>
<td>106</td>
<td>70</td>
<td>100</td>
<td>49</td>
</tr>
</tbody>
</table>

northern study sites, high intensity or protracted falls are required to guarantee the movement of significant flood waters into the southern sites. Floods moving through the study sites may or may not be accompanied by local rainfall. Rainfall in the region of the study sites rarely creates water flow substantial enough to connect waterholes and billabongs unless it accompanies water moving down the river from farther north in its catchment. However, local rainfall can replenish water levels in billabongs and submerge ephemeral swamps.

### 3.2.3 Topography and soils

The Paroo area, being dominated by the floodplain of the river, has little topographical relief. The area contains three distinct landforms defined by topography and soil type; (1) red soil dunes and plains, (2) grey soil clay-pans, and (3) black soil floodplains. Red soil areas are remnant dunefields and associated sand plains at the margin of the dune fields. Red soil areas are made up of aeolian red sands and, being higher than the floodplains which are interspersed through them, do not hold floodwaters. Grey soil clay-pans form in the swales of the remnant dune fields and in depressions throughout the sand plain areas. They contain silty clays or clay loams deposited more commonly by flooding through local rainfall than by accumulated flood waters. Floodplains comprise a mosaic of landforms on and around the floodplains, billabongs, swamps and creeks of the Paroo and Cuttaburra, and associated networks of braided streams. While higher islands and promontories of red soil occur...
throughout the floodplains, they are predominantly flat with occasional channels, waterholes and billabongs. The black soils which make up the floodplains are heavy-textured grey clays deposited as the river opens out across its broad floodplain and the movement of waters slows. Because grey clays expand when wet and crumble rather than powder when dry, the black soils they form become self-sealing under conditions of heavy rain or flooding, cracking deeply as they dry out. The black soils of these floodplains are consequently very resistant to erosion, are self-mulching and have a much higher organic content than the red sands which typically surround them.

3.2.4 Vegetation

In the region of the study sites, red soils supported either grasslands or more commonly shrublands. Shrublands were dominated by hopbush and other woody shrubs, usually emubush (Eremophila longiflora), budda (E. mitchelli), and turpentine (E. sturtii). Stands of taller timber, consisting of belah, rosewood and occasionally white cypress pine were distributed through these areas. While red soil areas did not hold flood waters, they produced substantial growth of annual and perennial grasses (notably Stipa spp.) following local rainfall. Grassland areas were dominated by speargrasses (Stipa spp.), common bottlewashers (Enneapogon avenaceus), and often woollybutt (Eragrostis eripoda). There was virtually no tree or shrub cover, although small isolated stands of white cypress pine or belah/rosewood occurred occasionally. Grasslands did not hold floodwaters, but also produced a luxuriant growth of annual and perennial grasses and forbs following local rain. Grass plains often link areas dominated by woody shrubs.

Grey soil clay-pans typically supported often monospecific stands of canegrass (Eragrostis australasica or Leptochloa digitata), and less commonly sparse stands of lignum or saltbush. During and following flood, these shallow clay pans produced a flush of grasses (mostly Aristida, Stipa and Poa), and various forbs including an often lush coverage of wild lettuce (Lattuca spp.).
Vegetation on black soil floodplains was typically dominated by lignum, interspersed with stands of black wattle (*Acacia stenophylla*). Yapunyah, coolibah and black box occurred largely around the edges of these floodplains, with river red gums and black box in often thick stands along the banks of deeper channels and around waterholes and billabongs. During and immediately following flood, these areas produced a luxuriant growth of grasses (largely *Aristida*, *Stipa*, *Panicum*, *Eragrostis*, *Sporobolus*, *Poa* and *Astrebla* spp.), legumes (*Medicago* and *Trigonella* spp.), nardoo (*Marsilea drummondii*) and a variety of forbs.

3.2.5 Fauna

The dominant terrestrial herbivores in the region of the study sites were sheep (*Ovis aries*), red and grey kangaroos, feral goats (*Capra hircus*) and feral pigs. While both eastern (*Macropus giganteus*) and western (*M. fuliginosus*) greys occurred in the region, Caughley et al. (1984) estimated that 75-91% of the grey kangaroos were eastern greys. Small numbers (probably <30) of feral horses (*Equus caballus*) and feral camels (*Camelus dromedarius*) occurred on two of the sites, while low densities of euros (*M. robustus*) were present on all sites. Most of the grazing properties maintained small herds of domestic cattle (*Bos taurus*). Rabbits and herbivorous insects were present on all sites but the abundance of both remained uniformly low throughout the study.

As all study sites were within the dog-proof fence, of the large carnivores present (red fox (*Vulpes vulpes*), feral cats (*Felis catus*) and wedge-tailed eagles (*Aquila audax*)), only the fox was considered capable of preying on feral pigs. Four dietary studies of foxes have been conducted in areas at least potentially inhabited by pigs (Coman 1973, Croft and Hone 1978, Green and Osborne 1981, Catling 1988, Lunney et al. 1990). Only Coman (1973) and Croft and Hone (1978) found evidence of pig consumption, and in both cases data indicated <1% occurrence by frequency in fox stomachs, suggesting that foxes are an insignificant predator of pigs.
Chapter 4. Pig density, pasture biomass and rate of population increase

4.1 Introduction

Two hypotheses related to the effects of food availability on variation in the abundance of large herbivore populations were identified in chapter 1: (1) the intrinsic food hypothesis and (2) the extrinsic food hypothesis. The intrinsic food hypothesis proposes that the density of a herbivore population is regulated at or around some equilibrium ($K$) through density dependent variation in its rate of change in abundance ($r$) through the effect of per capita food availability on the demographic rates of the population (Sinclair et al. 1985). Two models have been used to evaluate the applicability of the food hypothesis to herbivore populations and predict the dynamics of grazing systems to which it applies: (1) single-species models (derived from logistic population growth models) and (2) interactive models (derived from predator-prey theory) (Caughley 1976a). Single-species models imply the interaction of herbivores and their food resources through a density dependent decline in $r$ as populations approach $K$ (Caughley 1976a, 1977). In contrast, interactive models explicitly represent the interaction of herbivores and their food supply through the effects of parabolic plant productivity, and the functional and numerical responses of herbivores to variation in vegetation biomass (Caughley 1976a, 1987). The functional and numerical responses form a negative feedback loop between vegetation and herbivore abundance which imparts a tendency toward equilibrium (centripetality) through density dependent intraspecific competition for food resources (Caughley 1976a, 1987). In chapter 1 it was demonstrated that single-species models are a special case of interactive models where environmental variation is low enough and/or the demographic and grazing efficiency of herbivores high enough, that centripetality is absolute and $K$ and density dependence can be assumed constant.

Alternatively, the extrinsic food hypothesis proposes that herbivore populations do not affect the rate of renewal in the abundance of their food resources and hence are not regulated through density dependent variation in per capita food availability (Andrewartha and Birch 1954, 1984). Two models have been used to represent the dynamics of populations conforming to the extrinsic shortage hypothesis; (1) random-walk models in which variation
Chapter 4. Pig density, pasture biomass and rate of population increase

4.1 Introduction

Two hypotheses related to the effects of food availability on variation in the abundance of large herbivore populations were identified in chapter 1: (1) the intrinsic food hypothesis and (2) the extrinsic food hypothesis. The intrinsic food hypothesis proposes that the density of a herbivore population is regulated at or around some equilibrium ($K$) through density dependent variation in its rate of change in abundance ($r$) through the effect of per capita food availability on the demographic rates of the population (Sinclair et al. 1985). Two models have been used to evaluate the applicability of the food hypothesis to herbivore populations and predict the dynamics of grazing systems to which it applies: (1) single-species models (derived from logistic population growth models) and (2) interactive models (derived from predator-prey theory) (Caughley 1976a). Single-species models imply the interaction of herbivores and their food resources through a density dependent decline in $r$ as populations approach $K$ (Caughley 1976a, 1977). In contrast, interactive models explicitly represent the interaction of herbivores and their food supply through the effects of parabolic plant productivity, and the functional and numerical responses of herbivores to variation in vegetation biomass (Caughley 1976a, 1987). The functional and numerical responses form a negative feedback loop between vegetation and herbivore abundance which imparts a tendency toward equilibrium (centripetality) through density dependent intraspecific competition for food resources (Caughley 1976a, 1987). In chapter 1 it was demonstrated that single-species models are a special case of interactive models where environmental variation is low enough and/or the demographic and grazing efficiency of herbivores high enough, that centripetality is absolute and $K$ and density dependence can be assumed constant.

Alternatively, the extrinsic food hypothesis proposes that herbivore populations do not affect the rate of renewal in the abundance of their food resources and hence are not regulated through density dependent variation in per capita food availability (Andrewartha and Birch 1954, 1984). Two models have been used to represent the dynamics of populations conforming to the extrinsic shortage hypothesis; (1) random-walk models in which variation
in $r$ is entirely stochastic and (2) reactive vegetation-herbivore models in which population abundance is limited but not regulated by available resources (Caughley and Lawton 1981). Vegetation-herbivore systems cannot generally conform to random-walk models because herbivore populations are considered to have at least a notional equilibrium set by the effect of prevailing food availability on $r$ (Caughley and Lawton 1981). Caughley (1987) simulated an unregulated equilibrium grazing system by removing the functional response from an interactive model describing the variation in red kangaroo and pasture abundance. In this system, food availability limited kangaroo abundance through the numerical-response, but the lack of any reciprocal influence of kangaroos on pasture biomass negated any potential for regulation through density dependent intraspecific competition for pasture resources.

This chapter describes an experiment conducted to assess the applicability of the intrinsic and extrinsic food hypotheses to the dynamics of feral pig populations inhabiting the semi-arid rangelands of inland Australia. As stated in Chapter 1, predictions of the interactive and reactive vegetation-herbivore models were evaluated using a manipulative experiment in which the density of six feral pig populations was reduced to one of three densities (treatments) annually and variation in vegetation biomass and $r$ for pigs monitored quarterly over two and a half years. It was predicted that if the interactive model was an appropriate description of the dynamics of pigs grazing native pastures, variation in $r$ with density would be negative if the grazing system has strong centripetality (constant density dependence), or non-significant if centripetality is weak (shifting density dependence). In either case, higher densities of pigs should be associated with reduced pasture biomass. If the reactive model was a more appropriate description of the pig-pasture grazing system, there would be no significant change in either $r$ or pasture biomass with increasing pig density. A positive numerical response by pigs to increasing pasture availability should be observed for both models, and would confirm that the reactive model is more appropriate than a random-walk model to represent the extrinsic food hypothesis. These predictions were summarised in Table 1.1.
4.2 Methods

4.2.1 Study sites and conditions during the experiment

The six study sites used in this experiment were located on the Paroo River in northwestern New South Wales. Detailed descriptions of the Paroo area and the study sites were given in Chapter 3. This section describes patterns of rainfall and flooding for the six study sites over the duration of the experiment and provides additional details of site characteristics which proved important during the course of the experiment. Because continuous rainfall data were unavailable for individual study sites, records from Wanaaring, a village 20km to the north of sites NP and NC, were used. Total quarterly rainfall over the duration of the experiment is shown in relation to long-term quarterly averages and as deviations from long-term (66 year) averages in Figs 4.1(a) and (b) respectively.

In order to gain some idea of the incidence and magnitude of flooding on each site during the course of the study, the presence of high, moderate, low or no flood waters was scored monthly by landholders or land managers based on their long-term experience of flooding on the sites in their care. Monthly scores given for sites running from north to south are shown in Fig. 4.2. Flooding was more frequent on the northern sites because lower level floods reached these areas but did not travel farther south. Extreme flood events (ie: during 1990) were more uniform in their effects, though arriving somewhat later on sites progressively farther south.

With the exception of the first quarter of the experiment when no rain fell, summer rainfall was consistently higher than average. Above average rainfall in northwestern New South Wales during the summer of 1989/90 was followed by extremely high rainfall throughout inland Australia in the autumn, which led to extensive flooding in many river systems including the Paroo. Floodwaters persisted on all sites until the spring. Autumn rainfall was also above average in 1989 and 1990, but was below average in 1991 and 1992. Winter rainfall was below average in all years except during the final quarter of the experiment. Spring rainfall was consistently higher than winter rainfall, but was below average in every year of the experiment.
Fig. 4.1  Total quarterly rainfall (mm) for the village of Wanaaring over the course of the experiment (a) compared to long-term quarterly averages (continuous line), and (b) as deviations from long-term quarterly averages.
Fig. 4.2 Monthly flood scores for each study site over the course of the experiment. Scores are a subjective assessment by land managers familiar with each site of whether floodwaters were (0) non-existent, (1) low, (2) moderate or (3) high over the majority of each month.
Conditions along the Paroo at the beginning of the experiment were poor, the area having like the rest of northwestern New South Wales, experienced a moderate drought during 1986 and 1987. Good rainfall in the autumn and spring of 1988 and the autumn of 1989 improved conditions markedly through 1989, despite below average rainfall in the winter and spring of 1989. Above average rainfall at the beginning of 1990 saw extensive flooding throughout western New South Wales. Flood waters in the Paroo area did not decline substantially until late in the winter of that year. There followed a period of relatively dry weather, with above average rainfall in the summer of 1990/91 coming mostly as sporadic and patchy storms in January. Conditions on sites NC and TO were alleviated slightly during autumn by a small flood coming down the Cuttaburra Creek, but overall conditions continued to deteriorate through 1991 until reasonable rains fell in the summer of 1991/92. The following autumn was dry but substantial rain fell over winter in the final quarter of the experiment leading to a minor flooding on most sites.

Because preliminary surveys of pig abundance indicated a strong association between pig density and floodplain habitat (see below), some variation in pig density between study sites appeared to be related to between-site differences in the area of floodplain. To estimate the percentage of each site covered by floodplain habitat, a transparent sheet with a 1x1mm grid was placed over a 1:100,000 orthophotographic map of each site, and the number of grid squares (each representing 1ha) containing floodplain counted. Floodplain habitat was identified from a combination of vegetation, proximity to obvious water courses and the shade of soil. Landsat imagery and aerial photographs were used to resolve any grid squares where differentiation of floodplain was unclear or confused on the orthophotographic map.

4.2.2 Experimental design

Pig density, pasture biomass, and the abundance of other large herbivores were monitored on the six study sites over 12 months (summer 1988/89 to summer 1989/90) prior to implementation of treatments (see sections 4.2.3 and 4.2.4 for survey methods). Pasture biomass was measured over three quarters, the abundance of other herbivores over two
quarters, and pig density over five quarters. Site characteristics and conditions prevailing at the time of the first surveys in summer 1988/89 are given in Table 4.1.

Daily pasture offtake by other herbivores was calculated from estimates of kangaroo and goat density based on aerial counts, and from mustering returns for sheep. Visibility bias associated with aerial counts of kangaroos and goats was accounted for using correction factors derived from double-count surveys (Choquenot 1994 and unpublished data). Daily per capita pasture offtake by kangaroos, goats and sheep was calculated from estimates of the pasture intake of each species at given pasture biomass using the functional responses of sheep and red and western grey kangaroos measured by Short (1986, 1987). It was assumed that red and grey kangaroos weighed 35kg, goats and sheep 65kg, that eastern grey kangaroos had the same functional response to native pasture as western grey kangaroos, and goats the same as sheep.

<table>
<thead>
<tr>
<th>Site</th>
<th>Total area (ha)</th>
<th>Percent floodplain</th>
<th>Pasture (kg/ha) (overall)</th>
<th>Pigs/km² (floodplain)</th>
<th>Pigs/km² other herbivores</th>
</tr>
</thead>
<tbody>
<tr>
<td>NP</td>
<td>27,000</td>
<td>10</td>
<td>484</td>
<td>3.7</td>
<td>22</td>
</tr>
<tr>
<td>NC</td>
<td>21,000</td>
<td>7</td>
<td>396</td>
<td>2.9</td>
<td>21</td>
</tr>
<tr>
<td>TO</td>
<td>20,000</td>
<td>18</td>
<td>477</td>
<td>4.9</td>
<td>25</td>
</tr>
<tr>
<td>GO</td>
<td>16,500</td>
<td>15</td>
<td>501</td>
<td>4.8</td>
<td>23</td>
</tr>
<tr>
<td>LA</td>
<td>16,000</td>
<td>14</td>
<td>411</td>
<td>3.9</td>
<td>21</td>
</tr>
<tr>
<td>NA</td>
<td>14,000</td>
<td>5</td>
<td>458</td>
<td>1.8</td>
<td>14</td>
</tr>
</tbody>
</table>

Table 4.1: Total area, percentage of floodplain habitat, pasture biomass, pig density over the entire site and over floodplain habitat, and pasture offtake by other herbivores on each site in summer 1988/89.
Table 4.2 Sites ranked by the percentage of their floodplain habitat, with average pig densities (for the three sites with more and the three sites with less floodplain) immediately before implementation of treatments, the treatment imposed, and the actual percentage reduction in pig density achieved.

Estimates of feral pig density during initial surveys (Table 4.1) indicated a strong affinity of pigs for black soil floodplain habitat, suggesting that the proportion of floodplain on each site may influence the local dynamics of pig populations. Hence, treatments were applied in a randomised block design which accounted for potential floodplain effects by ranking sites according to their percentage area of floodplain habitat (see section 4.2.1) and randomly allocating treatments amongst the three sites with more and three sites with less floodplain. Treatments were high (>90%), moderate (50-65%) or low level (<35%) reduction in pig density (2 sites each), based on average pig density for the three sites with more and three
sites with less floodplain, measured immediately prior to imposition of treatments in summer 1989/90 (Table 4.2). Treatments were reimposed each summer until 1991/92, wherever pig abundance had increased beyond target densities. All imposed reductions in pig density were carried out by shooting from helicopters, with the exception of two surveys on site NP and one survey on LA where a combination of cage trapping and helicopter shooting were used. Details of the cage trapping technique are given in Choquenot et al. (1990) and Saunders (1993a).

Pig density and pasture biomass were monitored quarterly on all sites following the initial imposition of treatments until winter 1992, two quarters after final reductions in pig density had taken place. Pasture biomass could not be estimated in autumn 1990 because of extreme flooding on all sites. The abundance of other herbivores was estimated less frequently (in 10 of 15 quarters).

4.2.3 Estimating the abundance of pigs and other herbivores

Pig density was estimated from either (1) corrected helicopter counts (10 quarters) or (2) an indirect index of abundance based on the maximum percentage of bait trails taken (MPBT) (5 quarters). The abundance of other herbivores was estimated using helicopter counts only. Helicopter counts were standardised to account for potential bias in the sightability of pigs (visibility bias) associated with time of day, cloud cover and prevailing ambient temperature. Visibility bias related to sightability of pig groups in different habitats was estimated and removed from counts using multiplicative correction factors. Variation in MPBT due to food availability (indexed as pasture biomass) was estimated and accounted for using 6 simultaneous estimates of MPBT and absolute pig density (estimated from helicopter counts) for each site. A regression predicting pig density from MPBT was derived from these data. Experimental evaluations of the two techniques, and derivation of all relevant correction factors allowing estimation of total population densities from both helicopter counts and MPBT are described in appendix 1.
On each occasion a site was surveyed from helicopter, transects were placed randomly without replacement across study sites, with the number of transects estimated to return sampling rates of around 15%. Actual sampling rates were calculated later from start and end time for each transect and known airspeed. Transects were placed so as to be perpendicular to the general orientation of floodplain habitat on each site. This entailed east-west transects on all sites except NA where southeast-northwest transects were used. All surveys were conducted at an altitude of 30.5m (100ft), an airspeed of 80km/hr and during the first and last three hours of daylight under conditions of little or no cloud (<1 octal). Air temperature, recorded at the beginning of each transect, did not exceed 21°C. Left and right observers, seated in the rear of Kawasaki/Bell 47 or Hughes 500C helicopter, counted feral pigs, red kangaroos, grey kangaroos, emus and feral goats in groups as they occurred in 150m-wide transects demarked by right-angled poles attached to either side of the helicopter. Groups of animals represented sighting entities rather than biologically meaningful associations of animals. Counts were made onto a continuously running tape recorder and collated at the completion of each survey. The number of pig groups counted in each transect was corrected for habitat effects (see appendix 1), then multiplied by the average size of pig groups for the survey. The 'simple' method (Caughley 1977) was used to derive population estimates from corrected transect totals.

For each MPBT survey, bait trails were distributed along tracks and trails on each site. Ninety trails were distributed on site NP, 80 on sites NC and TO, 70 on sites GO and LA, and 60 on site NA. In most cases, bait trails were placed in locations where pigs, if present, would be likely to find them. These locations included the edge of waterholes, distinct rubs under fences, clear animal pads, areas dominated by lignum and along ephemeral drainage lines. Before treatments were implemented, most locations where bait trails were placed had sign of recent pig activity. The minimum distance between bait trails was 1.5km and the same bait trail locations were used for each site throughout the study. A bait trail consisted of approximately 8kg of fermented wheat, distributed along a 70-100m trail consisting of 7-10 discrete piles with wheat trickled between (Choquenot et al. 1990, Saunders 1993a). Bait trails were inspected daily and either freshened or replaced. Those that had been consumed by pigs (indicated by the presence of tracks and/or the complete consumption of wheat) were
recorded and expressed as a proportion of all bait trails on offer. Once pigs began consuming bait trails they were rarely abandoned, as long as the trail continued to be offered. Bait trails continued to be offered until 3-7 days after maximum percentage bait take, ascertained visually from plots of percentage bait take over time, was achieved. Average percentage bait take following attainment of this maximum (MPBT) was used as an index of pig density following frequency-density transformation (Caughley 1977).

4.2.4 Estimating pasture biomass

Pasture biomass for the three generic soil types which made up all sites (black soils on riverine floodplain, grey soils on cane grass flats and red soil areas elsewhere) was estimated quarterly on each site. The three soil types corresponded to habitat types identified during aerial surveys (see appendix 1), except that red soil shrubs and red soil grass plains were combined into a single red soil type. On each sampling occasion pasture biomass on each soil type was sampled randomly throughout each site, until soil-type specific biomass estimates achieved a coefficient of variation (CV%) of <15%. Actual sample sites were re-randomised at each quarterly survey.

For each pasture biomass sample, the above-ground biomass of grasses and forbs, estimated using a modified version of the comparative yield technique (Haydock and Shaw 1975), was averaged across three 0.25m² quadrats positioned at random in an area of 0.01ha. During each survey, 20 additional quadrats for each of the 3 soil types sampled, selected to span the range of biomass for dominant plant associations observed during sampling, were scored according to the comparative yield techniques, photographed, cut, oven-dried and weighed. These series were accumulated into sets of photographic standards against which the biomass in sampled quadrats was assessed visually. Seven sets of standards were used in assessing pasture biomass over the course of the study.
4.2.5 Analysis

Sequential estimates of pig density and pasture biomass from individual sites were potentially autocorrelated (Snedecor and Cochran 1967). To examine the degree of autocorrelation in estimates of pig density and pasture biomass, correlograms of series of estimates, log-transformed to normalise variances, were plotted and examined for each site. The shortest interval between quarterly estimates which returned correlation coefficients <0.15, averaged across study sites, was used to determine the period between quarters which maximised independence for each measure. This reduced data set was used to test for treatment and pig density effects on the rate of increase for pig populations and the grazed biomass of pasture using inferential statistics. However, because assessment of the effects of soil type, rainfall and flooding on grazed pasture biomass, and of pasture biomass on rate of increase for pig populations sought to develop predictive models, it was considered appropriate to evaluate variation in the entire data set.

Estimates of annual exponential rates of pig population increase \((r)\) for all sites were calculated by subtracting the logged pig density estimate for a given quarter \((\ln N)\) from the logged density estimate in the subsequent quarter \((\ln N_{t+1})\), and multiplying by four. The effect of treatments, time since implementation of treatments and their interaction on variation in \(r\) was evaluated using fixed factor analysis of variance (anova), and the direct effect of pig density on \(r\) using regression analysis. The effect of soil type on grazed pasture biomass was assessed using fixed factor anova, and the effects of rainfall and flooding using multiple regression analysis. The resultant regression model was used to remove variation in grazed pasture biomass due to these factors, before the effect of treatments, time since implementation of treatments, and their interaction were evaluated using anova. The direct effect of pig density on grazed pasture biomass was evaluated using regression analysis. The effect of grazed pasture biomass on \(r\) was evaluated using regression analysis and an inverted exponential model of Ivlev form was fitted to the relationship.

The coefficient of determination for least squares lines of best fit is given as \(R^2\) throughout to avoid confusion with exponential rate of population increase, \(r\).
4.3 Results

4.3.1 Variation in pig density

Variation in pig density over the course of the experiment is shown for the three sites with more and three sites with less floodplain in Figs 4.3(a) and (b) respectively. There was a general increase in pig abundance through 1989 prior to imposition of treatments in summer 1989/90. Pig abundance increased on most sites through 1990, and treatments were reimposed on all sites except NA in summer 1990/91. Pig densities on NA declined from 0.43 to 0.37 during 1990, so no reduction was necessary to maintain the population at <10% of average starting density for sites with less floodplain. Because the density of all populations declined during 1991, some dramatically, pig density was reduced on site TO only in summer 1991/92. With the exception of TO and GO, the density of all populations increased slightly between summer 1991/92 and the conclusion of the experiment in winter 1992.

4.3.2 Effect of treatment and pig density on $r$

Serial correlograms of logged density estimates for each site indicated that the interval between quarterly estimates of pig density which maximised independence ranged from 2 to 5. An interval of 3 quarters was selected for analyses of the effects of treatment and time on $r$. This allowed 4 independent estimates of $r$ for each site following implementation of treatments and 5 for the entire monitoring period.

Estimates of $r$ for the entire data set ranged from -2.30 to 1.24. Analysis of variation in $r$ with treatment and time since implementation of treatments for the independent subset of data indicated no significant variation with treatment, time or their interaction (Table 4.3). This suggests that $r$ varied independently of the magnitude of reductions in pig density corresponding to treatments, and the time since their imposition.
Fig. 4.3 Variation in estimated pig density over the course of the experiment for (a) the three sites with more and (b) three sites with less floodplain habitat. Discontinuous lines indicate reductions in pig density associated with implementation and maintenance of experimental treatments. Low, moderate and high level reductions in pig density are shown by the symbols ●, ▲ and ■ respectively. In (a) sites are GO (●), LA (▲) and TO (■); and in (b) sites are NC (●), NP (▲) and NA (■).
Table 4.3  Analysis of variation in annual exponential rates of population increase \((r)\) associated with treatment, time since implementation of treatments and their interaction.

Because pig density varied somewhat independently of imposed treatments (Fig. 4.3 (a) and (b)), systematic variation in \(r\) with treatment may have been obscured. To examine the direct relationship between \(r\) and pig density, \(r\) was regressed on logged pig density lagged from 0 to 4 quarters (12 months). Given the reproductive potential of feral pigs in this environment (Giles (1980) estimated that sows produce 1.93 litters/year under good conditions), 4 quarters was considered the longest likely lag in feedback between pig density and a detectable change in \(r\). None of the regressions was significant (Table 4.4) suggesting that \(r\) was not related to prevailing or lagged pig density.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Anova SS</th>
<th>Mean Square</th>
<th>F-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>2</td>
<td>0.7154</td>
<td>0.3577</td>
<td>0.62</td>
<td>0.553</td>
</tr>
<tr>
<td>Time</td>
<td>3</td>
<td>4.1378</td>
<td>1.3793</td>
<td>2.40</td>
<td>0.118</td>
</tr>
<tr>
<td>Treatment*Time</td>
<td>6</td>
<td>0.0947</td>
<td>0.0158</td>
<td>0.03</td>
<td>1.000</td>
</tr>
<tr>
<td>Error</td>
<td>12</td>
<td>6.8865</td>
<td>0.5739</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td>11.8345</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4.4  Summary of regressions of \(r\) on logged pig density, lagged 0 to 4 quarters.
The lack of any relationship between $r$ and either treatment or pig density corresponds with predictions of the intrinsic food hypothesis where centripetality is weak and the extrinsic food hypothesis, but not the intrinsic food hypothesis where centripetality is strong (see Table 1.1).

4.3.3 Variation in grazed pasture biomass

Variation in grazed pasture biomass over the course of the experiment, averaged across the 3 soil types, is shown for the 3 sites with more and less floodplain in Figs 4.4(a) and (b) respectively. Over the course of the experiment, estimated pasture biomass ranged from 23 to 1,396 kg/ha. There was a modest increase in pasture biomass on all sites through 1989 prior to imposition of treatments in summer 1989/90. Pasture biomass suffered a general decline over the first quarter of 1990, followed by a dramatic increase to peak levels on all sites during spring and summer in response to heavy rainfall and flooding over the previous summer and autumn. A universal decline occurred through 1991, biomass on all sites falling to its lowest levels of the entire monitoring period during spring and summer. Pasture responded to drought-breaking rains in summer 1991/92 and the following winter, displaying some recovery in biomass over the final two quarters of the experiment.

4.3.4 Effect of soil type, rainfall and flooding on pasture biomass

Analysis of variation in logged pasture biomass due to soil type, time since monitoring commenced and their interaction across the entire monitoring period, indicated no effect of soil type on pasture biomass over and above variation through time (Table 4.5). Pasture biomass was averaged across all soil types in subsequent analyses.

The effect of rainfall and flooding on variation in logged grazed pasture biomass was investigated using multiple regression analysis. Pasture biomass estimates for each study site were regressed on (1) rainfall accumulated over 1, 3, 6, 12 and 24 months prior to the month in which pasture biomass was estimated, and (2) a flooding index calculated from the number of months in each quarter that a site was considered to be at least partially flooded (flood score >0, see section 4.2.1). Pasture biomass was best associated with rainfall accumulated
Fig. 4.4  Variation in grazed pasture biomass estimated over the course of the experiment for (a) the three sites with more and (b) three sites with less floodplain habitat. Low, moderate and high level reductions in pig density are shown by the symbols ○, △ and ■ respectively. In (a) sites are GO (○), LA (△) and TO (■); and in (b) sites are NC (○), NP (△) and NA (■).
over the previous 12 months (Table 4.6), with the flooding index \((t=2.493, df=74, P=0.015)\), but not site \((t=0.354, df=74, P=0.724)\) contributing significantly to the relationship. Because the intercept of the least squares line of best fit describing the relationship between pasture biomass, 12 months accumulated rainfall and the flooding index was not significantly different from 0 \((t=0.242, df=74, P=0.809)\), the regression was forced through its origin.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Anova SS</th>
<th>Mean Square</th>
<th>F-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil</td>
<td>2</td>
<td>0.0291</td>
<td>0.0146</td>
<td>0.08</td>
<td>0.927</td>
</tr>
<tr>
<td>Time</td>
<td>11</td>
<td>85.3488</td>
<td>7.7590</td>
<td>40.15</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Soil*Time</td>
<td>22</td>
<td>0.2065</td>
<td>0.0094</td>
<td>0.05</td>
<td>1.000</td>
</tr>
<tr>
<td>Error</td>
<td>180</td>
<td>34.7838</td>
<td>0.1932</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>215</td>
<td>12.3683</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4.5  Analysis of variation in logged pasture biomass associated with soil type, time since monitoring commenced and their interaction.

<table>
<thead>
<tr>
<th>Rainfall interval (months)</th>
<th>(R^2)</th>
<th>F-value</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.101</td>
<td>3.887</td>
<td>3,74</td>
<td>0.012</td>
</tr>
<tr>
<td>3</td>
<td>0.054</td>
<td>2.475</td>
<td>3,74</td>
<td>0.068</td>
</tr>
<tr>
<td>6</td>
<td>0.064</td>
<td>2.760</td>
<td>3,74</td>
<td>0.048</td>
</tr>
<tr>
<td>12</td>
<td>0.299</td>
<td>11.959</td>
<td>3,74</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>24</td>
<td>0.112</td>
<td>4.226</td>
<td>3,74</td>
<td>0.008</td>
</tr>
</tbody>
</table>

Table 4.6  Variation in grazed pasture biomass accounted for by regression on rainfall accumulated over previous intervals (effects of flooding removed).

The influence of flooding on the relationship between grazed pasture biomass and rainfall was investigated further by assessing the coefficient of determination \((R^2)\) for the regression
of grazed pasture biomass and 12 months accumulated rainfall, as the effect of the flooding index was lagged over progressively longer intervals. A lag of 2 quarters maximised the $R^2$ of the regression at 0.313, suggesting that flooding took around 6 months to have its most profound effect on grazed pasture biomass, over and above variation due to the preceding years rainfall (Table 4.7). However, variation in $R^2$ was low, suggesting that although flooding contributed significantly to variation in grazed pasture biomass, this influence was relatively minor, and clearly subordinate to that of accumulated rainfall.

<table>
<thead>
<tr>
<th>Lag in flood effects (quarters)</th>
<th>$R^2$</th>
<th>F-value</th>
<th>df</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.300</td>
<td>18.115</td>
<td>2,76</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1</td>
<td>0.311</td>
<td>17.650</td>
<td>2,70</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2</td>
<td>0.313</td>
<td>16.399</td>
<td>2,64</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>3</td>
<td>0.294</td>
<td>13.845</td>
<td>2,58</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 4.7 Variation in grazed pasture biomass accounted for by regression on rainfall accumulated over 12 months, with the effects of the flooding index lagged from 0 to 3 quarters.

The final model relating grazed pasture biomass ($V_g$) to rainfall over the preceding 12 months ($RF$) and the flooding index 2 quarters previously ($FI$) was $V_g = 2.197(RF) + 26.684(FI)$, which explains 31.3% of the variation in pasture biomass, leaving a residual standard deviation of 272kg/ha around the regression. Predictive relationships between 12 months accumulated rainfall and pasture biomass for the 4 possible flood indices are shown in Fig. 4.5. The regression model predicts that grazed pasture biomass increased by 2.197kg/ha for every 1mm increase in rainfall over the preceding 12 months, while an increase of 1 in the flooding index 6 months previously increased pasture biomass by 26.684kg/ha. The residual variance around the generalised regression of grazed pasture biomass on accumulated rainfall would exceed differences between models predicted by the four flood scores.
4.3.5 Effect of treatment and pig density on grazed pasture biomass

Serial correlograms of logged grazed pasture biomass for each site indicated that the interval between quarterly estimates of biomass which maximised independence of estimates ranged from 1 to 5. An interval of 3 quarters was used to obtain independent estimates of pasture biomass for analyses of the effects of treatment and pig density. This allowed 4 independent estimates of pasture biomass for each site following implementation of treatments, and 5 for the entire monitoring period.

Because rainfall was measured at only one location, variation over time was identical among sites and treatments. This meant that the effects of rainfall and time since implementation of treatments on pasture biomass were co-linear and could not be separated in analyses of variance. Since both factors could potentially affect grazed pasture biomass, the relative
contribution of each factor to variation in logged grazed pasture biomass was assessed in a partial regression analysis (Table 4.6)

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Regression coefficient</th>
<th>Standard Deviation</th>
<th>t-ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>0.03088</td>
<td>0.0354</td>
<td>0.87</td>
<td>0.392</td>
</tr>
<tr>
<td>Rainfall</td>
<td>0.005792</td>
<td>0.0013</td>
<td>4.42</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 4.6 Relative contribution of time since implementation of treatments (Time) and rainfall accumulated over the previous 12 months (Rainfall) to variation in logged pasture biomass assessed by multiple regression analysis.

Antecedent rainfall clearly explained more variation in grazed pasture biomass than did time. Variation in logged pasture biomass due to treatment, 12 months accumulated rainfall and their interaction, with the flooding index 6 months previously entered as a covariate, indicated that treatment had no significant effect on grazed pasture biomass or on the effect of rainfall on grazed pasture biomass (Table 4.7). This suggests that although pasture biomass varied significantly after the implementation of treatments, this variation was due to the effects of antecedent rainfall and flooding, and independent of the magnitude of reductions in pig density corresponding to treatments.

Because pig density varied somewhat independently of experimental treatments (Figs 4.3(a) and (b)), variation in pasture biomass with pig density may have obscured variation due to treatments per se. To examine the direct relationship between grazed pasture biomass and pig density since imposition of treatments, logged grazed pasture biomass was regressed on 12 months antecedent rainfall, the flooding index 6 months before the pasture biomass estimate and logged pig density at the start of the quarter in which pasture biomass was measured. While the regression was significant ($F=8.09$, $df=3,20$, $P=0.001$), logged pig density did not contribute significantly to explanation of variation in grazed pasture biomass (Table 4.8).
Table 4.7 Analysis of variation in logged pasture biomass after implementation of treatments with treatment, rainfall accumulated over the previous 12 months (Rainfall) and their interaction. The flood score 6 months before the quarter in which grazed pasture biomass was estimated is included as a covariate.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Anova SS</th>
<th>Mean Square</th>
<th>F-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flood score</td>
<td>1</td>
<td>0.0009</td>
<td>0.0009</td>
<td>0.00</td>
<td>0.948</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>0.0121</td>
<td>0.0060</td>
<td>0.03</td>
<td>0.970</td>
</tr>
<tr>
<td>Rainfall</td>
<td>3</td>
<td>8.0585</td>
<td>2.6862</td>
<td>13.40</td>
<td>0.001</td>
</tr>
<tr>
<td>Treat*Rain</td>
<td>6</td>
<td>0.9143</td>
<td>0.1524</td>
<td>0.76</td>
<td>0.616</td>
</tr>
<tr>
<td>Error</td>
<td>11</td>
<td>2.2051</td>
<td>0.2005</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td>11.6553</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4.8 Relative contribution of logged pig density, rainfall accumulated over the previous 12 months (Rainfall) and flood score 6 months previously to variation in logged pasture biomass since the implementation of treatments assessed by multiple regression analysis.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coefficient</th>
<th>Standard deviation</th>
<th>t-ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ln Pig density</td>
<td>-0.0877</td>
<td>0.1045</td>
<td>-0.85</td>
<td>0.411</td>
</tr>
<tr>
<td>Rainfall</td>
<td>0.0066</td>
<td>0.0014</td>
<td>4.65</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Flooding</td>
<td>0.1496</td>
<td>0.1002</td>
<td>1.49</td>
<td>0.151</td>
</tr>
</tbody>
</table>

Variation in grazed pasture biomass over and above that due to rainfall and flooding was not related to treatments, or to pig density. This corresponds to the prediction of the extrinsic food hypothesis but not the intrinsic food hypothesis (Table 1.1). Testing the applicability of the interactive model to pig populations by measuring responses in grazed pasture biomass assumes that any response in pasture biomass to manipulation of pig density would be detectable. Increases in pasture offtake by other herbivores in response to any increased
pasture availability associated with decreased pig density could have potentially obscured or completely negated vegetation responses to treatments. Other herbivores may have increased their pasture offtake rates through a numerical and/or a functional response to increased pasture availability. To examine the response of other herbivores to reductions in pig density, daily pasture offtake by other herbivores in kg/ha was calculated from estimates of kangaroo and feral goat density obtained from corrected aerial surveys, and from sheep densities estimated from mustering returns (see section 4.2.2). Sheep density on sites located on pastoral properties (TO, GO, LA, NA) was estimated annually in the spring from mustering returns provided by landholders. Because mustering returns varied according to whether flock size increased or decreased over the intervening 12 months, it was assumed that rates of gain or loss were constant and sheep densities at the time of aerial surveys were estimated accordingly. This allowed 8 estimates of daily pasture offtake by other herbivores to be made following imposition of treatments (Fig. 4.6). No general pattern in pasture offtake by other herbivores was apparent, with the exception of site LA for which offtake was lower than for other sites on 3 of 8 occasions. LA was the only site where commercial kangaroo harvesting occurred over the duration of the experiment. Lower pasture offtake on LA was attributable to consistently lower densities of red kangaroos relative to other sites.

Serial correlograms of log(+1) daily pasture offtake by other herbivores for each site indicated that the interval between quarterly estimates which maximised independence ranged from 1 to 4. An interval of 3 quarters was selected for analyses of the effects of treatment on log(+1) daily pasture offtake by other herbivores. This allowed 4 independent estimates for each site following implementation of treatments. Analysis of variation in log(+1) daily pasture offtake by other herbivores indicated no significant effect of treatment (Table 4.9), suggesting that any increase in pasture biomass due to treatments was not removed by other herbivores.
Fig. 4.7 Variation in estimated daily pasture offtake by herbivores other than pigs after imposition of experimental treatments. Sites are GO (●), LA (▲), TO (■), NC (○), NP (△) and NA (□).

Table 4.9 Analysis of variation in log(+/1) daily pasture offtake by other herbivores after implementation of treatments associated with treatment.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Anova SS</th>
<th>Mean Square</th>
<th>F-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>2</td>
<td>0.005999</td>
<td>0.002999</td>
<td>0.71</td>
<td>0.504</td>
</tr>
<tr>
<td>Error</td>
<td>21</td>
<td>0.089069</td>
<td>0.004241</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td>0.095068</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

4.3.6 Effect of pasture biomass on \( r \)

Both of the hypotheses addressed in this study predict a positive relationship between the exponential rate of population increase for pigs and food availability (the numerical
response). To test for this relationship, \( r \) was regressed on logged pasture biomass lagged from 0 to 3 quarters (9 months), and variation in the coefficient of determination (\( R^2 \)) for regressions used to measure the strength of any relationship. Given that gestation for feral pigs is just under 4 months (Giles 1980) and that surveys were conducted quarterly, 9 months was considered the longest likely lag between a change in pasture biomass and a detectable change in \( r \). Variation in \( r \) was significantly related to pasture biomass across three of four lags considered, but most strongly related to pasture biomass with a 1 quarter (3 month) lag (Table 4.9).

<table>
<thead>
<tr>
<th>Lag (quarters)</th>
<th>( R^2 )</th>
<th>( F )-value</th>
<th>( df )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.307</td>
<td>13.820</td>
<td>1,28</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1</td>
<td>0.581</td>
<td>32.928</td>
<td>1,22</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2</td>
<td>0.233</td>
<td>8.001</td>
<td>1,16</td>
<td>0.012</td>
</tr>
<tr>
<td>3</td>
<td>0.167</td>
<td>5.607</td>
<td>1,16</td>
<td>0.027</td>
</tr>
</tbody>
</table>

Table 4.9 Summary of regressions of \( r \) on logged pasture biomass, lagged 0 to 3 quarters.

A polynomial regression analysis (Zar 1974) was used to test for deviations in linearity for the relationship between pasture biomass lagged 1 quarter and \( r \). The quadratic term of the regression equation was negative (-0.0000036) and significant (\( t=-3.160, df=1, P=<0.001 \)), indicating that rate of change in \( r \) slowed at progressively higher pasture biomass. A consonant model of inverted Ivlev form (Noy-Meir 1975, Bayliss 1987) was fitted to the relationship. The parameters of consonant models can be interpreted biologically and compared between populations and/or species (Gilbert et al. 1976, Bayliss 1987). The inverted Ivlev model used here has the form:

\[
r = -a + c (1 - e^{-av})
\]

(4.1)

where \( r \) is defined above, \( V \) is pasture biomass in kg/ha, \( a \) is the maximum exponential rate of population decrease in the absence of food, \( c \) is the rate at which \( a \) is progressively
ameliorated with increasing $V$ and $d$ is a measure of the population's demographic efficiency, quantifying its ability to increase when $V$ is low. The maximum or intrinsic rate of population increase ($r_m$) (Caughley and Birch 1971) is given by $c-a$. The model was fitted using a derivative-free non-linear regression procedure (Freund and Littel 1986). Because the least-squares extrapolation used in the fitting procedure typically underestimates the maximum rate of decrease ($a$) in the numerical response (Caughley 1987), this parameter was fixed at the maximum rate of decline in abundance observed during the crash in pasture availability during the second half of 1991, averaged across all 6 sites ($a = -2.045$ (s.e. = 0.178)). Using the entire data set, the fitted model (Fig. 4.8) was $r = -2.045 + 2.730 (1 - e^{-0.025s})$ ($R^2 = 0.566$, $df = 270$, $P < 0.001$). This model indicates that pig populations increase in abundance when pasture biomass exceeds 251 kg/ha and decline when biomass is below that level. The intrinsic rate of increase on an annual basis ($r_m$) was estimated as $(2.730 - 2.045) = 0.685$.

![Graph](image)

**Fig. 4.7** The numerical response of pigs to variation in pasture biomass (kg/ha) in the preceding quarter. Points are estimates of $r$ derived from quarter-to-quarter changes in pig density as a function of pasture biomass lagged by 1 quarter, across all sites. The line is an inverted Ivlev model fitted by non-linear least squares.
4.4 Discussion

4.4.1 Variation in pig density

Pigs exhibited a strong numerical response to food availability, with variation in $r$ being closely linked to pasture biomass lagged by 1 quarter. Systematic variation in $r$ with pasture availability is coincident with predictions of both forms of the food hypothesis, although in the case of the extrinsic food hypothesis, this indicates that the reactive model is the form appropriate to feral pig populations. The numerical response indicates that pig density was limited by pasture availability, $r$ being positive when pasture biomass exceeded 251 kg/ha and attaining a maximum value on an annual basis ($r_m$) of 0.685 above pasture biomass of about 600 kg/ha. This corresponds with a finite rate of increase of 1.97, suggesting that under good seasonal conditions the density of pig populations can effectively double in a year.

Maximum rates of increase estimated for feral pig populations in the rangelands (0.6-0.7 and 0.57) by Giles (1980) and Hone (1983) respectively, and in northern Australia (0.78) by Caley (1993) were similar to that estimated here. Maximum exponential rate of decrease in this study was estimated to be -2.045, suggesting that in the absence of food pig abundance declines rapidly. Maximum exponential rates of decrease for pig populations in northern Australia (-0.16) and in the rangelands (-0.80) estimated by Caley (1993) and Giles (1980) respectively, were both substantially lower than that estimated here, although how close these populations were to completely exhausting food resources is unknown as neither of these studies estimated food availability.

Bayliss (1985b, 1987) estimated $r_m$ for red kangaroos, another generalist herbivore inhabiting the semi-arid rangelands, to be between 0.34 and 0.44 (mean 0.39), equivalent to an annual finite rate of between 1.40 and 1.55. Pig populations attain higher rates of increase under good seasonal conditions largely because they produce litters rather than single offspring. Bayliss (1987) found that like pigs, kangaroos displayed a strong numerical response to pasture availability, $r$ being positive when pasture biomass exceeded similar levels as that for pigs, 230 kg/ha. Caughley (1987) reported a maximum exponential rate of decline for red kangaroo populations over 4 months of a deep drought to be -1.6 on an annual basis. This is
substantially lower than that reported for pigs in this study, suggesting red kangaroos are much more resilient to declining seasonal conditions than are pigs. One reason that pigs may decline more rapidly during droughts is that they are less able to minimise their nutritional requirements by slowing rates of reproduction when seasonal conditions are poor. Shepherd (1987) reported that for red kangaroos the number of anoestrous females rose from 2 to 85% during the aforementioned drought. In contrast, Giles (1980) found that the percentage of anoestrous female pigs rose by only 9% on a site in the rangelands where $r$ had declined to -0.80.

4.4.2 Variation in pasture biomass

Grazed pasture biomass fluctuated widely over the course of this experiment, the variation being due to rainfall variation and to a lesser extent flooding, but not to soil type or pig grazing. Variation in grazed pasture biomass was best related to rainfall accumulated over the previous 12 months, with biomass increasing by about 2.2 kg/ha for every 1mm increase in antecedent rainfall. Flooding increased pasture biomass 2 quarters hence, by an average of 26.7 kg/ha for every month in which flood waters remained over a site. A comparable study undertaken by Robertson (1987a, b), investigated variation in pasture biomass on two sites, both of which contained areas of black soil floodplain broadly similar to that in the current study. Robertson (1987a, b) also found that variation in grazed pasture biomass was independent of soil type and highly dependent on the previous 12 months accumulated rainfall, although he estimated a slightly stronger response in biomass (3 kg/ha for every 1mm increase in rainfall). Robertson (1987a, b) did not formally investigate the effects of flooding.

4.4.3 Pig density, food availability and the extrinsic food hypotheses

In a recent review of animal population regulation, Sinclair (1989) concluded that where it had been sought, density dependence had been found for most large mammal populations and for all ungulates. Further, Sinclair (1989) predicted that density dependent mortality through food shortage would ultimately be found to regulate most populations of large mammals.
However in this study, rate of change in pig abundance ($r$) was not influenced by experimental reductions in pig abundance and was not related directly to pig density. This suggests that pig populations in the rangelands do not conform to Sinclair’s (1989) prediction, with $r$ showing no consistent relationship with population density, and hence indicating no density dependent variation in mortality.

Caughley and Gunn (1993) argued that although most populations of large herbivores could be expected to display density dependence, stochastic climatic variation in unpredictable environments such as the semi-arid rangelands would tend to obscure any relationship between population density and $r$. This is because in such environments per capita food availability is commonly more dependent on the density independent effects of weather than on the offtake of the herbivores themselves. Caughley and Gunn (1993) argue that for this reason the dynamics of herbivore populations in such environments will usually not conform to assumptions of logistic growth and hence cannot be represented by single-species models. This does not mean that such populations do not conform to the intrinsic food hypothesis. Rather, it implies that the effects of per capita food availability will not be manifested through constant density dependence and the existence of an equilibrium density ($K$). A test of the intrinsic food hypothesis robust to the effects of stochastic environmental variation must be cast in an interactive vegetation-herbivore rather than a single-species context (Caughley 1976a, 1981, Caughley and Gunn 1993). This requires assessment of reciprocal changes in the abundance of herbivores and their food supply. For example, Caughley (1987) used a stochastic simulation model to demonstrate that eliminating red kangaroos from a rangelands grazing system increased pasture biomass by 43% because of the effect their offtake had on variation in their food resources. Similarly, Skogland (1984) and Garre and Skogland (1980) demonstrated that food availability (measured as the per capita biomass of lichen during winter) declined with increasing reindeer density for hunted populations in Norway. The outcomes of both experiments conform to predictions of the intrinsic hypothesis, with reduced herbivore density leading to increased vegetation biomass (Caughley 1976a, 1987).
However in the current study, while grazed pasture biomass fluctuated widely over the course of the experiment, this variation was not related to pig abundance. Grazed pasture biomass varied with rainfall and to a lesser extent flooding, but showed no response to experimental reductions in pig abundance and no direct relationship with pig density. Moreover, the lack of response in vegetation biomass to manipulation of pig density was not related to increased pasture offtake by other herbivores. The lack of any apparent relationship between the abundance of pigs and their food resources conforms to predictions of the extrinsic food hypothesis. According to this hypothesis, $r$ for a herbivore population will not be influenced by intraspecific competition for food resources and hence cannot be density dependent. In the absence of such density dependence, these populations will be unregulated. The results of this experiment suggest that in the rangelands, pig abundance is limited but not regulated by pasture availability which varies stochastically with rainfall, flooding and probably offtake by other herbivores; but not offtake by pigs. Accordingly, pig populations cannot be regulated because they do not influence their per capita food availability, and hence there can be no negative feedback from density to $r$ (density dependence). This suggests that the vegetation-herbivore feedback loop which imparts centripetality to interactive grazing systems must be either non-existent or extremely inefficient. An experiment to estimate the functional response of pigs to pasture biomass in order to articulate this feedback loop fully is described in Chapter 5, along with some simulation modelling conducted to further interpret the results of the experiment described in this Chapter.
Chapter 5. The functional response and dynamics of pig populations grazing native pastures

5.1 Introduction

The experiment described in Chapter 4 found no evidence that feral pig populations influence the availability of their food resources measured as pasture biomass. This suggests that pig population abundance is limited but not regulated by food availability and that pigs conform to the extrinsic rather than intrinsic food hypothesis (Andrewartha and Birch 1954, 1984, and section 1.2.2). According to this hypothesis, the association between herbivores and their food resources is reactive, vegetation biomass determining the herbivore population's rate of increase (r) through the numerical response, but herbivores having no influence on vegetation biomass (Caughley and Lawton 1981, Caughley 1987).

The numerical and functional responses of animals to variation in food availability were described originally by Holling (1959). For herbivores, the combined effects of the numerical and functional responses to pasture biomass determine the influence they have on variation in pasture biomass (Caughley 1976a). The numerical response determines the number of herbivores consuming pasture, and the functional response the intake rate of each herbivore. According to the functional response, the rate of per capita vegetation offtake by herbivores declines from a constant (satiated) maximum at high vegetation biomass to 0 at low or no pasture biomass. Declining per capita offtake by herbivores eases grazing pressure when vegetation biomass is low. Because vegetation biomass influences r for herbivores through the numerical response, the reciprocal influence of herbivores on vegetation through the functional response provides a link between r and herbivore density. As such, variation in vegetation offtake, mediated through functional response, is integral to regulation of the herbivore population through density-dependent intraspecific competition for food resources (Caughley 1976a).

Caughley (1987) found that red kangaroos interacted with the pastures they graze through a vegetation-herbivore feedback loop comprising both the numerical and functional responses.
of kangaroos to variation in pasture biomass. Caughley (1987) demonstrated that despite substantial stochastic variation in food availability due to unpredictable variation in rainfall, the vegetation-herbivore feedback loop was strong enough that red kangaroo populations were regulated through interaction with their food resources in an essentially density dependent manner. As such, red kangaroo populations conformed to the intrinsic food hypothesis. The reciprocal influence of kangaroo and pasture abundance imparted by the vegetation-herbivore feedback loop gave the grazing system a tendency toward equilibrium, although the system rarely if ever attained this equilibrium because of stochastic environmental buffeting. Caughley (1987) termed this central tendency centripetality.

It seems likely that the relative strength of their respective vegetation-herbivore feedback loops may explain why pigs appear to conform to the extrinsic and red kangaroos to the intrinsic food hypotheses. While Caughley (1987) found that the red kangaroo grazing system could not persist in the absence of such a feedback loop, the experiment in chapter 4 suggests that for the pig-pasture grazing system the feedback loop is either (1) non-existent or (2) exceedingly inefficient. If (1) is correct, the outcome of the experiment described in chapter 4 is entirely accurate and the abundance of pigs is limited but not regulated by food availability. However, if (2) is correct, some tendency toward an equilibrium between pigs and pasture must exist, but this tendency is so slight (pig abundance is so poorly regulated) that the experiment described in chapter 4 could detect no evidence of it (neither pasture biomass or the abundance of other herbivores showed any numerical response to reductions in pig density). In either case, given that their abundance is at best poorly regulated, the question of how pig populations persist in a highly unpredictable environment such as the semi-arid rangelands, remains.

This chapter describes an experiment and some population modelling conducted to (1) determine the form of the functional response of pigs to variation in pasture biomass, and (2) differentiate between the alternative interpretations of the results from the experiment described in chapter 4. The functional response of pigs to pasture biomass was estimated from two graze down trials. A stochastic grazing model comprising pasture, pigs and red kangaroos (acting as a surrogate for other herbivores) was developed. The relative importance
of the pasture-pig feedback loop to regulation of pig populations was investigated by
alternately adding and omitting the functional responses of pigs and kangaroos. The model
was also used to examine whether centripetality was essential to persistence of pig
populations in rangelands grazing systems.

5.2 Methods

5.2.1 Graze down trials

Two graze-down trials were conducted in field enclosures at the Trangie Agricultural
Research Centre in western New South Wales. Details of pigs and starting pasture biomass
for each trial are given in Table 5.1. At their commencement, each trial had a similar ratio of
pig biomass to pasture biomass, trial 1 consisting of fewer larger pigs and trial 2 of more
smaller pigs. Larger pigs were held in captivity for at least 1 year prior to the trials, while
smaller pigs were born and raised in captivity. All pigs were either captive feral animals or
their offspring. Pigs were maintained in paddocks adjacent to the enclosures used for the
trials over 2 months prior to their commencement. During that time they were gradually
weaned from their normal diet of grain to the pasture available in the paddocks. The trial-
enclosures contained a mix of native grasses dominated by *Stipa, Eragrostis, Aristida,* and
*Poa* spp. A 4x4m pig-proof exclosure was established in the centre of each enclosure so that
pasture growth and die-back unrelated to pig grazing could be measured. Day-to-day
variation in pasture biomass in enclosures would result from (1) grazing by pigs, (2) pasture
growth or die-back not related to grazing, and (3) trampling by pigs and by people during
pasture biomass estimation (Short 1986).

Pigs were maintained in the enclosures until estimates of pasture intake had been uniformly
low for 3 days in succession (18 days for trial 1 and 16 days for trial 2). During trials pigs had
access to water and shade, but were given no feed to supplement the available pasture. On
each day of the trial pigs were removed from enclosures and pasture biomass was estimated
from the average of 50 randomly placed 0.25m quadrats using the non-destructive
comparative yield technique (see section 4.2.4 for additional detail). Rate of pasture growth
or die-back was assessed from the average of 20 additional quadrats placed randomly in the exclosures at the centre of each enclosure. Biomass reduction due to trampling was measured as the daily average dry weight of vegetation litter, estimated by subjectively scoring the amount of litter (on a scale of 0 to 12) for 20 of the 0.25m quadrats used to assess pasture biomass daily during each trial. At the completion of the trials, litter was collected from 50 quadrats representing the range of litter scores obtained during the trials, and a regression between scores and dried weight of litter calculated. Scores ($LS$) obtained during the trials were converted to dry weight estimates ($LB$) using a highly significant regression through the origin ($R^2 = 0.81, F = 96.05, df = 1.49, P < 0.001$) of the form:

$$LB = (33.25LS)$$

<table>
<thead>
<tr>
<th>Area (ha)</th>
<th>Starting pasture biomass kg/ha (enclosure)</th>
<th>Starting pasture biomass kg/ha (enclosure)</th>
<th>Pasture available kg (enclosure)</th>
<th>Starting pig biomass kg</th>
<th>No. of pigs</th>
<th>Average weight kg</th>
<th>kg pig/kg pasture</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trial 1</td>
<td>0.21</td>
<td>717.7</td>
<td>721.2</td>
<td>151</td>
<td>4</td>
<td>84.7</td>
<td>2.25</td>
</tr>
<tr>
<td>Trial 2</td>
<td>0.07</td>
<td>697.3</td>
<td>692.6</td>
<td>49</td>
<td>5</td>
<td>22.2</td>
<td>2.26</td>
</tr>
</tbody>
</table>

Table 5.1 Details of graze down trials for feral pigs.

Intake rate was estimated from the daily loss of pasture from each enclosure, corrected for natural growth or die-back and trampling. Daily losses were smoothed by calculating 4-point moving averages and converted to food intake ($g/kg^{0.75}/day$) by multiplying by the area of each enclosure and dividing by the number of animals and their average metabolic body
weight (kg^{0.75}). A consonant model of inverted Ivlev form (Noy-Meir 1975, Short 1985) was fitted to the relationship between pasture biomass and pasture intake rate. The parameters of consonant models can be interpreted biologically and compared between species (Gilbert et al. 1976, Short 1985). The model has the form:

\[ c_p = c_{sp} \{1 - e^{[(V - V_r)ld_p]}\} \]  

(5.1)

where \( c_p \) is the intake rate of pig at given pasture biomass \( V \), \( c_{sp} \) is the maximum (satiated) intake rate, \( V_r \) is the biomass of the ungrazable pasture residue, and \( d_p \) is a measure of grazing efficiency for pigs which dictates how long maximum intake can be maintained at progressively lower pasture availability. Models were fitted using a derivative-free non-linear regression procedure (Freund and Littel 1986).

### 5.2.2 Grazing system models

Four models which simulated the dynamics of feral pig populations and their food resources in the semi-arid rangelands were constructed to examine the effect of pasture offtake by pigs and other herbivores on the stability of the grazing system. Models were modified from the stochastic red kangaroo-pasture model developed by Caughley (1987). Models generated 100-year sequences of stochastic rainfall drawn at random from normal distributions with average and variance equivalent to that for each season according to the long-term rainfall records from Wanaaring (section 3.2.2). Pasture grew or died back in response to rainfall according to an empirically derived relationship which accounted for the effects of rainfall on soil moisture, and competition for space between pasture plants in rangelands pastures (Caughley (1987) modified from Robertson (1987b, 1988)). The relationship has the form:

\[ \Delta V = -55.12 - 0.01535V - 0.00056V^2 + 2.5R \]  

(5.2)

where \( \Delta V \) is the increment of growth or dieback in ungrazed pasture biomass over the subsequent quarter, \( V \) is the pasture biomass at the beginning of the quarter and \( R \) is rainfall in mm over the quarter. Robertson (1987b, 1988) found that pasture growth or dieback not
accounted for by $V$ and $R$ resulted in a standard deviation around the regression equation equivalent to 52kg/ha. The pasture growth increment was taken as a random draw from a normal distribution with a mean equal to the solution of equation (5.2) and a standard deviation of 52.

In all models, red kangaroos were used as a surrogate for all herbivores other than pigs, their numerical and functional responses being taken from Caughley (1987) who modified them after Bayliss (1987) and Short (1987). The numerical and functional responses of red kangaroos to pastures biomass are:

$$r_k = -1.6 + 2 \left(1 - e^{-0.007V}\right)$$  \hfill (5.3)

and

$$c_k = 66 \left(1 - e^{0.024}\right)$$  \hfill (5.4)

respectively, where $r_k$ is the annual exponential rate of increase for red kangaroos and $c_k$ is their daily pasture intake rate as a function of metabolic body weight (g/kg$^{0.75}$/day) at given pasture biomass, $V$. Pigs were added to models through their numerical response (estimated in section 4.3.6):

$$r_p = -2.045 + 2.730 \left(1 - e^{-0.0055V}\right)$$  \hfill (5.5)

and their functional response estimated in this chapter (see below). To simplify the model, both kangaroos and pigs were assumed to weigh 35kg. The four models constructed were:

1. **No grazing (NG)** - The grazing system with pasture offtake by both kangaroos and pigs eliminated by omitting their functional responses to pasture biomass. This represents the grazing system if neither kangaroos nor pigs were regulated by food availability, their pasture offtake having no influence on variation in pasture biomass.
2. **Pig only grazing (POG)** - The grazing system with pasture offtake by pigs included through their functional response, but omitting that of kangaroos. This represents the grazing system if only pigs were regulated by food availability, pasture offtake by pigs but not kangaroos contributing to variation in pasture biomass.

3. **Kangaroo only grazing (KOG)** - The grazing system with pasture offtake by kangaroos included through their functional response, but omitting that of pigs. This represents the grazing system if only kangaroos were regulated by food availability, pasture offtake by kangaroos but not pigs contributing to variation in pasture biomass. This model describes a grazing system in which pigs conform to the extrinsic food hypothesis.

4. **Both grazing (BG)** - The grazing system with pasture offtake by both kangaroos and pigs included through their respective functional responses. This represents the grazing system if both kangaroos and pigs were regulated by food availability, pasture offtake by both species contributing to variation in pasture biomass. This model describes a grazing system in which pigs conform to the intrinsic food hypothesis.

Each model was iterated 10 times. Initial values for each iteration were 0.07 pigs/ha, 0.4 kangaroos/ha and 250 kg/ha of pasture. Caughley (1987) found that for a similar grazing system model comprising pasture and red kangaroos, initial pasture biomass had little influence on subsequent dynamics, while initial herbivore density affected subsequent dynamics for only 5 to 10 years.

5.3 **Results**

5.3.1 **Graze down trials**

Pasture biomass in each enclosure declined steadily over the course of the 2 graze down trials (Fig. 5.1). A polynomial regression test was used to assess deviations from linearity in the relationship between intake rate on a metabolic body weight basis and pasture biomass for the
Fig. 5.1  Variation in pasture biomass (kg/ha) over the course of the 2 graze down trials.

Fig. 5.2  Predictive relationship between pasture biomass (kg/ha) and daily pasture intake rate on a metabolic body weight basis (g/kg$^{0.75}$/day). Points are 4-point moving averages and the line is an inverted Ivlev model fitted by non-linear least squares.
combined data set (Zar 1974). The quadratic term of the regression (-0.0001) was significant and negative ($t = -2.247$, $df = 230$, $P = 0.031$), suggesting that increase in intake rate slowed at progressively higher pasture biomass. An inverted Ivlev model fitted to the data (Fig. 5.2, $R^2 = 0.714$, $df = 329$, $P < 0.001$) had the form:

$$AV = 58\left(1-e^{((-0.02)t^{0.302})}\right)$$

(5.5)

5.3.2 Grazing system models

Figures 5.3a, b, c and d show typical 100-year runs for the four grazing system simulation models considered. For all models, the abundance of pasture and herbivores fluctuated widely in response to stochastic variation in rainfall, but neither pigs nor kangaroos were ever driven to extinction in any iteration of any of the models. The results of all iterations of each model are summarised in Table 5.2.

<table>
<thead>
<tr>
<th>Model</th>
<th>Pasture biomass (kg/ha)</th>
<th>Kangaroo density (n/ha)</th>
<th>Pig density (n/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>sd</td>
<td>CV%</td>
</tr>
<tr>
<td>NG</td>
<td>367</td>
<td>144</td>
<td>39</td>
</tr>
<tr>
<td>POG</td>
<td>302</td>
<td>133</td>
<td>44</td>
</tr>
<tr>
<td>KOG</td>
<td>297</td>
<td>147</td>
<td>50</td>
</tr>
<tr>
<td>BG</td>
<td>299</td>
<td>150</td>
<td>50</td>
</tr>
</tbody>
</table>

Table 5.2 Average mean, standard deviation (sd) and coefficient of variation (CV%) among years of 10 iterations of a 100-year stochastic model simulating an interactive plant-herbivore system comprising pasture, red kangaroos and feral pigs, with pasture offtake by neither species included (NG), that of pigs only included (POG), that of kangaroos only included (KOG), and that of both species included (BG).
Typical output from the grazing system models (a) NG, (b) POG, (c) KOG and (d) BG. For all models, the bottom histogram shows modelled annual rainfall (mm), the next line-plot variation in grazed pasture biomass (kg/ha) and the top 2 line-plots variation in kangaroo and pig density (n/ha) respectively.
(a) Model NG

Pigs/ha

Kangaroos/ha

Pasture biomass (kg/ha)

Rainfall (mm)

Years
(b) Model POG

- Pig/ha
- Kangaroos/ha
- Pasture biomass (kg/ha)
- Rainfall (mm)

Years
The model which omitted pasture offtake by kangaroos and pigs (NG) was not centripetal, the abundance of both kangaroos and pigs increasing indefinitely. Including pasture offtake by pigs (POG) decreased average pasture biomass by 16% and eliminated the tendency for the abundance of pigs but not kangaroos to increase indefinitely, although the average rate of increase by kangaroo populations declined by 82%. In contrast, both models which included pasture offtake by kangaroos (KOG and BG) were entirely centripetal, all components of the grazing system persisting, regardless of whether or not offtake by pigs was included. Including pasture offtake by pigs had no appreciable effect on pasture biomass or the abundance of kangaroos and pigs.

5.4 Discussion

5.4.1 The functional response

Fig. 5.4 shows the functional response of pigs measured in this study along with those from graze down trials for red and western grey kangaroos, estimated by Short (1986). Pasture biomass below which grazing ceased for pigs (92 kg/ha) was lower than that estimated for western grey kangaroos (180 kg/ha) but not as low as that for red kangaroos which continued to graze until pasture was virtually non-existent (<20 kg/ha) (Short 1986). Pigs had a lower saturated intake rate on a metabolic body weight basis (58 g/kg$^{0.75}$/day) than either western grey kangaroos (87 g/kg$^{0.75}$/day) or red kangaroos (66 g/kg$^{0.75}$/day) (Short 1986), although intake by pigs may not have reached maximum rates over the range of pasture biomass assessed in the current study (Fig. 5.2).

Short (1986) suggested that the inability of western grey kangaroos to graze pasture below 180 kg/ha may have reflected (1) an inability to graze species of low biomass on the specific soil type where his experiment was conducted, and/or (2) a preference by western greys for browse which was not assessed in his graze down experiment. Giles (1980) found that feral pigs inhabiting floodplains in Australia's rangelands did not consume significant amounts of browse, but did supplement grazing by consuming progressively more roots, tubers and other below-ground plant parts as pasture biomass declined. In the graze down trials described in
this Chapter, pigs did not attempt to consume below-ground vegetation when pasture biomass declined. However, the hardness of soils upon which the trials were carried out may have made it impossible for pigs to root up underground vegetation. Consumption of underground vegetation by pigs appears to be restricted by soil hardness, which depends on soil structure and/or saturation by flooding or rainfall (Giles 1980, Corbett 1994, D. Choquenot, personal observation). For example, following softening of soils by heavy rains, the pigs used in the graze down trial described here rooted extensive areas of the paddocks where they were held prior to the trials (D. Choquenot, personal observation).

Short (1986) suggested that differences in the functional response of red and western grey kangaroos made them differentially susceptible to food shortage during periods of low pasture availability, and that this probably had consequences for their relative rates of decline into droughts. In particular, the ability of red kangaroos to graze pasture to lower biomass than western greys and their propensity to dig for below-ground vegetation when pasture
biomass was low contributed to their ability to maintain higher levels of food intake at low levels of pasture availability (Short 1987). In the same way, the ability of pigs to dig up and consume below-ground vegetation when soil conditions allow could potentially mitigate the effects of food shortage on rates of population increase \((r)\) when pasture availability is low (Giles 1980). Corbett (1994) suggested that in northern Australia, access to underground vegetation in the soft soil of the ecotone formed as floodwaters contract across coastal floodplains during the late dry season determined the probability of female pigs successfully weaning young at foot. Flooding has the same effect in the semi-arid rangelands, with extensive areas often rooted up by pigs as flood waters contract (Giles 1980, D. Choquenot personal observation). However, the irregularity of flooding events in the rangelands means that access to below-ground vegetation will be less predictable than that reported for northern Australia by Caley (1993) and Corbett (1994). Giles (1980), comparing the crude protein and energy levels of pig diets as seasonal conditions varied over 17 months on a floodplain location in the semi-arid rangelands, concluded that as pasture biomass declined, protein-rich green feed was replaced by energy-rich but protein-poor roots and tubers wherever soil conditions allowed pigs to root. Giles (1980) suggested that as the proportion of below ground vegetation in the diet increased, the ability of pigs to maintain body condition declined, affecting demographic rates and \(r\). The unpredictable coincidence of recent flooding and low pasture biomass in the current study may have contributed to variation in \(r\) when pasture biomass was below that required to generate a positive rate of population increase (see section 4.3.6, Fig. 4.7).

5.4.2 Comparison of grazing system models

Caughley (1987) recognised that because ecological models oversimplify complex ecological systems, their predictions must be interpreted cautiously. Despite attempting to represent all of the important relationships which constitute the grazing system studied here, the simulation models described in this chapter lacked (1) the effects of the real suite of other herbivores (including rabbits and invertebrates), (2) any consideration of herbivore population age-structure, (3) variation in pasture species composition, and (4) long-term trends in pasture composition which may affect forage quality. Any or all of these omissions
could change or invalidate the outcomes predicted by some or all of the models summarised in Table 5.2. Hence, the following conclusions should be interpreted judiciously, with more emphasis on qualitative than quantitative predictions.

In the absence of pasture offtake (model NG), herbivores in the grazing system did not achieve centripetality, indicating that feedback between herbivore and pasture abundance is necessary for persistence of the grazing system. Caughley (1987) also found this to be the case for the modelled grazing system comprising red kangaroos and rangelands pastures. Including pasture offtake by pigs (model POG) reduced pasture biomass relative to the ungrazed system (model NG) by almost 20% and induced centripetality in pig populations, indicating that pigs will persist in the absence of other herbivores. However, the reduction in pasture biomass due to pasture offtake by pigs was insufficient to entirely eliminate the tendency for the abundance of red kangaroos to increase indefinitely, although their average rate of increase declined by over 80%. Addition of pasture offtake by kangaroos (models KOG and BG) reduced pasture biomass only slightly (2%) but increased its year-to-year variation by 12%. Increased variation in pasture biomass negated the tendency for kangaroo abundance to increase indefinitely and led to a 75% decline in average pig abundance. The dramatic reduction in average pig density was due to asymmetry in their numerical response. Asymmetry in the numerical response of both kangaroos and pigs means that an incremental decrease in food availability will reduce \( r \) more than an equivalent addition of food will increase it (Caughley 1987). However, the more rapid decline estimated for pigs (\( a = -2.045 \)) than for kangaroos (\( a = -1.60 \)) in the absence of food meant that increasing variation in pasture biomass reduced the average density of pigs to a much greater extent than it did kangaroos. However, despite the fact that increased variation in pasture biomass substantially reduced their abundance, pig populations persisted through all iterations of both models which included pasture offtake by kangaroos.

5.4.3 The intrinsic and extrinsic food hypotheses

The experiment described in Chapter 4 evaluated the applicability of the intrinsic and extrinsic food hypotheses to feral pig populations in the rangelands. In the modelling
presented here, the 2 hypotheses were represented by the models BG and KOG respectively. In the initial experiment, the applicability of the 2 hypotheses to the pig populations studied was evaluated by determining whether or not pasture availability declined with increasing pig density. However, the results of the modelling conducted here indicate little difference in average pasture biomass between modelled grazing systems conforming to the 2 hypotheses, suggesting that the relationship sought in the original experiment was unlikely to have been detectable. Pasture offtake by pigs contributes little to variation in pasture biomass because (1) pigs are less efficient grazers than kangaroos and (2) their higher rate of decline into droughts means that pigs occur at considerably lower average densities than do kangaroos. For example, offtake by pigs contributed just 2.11% of total pasture offtake when grazing by pigs and kangaroos was considered together (model BG). Because offtake by pigs appears to make only a minor contribution to variation in total pasture offtake (model KOG compared with model BG), reduction in pig density will have limited potential to increase pasture biomass. Further, it is unlikely that any slight increase in pasture biomass would be detectable in the wash of stochastic environmental variation to which rangelands grazing systems are subjected.

Hence, the applicability of the intrinsic and extrinsic food hypotheses to pig populations in this study remains unresolved, as does the question of whether or not these populations are regulated. However, the collective results of the modelling presented here and the experiment described in Chapter 4 suggest that tangible differences between the two food hypotheses reduce to a negligible difference in pasture offtake which has no demonstrable effect on average pasture biomass or the abundance of other herbivores. As such, the question of whether pig populations in the rangelands conform to the intrinsic or extrinsic food hypothesis, or whether in fact these populations are regulated through density dependent effects on the abundance of their food resources, seems to be of more semantic than functional relevance.
5.4.4 Centripetality and population persistence

Concepts of density dependence and regulation are considered to be central to the understanding of vegetation-herbivore dynamics and to herbivore population persistence in particular (Caughley 1976a, Sinclair 1989, Sinclair et al. 1985). A regulated population by definition will tend to return to some equilibrium when perturbed from it (Varley et al. 1973). Walker and Goodman (1983) extended this concept, terming the tendency to return toward an equilibrium density 'stabilisation' and added the notion that such a tendency can be stronger or weaker. Caughley (1987) suggested that centripetality was a more appropriate term than stability for the dynamics of a vegetation-herbivore system because it implied that the system was held in check by a central tendency, without the requirement that any point equilibrium ever be attained. Caughley (1987) stated "The forces of centripetality are those that dampen temporal variation; a centripetal system is one that would come to equilibrium if it were not buffeted continually".

In the absence of pasture offtake by kangaroos (model POG), the pig population in the modelled grazing system in this study was centripetal, its abundance being regulated through density-dependent intraspecific competition for food resources. As such, the grazing system was qualitatively identical to that described for red kangaroos and rangelands pastures by Caughley (1987). In both model POG and that described by Caughley (1987) the herbivore populations clearly conformed to the intrinsic food hypothesis, their abundance being regulated by essentially density dependent processes; although the herbivore populations seldom if ever occupied stable equilibria. This leads to the truism that centripetality is a necessary consequence of population regulation and vice-versa. However, although pigs persisted indefinitely in both grazing systems which included pasture offtake by kangaroos (models KOG and BG), the role of regulation through density dependent intraspecific competition became irrelevant to this outcome. In these grazing systems pigs were no longer strictly centripetal in the sense implied by Caughley (1987). Rather, persistence of these pig populations had more to do with their high intrinsic rate of increase \( r_m = 0.68 \) than any central tendency imparted through interaction with their food resources. For example, in both models which included pasture offtake by kangaroos, removing variation in rainfall and
pasture growth prompted kangaroos and pasture to move rapidly to a stable equilibrium where grazing by kangaroos held pasture at 232 kg/ha. At this level of food availability the rate of increase in pig density was negative and their population underwent deterministic extinction. This suggests that regardless of whether or not pigs influenced pasture availability, they could not attain equilibrium in the absence of stochastic environmental variation and the presence of another more efficient herbivore such as red kangaroos. Hence, while centripetality may be an inevitable consequence of population regulation, for pigs at least, populations appear able to persist in its absence.

Population persistence in the absence of centripetality corresponds closely with the intent of Andrewartha and Birch's (1954, 1984) theory of environment from which the extrinsic food hypothesis is more or less derived. This theory suggests that average population density and the probability of persistence depend on the amount of time a population spends increasing in abundance as opposed to decreasing, discounting the requirement for regulation through density dependent stabilising mechanisms. The ratio of time a population spends increasing relative to decreasing will depend on the form of its numerical response. However, population persistence will also depend on the absolute rate at which a population increases and decreases in abundance. In particular, a population's intrinsic rate of increase ($r$) and maximum rate of decrease ($a$) will determine how rapidly the population responds to incremental changes in resource availability.

For example, Fig. 5.5 shows the estimated numerical responses of pigs and red kangaroos used in the modelling described in this chapter. According to these responses, $r$ and $a$ estimated for pigs are 1.7 and 1.3 times higher respectively than those estimated for red kangaroos. Pigs increase in abundance when pasture biomass is above 251 kg/ha and kangaroos when above 230 kg/ha. However, as pasture biomass falls progressively below these levels the rate of decline in the pig population increases rapidly beyond that experienced by kangaroos. This accentuates the effect of asymmetry in the numerical response for pigs, restraining average density at levels substantially below that of red kangaroos.
The numerical responses of pigs (see chapter 4) and red kangaroos (Caughley (1987) modified from Bayliss (1987)) to variation in pasture biomass.

The relatively high rate of decline in pig abundance during droughts may be related to their apparent inability to slow their rate of reproduction as seasonal conditions deteriorate (see section 4.4.1). Given the constraint of such a high rate of decline during droughts, it is only by virtue of their impressive capacity for increase when seasonal conditions are good that pig populations can persist under rangelands conditions. For instance, if the intrinsic rate of increase for pigs \( r_m = 0.68 \) is reset to that estimated for red kangaroos \( r_m = 0.40 \) (i.e. The capacity of pigs to increase when pasture biomass exceeds 250 kg/ha is suppressed) the pig population in model BG inevitably undergoes extinction. The high intrinsic rate of increase of pigs is due to (1) the fact that they give birth to litters rather than single offspring and (2) they have a short generation length (see section 4.4.1). This suggests that a herbivore population with a substantially higher maximum rate of decrease and/or lower intrinsic rate of increase than pigs would have either a lower average density in the rangelands than pigs or would be unable to persist at all. To examine persistence in more detail, habitat-related variation in the
numerical response of pigs, and its effect on the probability of population persistence are described and discussed in Chapter 6.
Chapter 6 Habitat-related variation in the numerical response of pigs

6.1 Introduction

A series of simulation models described in chapter 5 suggested that the average density and probability of persistence of feral pig populations in the rangelands is highly sensitive to variation in their numerical response and in particular, the intrinsic rate of increase \( r_m \) and maximum rate of decrease \( a \). In the pre-manipulation surveys associated with the experiment described in chapter 4, the area of floodplain was found to explain a substantial degree of between-site variation in pig abundance. Hence it was considered likely that the spatial availability of floodplain habitat may affect the dynamics of pigs resident in these and other areas of the rangelands. In this chapter, systematic variation in maximum rates of increase and decrease with the percentage of an area covered by riverine floodplain habitat is examined. The effect of habitat-related variation in the numerical response of pig populations on their average density and their probability of persistence is assessed by extending the population models described in Chapter 5.

6.2 Methods

Initial aerial surveys of pig populations on the six study sites used in the experiment described in Chapter 4 indicated a strong affinity of pigs for riverine floodplain habitat (see Table 4.1). Consequently, the percentage area of floodplain habitat on each site was estimated using orthophotographic maps, aerial photography and Landsat imagery (see section 4.2.1). The numerical response of pig populations in rangelands habitat was estimated in chapter 4 from sequential estimates of \( r \) for each study site (see section 4.2.5), related to estimates of pasture biomass (kg/ha) lagged 1 quarter (see section 4.3.6). The estimated numerical response was based on the maximum observed rate of decline \( (a_o) \) averaged across all 6 study sites and an intrinsic (maximum) rate of increase \( (r_m) \) derived from an inverted Ivlev function fitted to the data by a non-linear least squares technique (Freund and Littel 1986).
6.3 Results

6.3.1 Observed variation in \( a \) and \( r_m \) with the percentage of floodplain habitat

Lagged pasture biomass at which \( a \) was measured for each site ranged from 23 to 389 kg/ha, suggesting that not all estimates of \( a \) represented absolute maximum rates of decline in pig abundance. As such, \( a \) for each of the six sites was regressed independently on (1) the percent coverage of floodplain and (2) pasture biomass from the previous quarter. Variation in \( a \) was not significantly related to lagged pasture biomass \((R^2=0.002, F=0.008, df=1,4, P=0.0002)\), but was significantly related to percent coverage of floodplain \((R^2=0.816, F=17.729, df=1,4, P=0.014)\). While this confirms that it is unlikely estimated \( a \) represented actual maximum rates of decline in abundance for pig populations on each site, it does indicate a tendency for populations suffering food shortage to decline more quickly where the availability of floodplain habitat is lower. Variation in \( a \) with percentage floodplain coverage alone for each site is shown in Fig. 6.1. The regression line on the Figure indicates that for every 1% increase in floodplain habitat on a study site, the maximum exponential rate at which the pig population declined under conditions of extreme food shortage \((a)\) decreased by 0.034.

![Figure 6.1](image.png)

**Fig. 6.1** Variation in observed maximum rate of decrease \((a)\) and the percentage of floodplain \((\%FP)\) on six study sites used in the experiment described in chapter 4. The line is the least squares regression line described by \( a = -2.438 + (0.034 \%FP) \) \((R^2 = 0.814)\).
Maximum observed rates of increase ($r_m$) for each of the six sites used in the experiment described in chapter 4 were regressed on the percentage of each site covered by riverine floodplain. Because $r_m$ is an asymptotic value fitted according to residual variation in the relationship between $r$ and lagged pasture biomass, food availability immediately prior to measurement of $r_m$ was considered to be of little consequence and it was not included in the regression analysis. Variation in $r_m$ with percent floodplain coverage for each site is shown in Fig. 6.2. There was no significant relationship ($F = 1.920, df = 1,4; P = 0.238$), suggesting that the spatial extent of floodplain on a site had little or no consequence for the maximum rate at which resident pig populations increased when food was plentiful.

![Graph](image)

**Fig. 6.2** Variation in observed intrinsic rate of increase ($r_m$) and the percentage of floodplain on six study sites used in the experiment described in chapter 4.

### 6.3.2 Population modelling

To examine the effect of variation in $a$ on the average density and probability of persistence for pig populations in the rangelands, two of the grazing system simulation models described in chapter 5 were extended by varying $a$ for pigs and monitoring model output. Only the models which included pasture offtake by kangaroos (models KOG and BG) were considered. Each model was iterated 10 times as $a$ for pigs was varied from -2.00 to -2.15, over steps of
Each model iteration had starting values of 0.07 pigs/ha, 0.40 red kangaroos/ha and 250 kg/ha pasture biomass. For each value of \( a \), time to extinction or pig density were averaged across iterations where populations did and did not go extinct respectively. The probability of extinction for each value of \( a \) was estimated as the proportion of iterations where the pig population went extinct within the 100 years considered.

Figs 6.3a and b show variation in average pig density and the probability of population extinction as a function of \( a \) for models with and without pasture offtake by pigs (models KOG and BG respectively). The two models provided almost identical outcomes, average pig density declining to minimum viable levels as \( a \) increased from -2.00 to -2.08, and the probability of population extinction increasing from 0 at \( a = -2.04 \) to 1 at \( a = 2.09 \). The overlap between average population density and probability of extinction suggests that populations with \( a \) between -2.05 and -2.08 may sometimes persist for over 100 years, but will do so at a low average density.

Variation in the time to extinction (in quarters) is shown in Fig. 6.4 as a function of \( a \) for models with and without pasture offtake by pigs (models KOG and BG respectively). There was a general decline in time to extinction with increasing \( a \) for both models, suggesting that both the probability of extinction and the speed with which it occurs increase with increasing \( a \). However, the decline in time to extinction with increasing \( a \) was not monotonic, more rapid declines tending to occur at higher values of \( a \) (-2.05 and -2.06) than at moderate to high values. This pattern reflects a tendency for extinction, where it does occur for populations modelled with relatively high \( a \), to proceed rapidly or not at all.

6.4 Discussion

6.4.1 Habitat-related variation in \( a \), pig density and population persistence

These results indicate that pig populations in the rangelands inhabiting areas with progressively lower percentage coverage of floodplain habitat will have increasingly higher rates of decline during periods of extreme food shortage. According to the modelling
Fig. 6.3 Variation in average pig density (pigs/ha) (bars) and the probability of population extinction (points) as a function of the pig population's maximum rate of decline ($a$), derived from a 100 year simulation model (a) without pasture offtake by pigs (model KOG from chapter 5) and (b) with pasture offtake by pigs (model BG from chapter 5). Pig densities are averages from iterations in which pig populations did not go extinct (maximum 10) and extinction probabilities are the proportion of 10 iterations in which the pig population went extinct within the 100 years considered.
Fig. 6.4  Variation in the time to extinction (quarters) as a function of the pig population's maximum rate of decline ($\alpha$), derived from 100 year simulation models without pasture offtake by pigs (model KOG from chapter 5) (●) and with pasture offtake by pigs (model BG from chapter 5) (○). Time to extinction is the average of all iterations which resulted in population extinction at given values of $\alpha$.

presented here, increasing rates of decline will mean that populations inhabiting areas with incrementally less floodplain habitat will occur at progressively lower average densities. Further, at some lower threshold percentage of floodplain coverage, resident pig populations will undergo periodic extinction. As percentage floodplain coverage decreases below this threshold the probability and speed of extinction both increase, suggesting that the demise of pig populations in such locations will be not only inevitable but increasingly rapid. Assuming that dispersal of pigs into such areas is the only source of recolonisation following local extinction, these areas will only contain pigs periodically between colonisation and extinction. As such, the effect of percentage coverage of floodplain habitat on pig density and
population persistence in the rangelands may determine both spatial variation in the average density of a population and limits to its geographic distribution at any point in time.

Fig. 6.5 summarises the links between availability of floodplain habitat, the maximum rate of population decline, average population density and the probability of population extinction in a conceptual model. The availability of floodplain habitat ultimately determines whether pig populations in the semi-arid rangelands will (1) persist in an area and at what density, or (2) occur periodically in an area before undergoing local extinction. Where floodplain availability is very low, maximum rate of decrease will be so high that pig population extinction will occur rapidly. Such areas could be considered as non-viable for pigs as they are unlikely to sustain populations for any protracted period of time. In reality, the difference between periodic and non-viable areas may have as much to do with the ability of pigs to recolonise an area as with the availability of floodplain habitat. In such cases, both floodplain availability and proximity of persistent pig areas will influence whether or not pigs occur periodically in an area, or how long such populations can sustain themselves. Information on rates of potential recolonisation of areas by pigs during favourable conditions is not available.

6.4.2 Percent floodplain coverage and maximum rate of decrease

The conceptual model summarised in Fig. 6.5 suggests that pig populations in the rangelands will be restricted largely to major river systems and their associated floodplains. Most sources of information on the local distribution of pigs in the rangelands confirm this (Hone and Waithman 1979, Giles 1980, Saunders 1988, Wilson et al. 1992), although Giles (1980) suggested that on occasion individual pigs (primarily large boars) occurred around permanent water sources isolated from floodplain habitat.

Giles (1980) suggested that in order to effectively thermoregulate during periods of hot dry weather, pigs require regular access to permanent sources of water for drinking and wallowing, and to thick vegetation to avoid prolonged exposure to direct sunlight. Giles (1980) speculated that this requirement restricted the distribution of pigs to floodplains during hot weather because only this habitat provided both water (in the form of permanent
A conceptual model of how the percent coverage of floodplain habitat, through its effect on the maximum rate of population decrease, influences average pig density and the probability of population extinction in the rangelands. The consequences for the persistence of pig populations in areas with given coverage of floodplain habitat are summarised at the bottom of the figure. Persistent pig populations never go extinct, while areas with less floodplain range from those where pigs occur periodically to those which are non-viable for pigs.
waterholes, billabongs and ephemeral swamps) and cover (in the form of extensive stands of
lignum and taller trees) (see Chapter 3). According to the conceptual model presented here,
the effect of any behavioural constraint (related to the use of different habitats) on the
abundance and distribution of pigs will be linked to variation in the rate of population
decrease under conditions of food shortage. An obvious candidate would be the effect of
some constraint on foraging behaviour imposed by an overriding need to restrict movements
to floodplain habitat over all or part of the day during hot weather. Belovsky (1984) described
a continuum in the potential foraging behaviour of animals which related decisions about how
long and where to forage, to a trade off between nutrient/energy accumulation and risk
minimisation. At one end of this continuum, nutrient maximisers attempt to ingest the
greatest quantity of some nutrient in the time available for foraging. At the opposite extreme,
time minimisers achieve their minimum nutritional requirement in the least amount of
foraging time. If more efficient nutrient intake incrementally improves survival and
reproductive output, a species will be inclined to the nutrient maximiser end of the
continuum. If time spent foraging incrementally increases exposure to sources of direct
mortality such as predators or adverse weather, a species will tend to the time minimiser end
of the continuum.

For many species, compromise between nutrient accumulation and risk of exposure to
sources of direct mortality results in foraging behaviour which is suboptimal for these factors
in isolation, but optimal when their effects are considered together (Sih 1982, Dill 1983,
Krebs 1986). These and other studies have considered the consequences of habitat selection,
modified by risk of exposure to sources of direct mortality, on the fitness of individuals in
wild populations. For example, Skogland (1991b) demonstrated that female reindeer
dispersed to higher altitudes at parturition to avoid predation by wolves, thereby foregoing
more nutritious forage available at lower altitudes. Skogland (1991b) argued that
disadvantages accruing to females by forsaking better foraging conditions at lower altitudes
were more than balanced by the reduction in risk of predation to both the female and her
offspring. Skogland (1991b) pointed out that for long-lived animals predation generally has a
more profound effect on individual fitness than do the incremental effects of better or worse
foraging conditions. Hence risk of predation or some other source of direct mortality may influence habitat preference more than optimal foraging decisions alone.

In this sense, pigs may seek to enhance individual fitness by restricting their activities to floodplain habitat over part of the day during hot weather, despite the fact that this may reduce their ability to forage optimally by constraining (1) the area over which they can forage and/or (2) the types of habitat in which they can forage. As such, the spatial extent of floodplain habitat in an area could determine the amount of food accessible to pigs during hot, dry weather, without influencing its absolute availability. Where the availability of floodplain habitat is low, this could have the effect of exacerbating food shortage. While this would influence the fitness of individual pigs, the fate of these individuals would also result in a population response to food shortage which would be linked to floodplain availability. This may explain the apparent association of percent floodplain coverage and maximum rate of population decline. In order to test this hypothesis, the movements and habitat choices of pigs would need to be contrasted under conditions of high and low food availability and high and more moderate ambient temperatures. The hypothesis predicts that high temperatures will override any tendency for pigs to choose habitats on the basis of their relative food availability, while more moderate temperatures will not compromise optimal foraging behaviour.

6.4.3 Maximum rate of decrease and the edge of a populations range

According to the modelling presented here, habitat-related variation in rate of decrease influences the local geographic distribution of pigs in the rangelands and variation in this distribution through time. Caughley et al. (1988) considered that population ranges which are determined by the availability of a resource that is used consumptively will display a step function in $r_m$ at the edge of their range, the population having the same maximum potential rate of growth wherever they and the limiting resource occur together. For the same reason, Caughley et al. (1988) argued that the body condition of animals in such populations will also step at the population boundary. In this respect, Caughley et al. (1988) suggested a population equivalent of Fretwell's (1972) ideal free distribution, which proposes that individual animals
will assort amongst habitats in such a way that resource availability leads to equal fitness amongst all individuals in a population. If individuals achieve such an assortment, the populations they make up will have the same $r_m$ and average body condition across a species range, but an average density which reflects variation in resource availability across this range. However, the prediction that individual fitness, $r_m$, and average body condition will be constant across a population's range, while density will vary with resource availability, implies that the population is consistently at ecological carrying capacity ($K$) (Caughley et al. 1988, Pulliam 1989). The pig populations modelled here did not to maintain any real equilibrium, their density tending to be over- or under-abundant in relation to their food resources at any point in time. As such, the average density and probability of persistence of these populations were determined by the cumulative effects of rates of change in their abundance, which reflected temporal variation in the abundance of resources rather than any constant spatial pattern in their availability. Consequently, any factors which influence the spatial pattern of resource availability (either through direct effects on the resources or on an animal's ability to procure them) have the potential to influence both the density distribution of the population or the ability of a population to permanently or periodically inhabit a given area. For example, in the current study the availability of floodplain habitat appeared to influence the accessibility of food resources to pigs during hot weather. This modified the numerical response, increasing maximum rates of decline in pig density when food was scarce in areas with less floodplain habitat. Because the rate of decrease in abundance influences a population's average density, probability of persistence and time to extinction, the availability of floodplain habitat in an area ultimately determines whether pigs will occur (1) persistently, (2) periodically or (3) never. Hence, the spatial extent of pig populations in the rangelands appears more dependent on factors which determine accessibility of limiting resources, than on some underlying spatial pattern of availability of those resources. To what degree habitat or other constraints on accessibility to limiting resources restrict the range of other species is unknown. However, such constraints may explain why many ostensibly generalist herbivores do not occur wherever forage, water and climatic conditions allow.
Caughley et al. (1984) examined variation in exponential rates of increase ($r$) over 6 years for red kangaroos in far western and central New South Wales, as a function of local rainfall accumulated over the previous 12 months. The two sampling locations represented the geographic centre and eastern edge of the species range in eastern Australia, respectively.

Caughley et al. (1984) fitted parabolas to relationships between $r$ and rainfall for the two locations. These parabolas indicated that maximum rate of increase ($r_m$) was similar for kangaroos in the centre and at the edge of their range (0.40), but an index of the hypothetical maximum rate of decline (estimated from the intercept of fitted parabolas which predict $r$ for each population if no rain fell over the previous 12) was 39% higher at the edge (intercept = -2.8) than at the centre of the species range (intercept = -1.7). If this index is a reasonable approximation of $a$ (Caughley (1987) reported an exponential rate of decline of $a = -1.6$ for a population of red kangaroos in the centre of their distribution over 4 months of an extreme drought), demographic processes leading to lower red kangaroo abundance at locations progressively further east in New South Wales may be qualitatively similar to those which lead to lower densities of pigs as one moves away from river systems in the rangelands. That is, demographic mechanisms which determine average population density and the probability of population persistence may have more to do with factors which affect the accessibility of limiting resources than with any underlying spatial pattern to the abundance of those resources. Similarly, Jarman and Jarman (1974) and Sinclair (1985) demonstrated that predation risk influenced the foraging behaviour of ungulate species in eastern Africa.

Although demographic consequences of modified grazing behaviour were not measured, Sinclair (1985) provided evidence that such behaviour increased interspecific competition between ungulates, and that this may have affected species' distributions and consequently ungulate community composition. An unequivocal test of the role of constraints on foraging behaviour in determining species or population ranges would require evidence of a direct link from the constraint, through foraging behaviour to demographic processes which affect the populations' density and/or probability of persistence in given areas.
Chapter 7 Conclusions and general discussion

The purpose of this study was to test the applicability of two hypotheses explaining variation in the abundance of large herbivores to populations of feral pigs inhabiting the semi-arid rangelands of inland Australia. The first, the intrinsic food hypothesis, proposes that the density of herbivores is regulated at or around some equilibrium ($K$) through density dependent variation in the rate of change in their abundance ($r$) through the effect of per capita food availability on their demographic rates (Sinclair et al. 1985). The second, the extrinsic food hypothesis, proposes that herbivores do not affect variation in the abundance of their food resources and hence are not regulated through density dependent variation in per capita food availability (Andrewartha and Birch 1954, 1984). The essential difference between the two hypotheses is whether or not herbivores influence the availability of their food resources. If they do, their abundance will be regulated through density dependent intraspecific competition. If they do not, rates of change in their abundance are independent of population density, there can be no intraspecific competition for food and hence no regulation of their abundance.

The applicability of these two hypotheses to feral pig populations in the rangelands was tested by evaluating predictions of two models which represent them; an interactive model for the intrinsic food hypothesis and a reactive model for the extrinsic food hypothesis. The interactive model proposes that the reciprocal effect of vegetation and herbivore abundance, through the functional and numerical responses of herbivores to variation in vegetation biomass, forms a vegetation-herbivore feedback loop (Caughley 1976a). While interaction between herbivores and their food resources can lead to different outcomes for different grazing systems, one such outcome is a tendency toward some equilibrium between vegetation and herbivore abundance (centripetality) which promotes grazing system persistence through essentially density dependent processes (Caughley 1976a, 1987). The strength of centripetality will depend on the intrinsic variability of the environment of the grazing system and the strength of the vegetation-herbivore feedback loop which depends on the relative efficiency of the functional and numerical responses. In contrast, the reactive model involves only the numerical response of herbivores to vegetation biomass, there being
no reciprocal effect of vegetation offtake by herbivores on the abundance of vegetation (Caughley and Lawton 1981). Because the functional response is ineffective or inoperative in the reactive model, the vegetation-herbivore feedback loop of the interactive model is incomplete, and the grazing system cannot be centripetal.

Predictions of the interactive and reactive models were tested using an experiment where the density of 6 feral pig populations was manipulated in order to measure (1) the relationship between pig density and the rate of increase in their populations, (2) the relationship between pig density and pasture biomass, and (3) the relationship between pasture biomass and the rate of increase for the pig populations. Table 7.1 summarises predictions and outcomes of the 2 models. The results of the experiment indicated that the pig-pasture grazing system was reactive, pig populations in the rangelands conforming to the extrinsic food hypothesis, their abundance being limited but not regulated by food availability.

<table>
<thead>
<tr>
<th>Food hypothesis</th>
<th>Model</th>
<th>$r$ with pig density</th>
<th>Outcome</th>
<th>$r$ with pasture biomass</th>
<th>Outcome</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intrinsic</td>
<td>Interactive</td>
<td>-/0</td>
<td>0</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Extrinsic</td>
<td>Reactive</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
</tbody>
</table>

Table 7.1 Predictions and outcomes of 2 models for 3 relationships measured using a manipulative experiment on feral pig populations. Relationships which are positive, negative or non-significant according to each model are indicated as +, - and 0 respectively.

However, a subsequent experiment which measured the functional response of pigs and used a series of stochastic simulation models to assess the influence of the vegetation-herbivore loop on variation in pig abundance indicated that differences in the relationship between pig abundance and pasture biomass predicted by the 2 models were so slight as to be virtually unmeasurable. Outcomes for models equivalent to the intrinsic and extrinsic food hypotheses
were virtually coincident because pigs are relatively inefficient grazers, but more importantly because pigs were numerically scarce relative to other herbivores in the grazing system (represented by red kangaroos in the simulation models). Pigs occurred at lower average densities than other herbivores because of their much higher rates of decline during droughts. The high rate of decrease in pig populations when food was short compromised the efficiency of the numerical response. This reduced the efficiency of the vegetation-herbivore feedback loop, of which the numerical response is a component, to the extent that pigs had little ability to influence variation in the availability of their food resources over and above that due to rainfall and offtake by other herbivores.

Hence, it appears that the initial experiment did not resolve the issue of whether pigs in the rangelands conform to the intrinsic or extrinsic food hypothesis, or whether or not these populations are regulated. However, the similarity of outcomes predicted by simulation models representing these 2 hypotheses suggest that differences may be of little relevance to how the grazing system functions. This result suggests that differences between the intrinsic and extrinsic food hypotheses may be relative rather than absolute. Caughley (1987) in describing the concept of centripetality as it relates to grazing systems, implied that environmental variation buffets vegetation-herbivore systems away from any potential equilibrium between herbivore and vegetation abundance. However, the vegetation-herbivore feedback loop comprising the functional and numerical responses tends to dampen this buffeting, pushing the system back toward the equilibrium. The vegetation biomass feedback loop (resulting from parabolic plant productivity) may contribute to this dampening effect, but was subordinate to the vegetation-herbivore loop in the grazing system Caughley (1987) described.

The pasture-pig feedback loop in the current study was so inefficient that for all practical purposes, the grazing system was entirely reactive. However, if the efficiency of the feedback loop between pig and pasture abundance were enhanced, the pig-pasture system would become more functionally interactive, conforming more closely to the intrinsic food hypothesis. For example, by decreasing the maximum rate of decline of pig populations into droughts ($a = -2.045$) to that estimated for red kangaroos ($a = -1.6$), the pig-pasture system
becomes fully interactive, displaying strong centripetality. Hence, rather than being discrete, the intrinsic and extrinsic food hypotheses are likely to represent two ends of a continuum (Fig. 7.1).

Fig. 7.1 Hypothetical continuum between the extrinsic and intrinsic food hypotheses. Toward the extrinsic end of the continuum, the magnitude of environmental stochasticity and inefficiency of the vegetation-herbivore feedback loop (centripetality) mean that extrinsic food shortages dominate the dynamics of the herbivore population. In contrast, toward the intrinsic end of the continuum, reducing environmental stochasticity and the increasing strength of centripetality mean that food shortages are increasingly intrinsic in origin. Examples of grazing systems from this study and the literature (red kangaroos (Caughley 1987), caribou (Skogland 1985, 1989, Caughley and Gunn 1993) and African buffalo (Sinclair 1985)) are placed in approximate positions along the hypothetical continuum.
The position of a grazing system along such a continuum will depend on the intrinsic variability of the environment it occupies and the efficiency of its vegetation-herbivore feedback loop (i.e. the strength of centripetality). As such, the interactive model is the general case for all grazing systems, the degree of environmental stochasticity and relative strength of the functional and numerical responses it represents determining where along the continuum it settles. At the intrinsic extreme of the continuum, centripetality of a grazing system will be absolute and density dependence constant. Such grazing systems can be portrayed by single-species models based on logistic population growth, which effectively represent a "short-hand" version of the interactive model under conditions of little or no environmental variability and/or extreme efficiency in reciprocal feedback between herbivore and vegetation abundance. The dynamics of African buffalo described by Sinclair (1977) and Dublin et al. (1990) would tend toward this end of the hypothetical continuum. At the extrinsic extreme of the continuum, centripetality and density dependence will be non-existent and variation in herbivore abundance will be totally reactive to the influence of extrinsic factors on food availability. Because herbivore populations in such grazing systems are unregulated, they will tend to be less stable although they may persist for considerable periods (Andrewartha and Birch 1984, Den Boer 1991). Persistent herbivore populations conforming to the extrinsic food hypothesis should generally tend to have high rates of increase, particularly if they inhabit unpredictable environments. The feral pig populations described in this study would tend toward this end of the continuum. Between these two extremes, herbivore populations will vary in abundance according to the availability of their food resources, the biomass of which they exert some but not absolute influence over. The vegetation-herbivore feedback loop in such systems is strong enough to dampen some variation in food availability, but not strong enough to completely dampen the effects of stochastic environmental buffeting. As such, these systems will be centripetal but will not occupy vegetation-herbivore equilibria long enough or often enough that their dynamics can be described by single-species models. The grazing systems comprising red kangaroos and rangelands pastures and caribou and alpine/arctic tundra pastures described by Caughley and Gunn (1993) would occupy this middle region of the hypothetical continuum.
The hypothetical continuum between the concepts of intrinsic and extrinsic food limitation will have consequences for spatial as well as temporal variation in herbivore abundance. In the current study the maximum rate at which pig populations declined increased as floodplain habitat (evidently necessary for thermoregulation) became more scarce. Modelling indicated that as the maximum rate of population decline increased, average population decreased and the probability of population extinction rose. A similar trend was found across the species range for red kangaroos in Australia's eastern rangelands (Caughley et al. 1984). Elevating a herbivore population's maximum rate of decrease has the effect of lowering the efficiency of the vegetation-herbivore feedback loop. Hence, moving from the centre to the edge of the range of a population whose abundance is limited by consumptively exploited resources will be equivalent to moving toward the extrinsic end of the hypothetical continuum. This has the effect of decreasing the efficiency of the vegetation-herbivore loop which leads to declining average herbivore density. As the grazing system moves progressively further toward the extrinsic end of the continuum (i.e: toward the edge of its range), the vegetation-herbivore feedback loop becomes still less efficient and herbivore population extinction becomes probable and ultimately inevitable, defining where a herbivore population will and will not persist.
Appendix 1 Estimating feral pig abundance using aerial survey and maximum percentage bait take

Introduction

As part of the manipulative experiment described in Chapter 4, pig density was monitored quarterly on six study sites. This required development of reliable techniques for rapidly estimating pig density which accounted for the vagaries of seasonal conditions and other potential sources of bias. In this appendix the development of two techniques for estimating pig abundance, one a direct count (aerial survey) and the other an indirect index (maximum percentage bait take), is described.

Three general approaches have been used to estimate the abundance of wild animals: (1) direct counts, (2) indirect indices and (3) mark-recapture techniques (Caughley 1977). In order to estimate the absolute abundance of a wild animal population from either a direct count or an index the difference between the count or index and the true abundance of the population from which it was obtained must be established and corrected for. This requires either (1) application of the count or index to populations of known size or (2) independent estimation of bias associated with the count or index (Caughley 1977).

Visibility bias in aerial survey

Aerial survey is a widely used technique for estimating the actual or relative abundance of large mammals (Petrides 1954, Siniff and Skoog 1964, Caughley and Grigg 1981). Aerial counts of animals underestimate true abundance because observers do not see all animals (Jolly 1969). The systematic underestimation of true abundance during aerial surveys is called visibility bias. Visibility bias will be consistent under given conditions, and hence is distinct from random sampling error (Short and Bayliss 1985). If aerial counts are to be used

---

1The content of this appendix has been submitted as to Wildlife Research as two papers.
to estimate actual animal abundance, visibility bias must be estimated and accounted for (Caughley 1974).

Visibility bias associated with aerial counts has been estimated using regression techniques (Caughley et al. 1976), comparison of aerial counts and independent population estimates (Goddard 1967, Leighton et al. 1979, Short and Bayliss 1985, Short and Hone 1988), sightability estimates for marked or radio-collared animals (Rice and Harder 1977, Gasaway et al. 1985, Packard et al. 1985), and double-count survey techniques (Magnusson et al. 1978, Caughley and Grice 1982, Bayliss and Yeomans 1989, Choquenot 1995). Using these techniques, visibility bias has been shown to vary systematically with survey parameters such as aircraft height and speed, the width of transect scanned (Caughley et al. 1976) and time of day (Hill et al. 1985, Short and Hone 1988); and with environmental parameters such as temperature (Bayliss and Giles 1985), cloud cover (Short and Bayliss 1985) and habitat and/or vegetation cover (Caughley et al. 1976, Short and Bayliss 1985, Hill et al. 1985).

In this part of the study a double-count survey method which directly measures visibility bias, was used to investigate bias associated with habitat type during standardised helicopter surveys for pigs. Multiplicative correction factors to account for habitat-related bias were developed from estimates of visibility bias. In addition, a series of removal experiments was used to investigate the potential effect of population reduction using helicopter shooting on sightability of pigs during helicopter surveys. Saunders (1988) suggested that harassment by helicopters reduced subsequent helicopter counts by as much as 30%.

Maximum percentage bait take

Because aerial survey could not always be used during the study, a ground-based survey technique which provided estimates of pig abundance comparable with those obtained through aerial survey was required. Choquenot et al. (1990) successfully used an index based on the maximum percentage of bait trails consumed by pigs (MPBT) to assess pig abundance when evaluating the efficacy of a warfarin poisoning program in western New South Wales.
However, they suggested that (1) the index would be site-specific, and (2) that the effect of prevailing seasonal conditions on the propensity of pigs to find and/or accept bait would likely influence the relationship between MPBT and true population abundance. Hone (1983) also suggested that seasonal conditions, through their effect on the availability of alternative food, were at least partially responsible for variation in the success of 1080 poisoning campaigns.

This part of the study measured the relationship between MPBT, seasonal conditions (indexed by prevailing pasture biomass) and pig density on all six study sites. The influence of prevailing seasonal conditions on the form of the relationship between MPBT and pig density was examined and a predictive relationship between MPBT, which accounts for prevailing seasonal conditions, was derived.

Methods

Aerial surveys

All surveys were conducted at an altitude of 30m (100ft), and an airspeed of 80km/hr. For double-count surveys tandem observers seated in the right-hand front and rear positions, and a single observer in the left-hand rear positions counted feral pigs, red kangaroos, grey kangaroos, emus and feral goats in groups as they occurred in 150m-wide transects demarked by right-angled poles attached to either side of a Hughes 500 helicopter. For conventional (single-count) surveys, left and right observers only counted from the rear seat of a Kawasaki/Bell 47 helicopter. Groups of animals counted represented sighting entities rather than biologically meaningful associations of animals. Eastern and western grey kangaroos, both of which occur in the region, could not usually be distinguished from the air and were identified collectively as grey kangaroos. Caughley et al. (1984) determined that 75 to 91% of grey kangaroos in the region were eastern greys. Counts were made onto a continuously running tape recorder and collated at the completion of each survey.
For each survey, east-west transects were placed randomly without replacement across study sites, with the number of transects estimated to return sampling rates of around 15%. Actual sampling rates were calculated later from start and end time for each transect and known airspeed. All counts were made during the first and last three hours of daylight, under conditions of little or no cloud (<1 octal). Air temperature, recorded at the beginning of each transect, did not exceed 21°C.

All groups of animals observed in transects were placed into one of four generic habitat types readily identifiable from the air:

1. **Black soil floodplain.** Heavy black soil areas associated with river channels or their immediate floodplains. Vegetation is typically dominated by lignum (*Muehlenbeckia cunninghamii*), interspersed with stands of black wattle (*Acacia stenophylla*). Yapunyah (*Eucalyptus ochropholia*), coolibah (*E. microtheca*) and black box (*E. largiflorens*) occur largely around the edges of these floodplains, with river red gums (*E. camaldulensis*) and black box in often thick stands along the banks of deeper channels.

2. **Red soil shrubs.** Higher red soil areas, dominated by hopbush (*Dodonaea* spp.) and other woody shrubs including emubush (*Eremophila longiflora*), budda (*E. mitchelli*), and turpentine (*E. sturtii*). Stands of taller timber are distributed through these areas, consisting of belah (*Casuarina cristata*), rosewood (*Heterodendrum oleifolium*), and occasionally white cypress pine (*Callitris columellaris*).

3. **Cane grass flats.** Loamier grey soil flats, more commonly flooded by local rains than by accumulated floodwaters. Typically, these flats support often monospecific stands of canegrass (*Eragrostis australasica* or *Leptochloa digitata*), and less commonly sparse stands of lignum or saltbush (*Atriplex* spp.).
4. Red soil grass plains. Extensive red soil plains, dominated by speargrasses (*Stipa* spp.), common bottlewashers (*Enneapogon avenaceus*), and often woollybutt (*Eragrostis eripoda*). There is virtually no tree or scrub cover, although small isolated stands of white cypress pine or belah/rosewood may occur.

Although not specifically estimated, the degree of cover associated with the canopy of these habitat types decreases from black soil floodplain to red soil grass plains.

Double-count surveys

Three double-count surveys were conducted in three areas, corresponding to four of the study sites described in Chapter 2. The first area comprised site NP and site NC, the second, site TO and the third, site GO. During all surveys observers sitting in the right hand front and rear seats of the helicopter counted groups of animals in the same transect. Several passes over stationary objects ensured that the two observers had identical transect boundaries. During collation of data from survey tapes, the numbers of groups of pigs falling into each of three categories were recorded:

- $S_1$ Groups seen by the front observer, but missed by the rear.
- $S_2$ Groups missed by the front observer, but seen by the rear.
- $B$ Groups seen by both observers.

Groups recorded simultaneously, or nearly so, by the two observers were considered to be the same pigs and placed in category $B$. Densities of pigs encountered were low enough, and the speed of the helicopter slow enough, that cases of uncertainty were minimal (<5% across all surveys). Where it was unclear whether closely recorded observations were in fact the same group of pigs, the observations were treated as separate sightings.

Counts made by the tandem observers on the right-hand side of the helicopter were used to estimate visibility bias. Seber's (1973) Petersen estimation was used to derive estimates of pig
abundance ($N$), and the probability that the front or rear observer will see a group of pigs ($P_1$ and $P_2$ respectively) (Caughley and Grice 1982). Visibility bias was considered to be the inverse of these sighting fractions averaged across the front and rear observers $\left(1 - \frac{(P_1 + P_2)}{2}\right)$. Between-transect (n=350) variation in visibility bias was used to test for effects of habitat, study site and survey number using analysis of variance. A non-weighted mean solution (Snedecor and Cochran 1967) was used to account for unbalanced sample sizes in cells, because groups of pigs were not sighted in every habitat on every transect.

Removal experiments

Seven removal experiments were conducted. All were associated with the manipulation of pig density carried out in order to impose the large-scale population experiment discussed in chapter 4. Removal experiments involved a conventional (single-count) aerial survey before and after the abundance of the pig population on a study site was reduced. Of the seven removal experiments, four involved helicopter shooting and three trapping.

Pre- and post-removal counts of pig groups were multiplied by average group size to estimate the number of pigs in each transect sampled, uncorrected for visibility bias. The 'simple' method (Caughley 1977) was used to derive uncorrected population estimates from transect totals. Uncorrected population estimates were used as indices for index-manipulation-index analysis (Caughley 1977), the manipulation being the intervening removal of pigs either by helicopter shooting or trapping. Differences between uncorrected population estimates and those derived from index-manipulation-index analyses were attributed to visibility bias associated with counts of pig groups. Estimates of visibility bias derived from the seven experiments were used to examine the effects of method of removal (helicopter shooting or trapping) on the sightability of pig groups.
Maximum percentage bait take

On each of the six study sites described in section 3.2, between 60 and 90 bait-trails were distributed along tracks and trails (see section 4.2.3). In most cases, bait trails were placed in locations where pigs, if present, would be likely to find them. These locations included the edge of waterholes, distinct rubs under fences, clear animal pads, areas dominated by lignum and along ephemeral drainage lines. The minimum distance between bait trails was 1.5km. The same bait trail locations were used throughout the study.

A bait trail consisted of approximately 8kg of fermented wheat, distributed along a 70-100m trail consisting of 7-10 discrete piles with wheat trickled between (Choquenot et al. 1990). Bait trails were laid at the beginning of each assessment and inspected daily and either freshened or replaced. Those that had been consumed by pigs, as indicated by the presence of tracks and the complete consumption of wheat, were recorded and expressed as a proportion of all bait trails on offer. Once pigs began consuming bait trails they were rarely abandoned, as long as the trail continued to be offered. Bait trails continued to be offered until 3-7 days after maximum proportional bait take was achieved, ascertained visually from plots of percentage bait take over time. Average percentage bait take following attainment of this maximum (MPBT) was used as an index of pig density following frequency-density transformation (Caughley 1977).

MPBT was measured simultaneously with standard quarterly estimates of pasture biomass and pig density on six occasions for each of the six study sites. Pig density was estimated from corrected aerial counts (see section 4.2.3) and pasture biomass using a non-destructive technique applied in a semi-random design (see section 4.2.4). MPBT was measured on two occasions each when pasture biomass was relatively high, moderate and low as indicated by quarterly estimates. Measurements of MPBT and estimates of pasture and pig abundance were divided into three subgroups based on pasture biomass: low (range: 23-409kg/ha), medium (range: 452-798kg/ha) and high (range: 801-1,396kg/ha). The influence of prevailing seasonal conditions on the relationship between MPBT and pig density was assessed by
comparing the intercept of the regression of pig density on MPBT between pasture biomass subgroups. After accounting for the effects of seasonal conditions, predictive relationships between MPBT and pig density were derived using linear models to test for between site differences.

Results

Double-count surveys

Visibility bias for counts of pig groups varied significantly only with habitat (Table 1). To examine how visibility bias varied between habitats, average bias for each of the four habitats was estimated separately (Table 2), and multiple comparisons between estimates performed (Table 3). Bias was significantly higher for black soil floodplain compared to all other habitats. Bias was not significantly different amongst the three non-riverine habitats.

Results from double-count surveys suggest that 2 multiplicative correction factors be used to account for visibility bias in helicopter counts of pig groups: 3.61 for black soil floodplains and 1.47 for all other habitats.

Removal experiments

Table 4 summarises the site, time, magnitude and method of removal, and outcomes for each of the removal experiments undertaken. The seven experiments indicated that average visibility bias for counts of pig groups was 0.462, equivalent to a multiplicative correction factor of 1.859. There was no significant difference in visibility bias between sites which had been shot from helicopters and those which had been trapped ($t = 0.016$, $df = 3.507$, $P = 0.988$).
<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Anova SS</th>
<th>Mean Square</th>
<th>F-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>3</td>
<td>11.109</td>
<td>3.703</td>
<td>75.07</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>0.183</td>
<td>0.092</td>
<td>1.86</td>
<td>NS</td>
</tr>
<tr>
<td>Hab*Site</td>
<td>2</td>
<td>0.012</td>
<td>0.006</td>
<td>0.13</td>
<td>NS</td>
</tr>
<tr>
<td>Survey</td>
<td>6</td>
<td>0.148</td>
<td>0.025</td>
<td>0.50</td>
<td>NS</td>
</tr>
<tr>
<td>Hab*Surr</td>
<td>6</td>
<td>0.255</td>
<td>0.043</td>
<td>0.86</td>
<td>NS</td>
</tr>
<tr>
<td>Site*Surr</td>
<td>4</td>
<td>0.155</td>
<td>0.039</td>
<td>0.79</td>
<td>NS</td>
</tr>
<tr>
<td>Hab<em>Site</em>Surr</td>
<td>12</td>
<td>0.324</td>
<td>0.027</td>
<td>0.55</td>
<td>NS</td>
</tr>
<tr>
<td>Error</td>
<td>359</td>
<td>17.709</td>
<td>0.049</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>349</td>
<td>31.546</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1  Analysis of variation in visibility bias associated with counts of pig groups due to habitat (black soil floodplain, red soil shrubs, cane grass flats or red soil grass plains), study site (NP/NC, TO or GO) and survey number (1, 2 or 3).

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Average Visibility Bias</th>
<th>Standard Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black soil floodplain</td>
<td>0.723</td>
<td>0.234</td>
</tr>
<tr>
<td>Red soil shrubs</td>
<td>0.315</td>
<td>0.231</td>
</tr>
<tr>
<td>Cane grass flats</td>
<td>0.318</td>
<td>0.232</td>
</tr>
<tr>
<td>Red soil grass plains</td>
<td>0.322</td>
<td>0.240</td>
</tr>
</tbody>
</table>

Table 2  Mean visibility bias and associated standard deviations for counts of pig groups in four habitats.
### Table 3

Summary of multiple comparisons of mean visibility bias between habitats for counts of pig groups. Comparisons are $t$-tests referred to the Bonferroni $t$-distribution ($k =$ maximum comparisons (6), $df = df$ of the MS error (359)).

<table>
<thead>
<tr>
<th>Habitat Comparison</th>
<th>$t$-value</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black soil floodplain : red soil shrubs</td>
<td>13.02</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Black soil floodplain : Cane grass flats</td>
<td>12.795</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Black soil floodplain : Red soil grass plains</td>
<td>12.669</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Red soil shrubs : Cane grass flats</td>
<td>-0.095</td>
<td>NS</td>
</tr>
<tr>
<td>Red soil shrubs : Red soil grass plains</td>
<td>-0.222</td>
<td>NS</td>
</tr>
<tr>
<td>Cane grass flats : Red soil grass plain</td>
<td>-0.125</td>
<td>NS</td>
</tr>
</tbody>
</table>

### Table 4

Summary of seven removal experiments conducted to estimate visibility bias associated with counts of pigs during standardised helicopter surveys. The Table gives the method of removal employed, the size of the removal imposed, pre- ($Pre$) and post-removal ($Post$) indices of pig abundance, pre- ($Pre$) and post-removal ($Post$) estimates of true abundance, and visibility bias ($VB=1-1/(N/\tilde{N})$) estimated for the seven experiments conducted at given sites (see section 3.2) over two summers.

<table>
<thead>
<tr>
<th>Site</th>
<th>Summer</th>
<th>Method</th>
<th>Pigs removed</th>
<th>Pre $I$</th>
<th>Post $I$</th>
<th>Pre $N$</th>
<th>Post $N$</th>
<th>$VB$</th>
</tr>
</thead>
<tbody>
<tr>
<td>NP</td>
<td>89/90</td>
<td>Trap</td>
<td>215</td>
<td>240</td>
<td>134</td>
<td>487</td>
<td>272</td>
<td>0.507</td>
</tr>
<tr>
<td>NC</td>
<td>89/90</td>
<td>Shoot</td>
<td>14</td>
<td>121</td>
<td>111</td>
<td>169</td>
<td>155</td>
<td>0.286</td>
</tr>
<tr>
<td>TO</td>
<td>89/90</td>
<td>Shoot</td>
<td>1,498</td>
<td>777</td>
<td>243</td>
<td>2,179</td>
<td>682</td>
<td>0.644</td>
</tr>
<tr>
<td>GO</td>
<td>89/90</td>
<td>Shoot</td>
<td>48</td>
<td>320</td>
<td>297</td>
<td>668</td>
<td>620</td>
<td>0.521</td>
</tr>
<tr>
<td>LA</td>
<td>89/90</td>
<td>Trap</td>
<td>115</td>
<td>261</td>
<td>196</td>
<td>462</td>
<td>347</td>
<td>0.435</td>
</tr>
<tr>
<td>NA</td>
<td>89/90</td>
<td>Shoot</td>
<td>102</td>
<td>78</td>
<td>17</td>
<td>130</td>
<td>28</td>
<td>0.402</td>
</tr>
<tr>
<td>NP</td>
<td>90/91</td>
<td>Trap</td>
<td>223</td>
<td>223</td>
<td>154</td>
<td>401</td>
<td>277</td>
<td>0.444</td>
</tr>
</tbody>
</table>
Maximum percentage bait take

Intercepts of the regression of MPBT on pig density plotted against average pasture biomass for the three biomass subclasses along with the least squares line of best fit are shown in Fig. 1. Although insufficient data were available to establish a significant relationship, the least squares line of best fit strongly indicates a decline in the density of pigs when MPBT = 0 (i.e. the number of pigs which would not take bait) with increasing pasture biomass. The relationship was described by:

\[ a = 0.66727 + (-0.00231PB) \]  \hspace{1cm} (1)

where \( a \) is the intercept of the least squares line of best fit for the relationship between MPBT and pig density, and \( PB \) is pasture biomass in kg/ha. Data relating estimated pig density to MPBT for each site were corrected for the effect of pasture availability on the propensity of pigs to accept bait by subtracting \( a \) corresponding to prevailing pasture biomass from pig density estimates. A linear model relating corrected pig density to MPBT indicated no significant between-site effects (\( t = -1.437, df = 33, P = 0.161 \)), suggesting that the slope of the relationship between MPBT and corrected pig density was similar for all sites. A linear model relating corrected pig density to MPBT for all sites was highly significant (\( F = 91.375, df = 1,34, P < 0.01 \)), accounting for 72% of the variation in corrected pig density. This model and equation (1) were combined into an equation which predicts variation in pig density (\( PD \)) from MPBT and \( PB \) by:

\[ PD = (0.44633 + (0.08895MPBT)) - (0.66727 + (-0.00231PB)) \]  \hspace{1cm} (2)

This equation was used to estimate pig density from MPBT and pasture biomass for all sites used in this study.
Fig. 1 Intercepts of regressions of MPBT on pig density, plotted against average biomass for the 3 pasture subclasses.

Discussion

Helicopter surveys of feral pig abundance

Research on helicopter surveys to estimate pig abundance was first conducted by Hone (1987). This work used a known-size population of pig carcasses to test one strip transect estimator (the ratio method), and eight line transect estimators (Cox's method, the Fourier series, negative exponential, half-normal, exponential power series, exponential polynomial, hermite polynomial and hazard rate) for correcting visibility bias associated with counts of pigs in an area of the Northern Territory consisting of a mixed flood plain/open woodland. The influence of cloud cover, time of day and observer effects on visibility bias were also investigated. Hone (1987) found that the most accurate estimators were the ratio method
using a 25m-wide transect for floodplain habitat, and the Fourier series for the combination of floodplain and woodland habitats, although all estimators returned reasonably accurate population estimates. No effects of cloud cover or time of day on visibility bias were detected, although significant observer differences in the shape of sightability functions for line transect counts were apparent.

Using a survey height of 46m (150ft) and a transect width of 100m, he estimated maximum visibility bias for counts of pig carcasses to be 0.545 and 0.454 in combined floodplain/open woodland and floodplain respectively. These estimates are similar to the average estimate of bias for the seven removal experiments in this study (0.462) using a survey height of 30.5m (100ft) and a strip width of 150m. In contrast, Saunders (1993b) using a survey height of 100m (324ft) and unbounded transects estimated the abundance of a pig population before and after 2 helicopter shoots. Saunders (1993b) used an index-manipulation-index approach, such as that employed in the removal experiments in this study, to correct for visibility bias. Although Saunders (1993b) did not specifically estimate visibility bias, his data indicate bias of 0.645 and 0.796 (mean=0.721) respectively for surveys associated with his first and second helicopter shoot.

At least some of the discrepancy in estimates of visibility bias between these and the current study could be attributable to the differences in aircraft height and survey strip width employed, and the fact that Hone (1987) counted carcasses as opposed to live pigs. Hone (1987) found that visibility bias associated with counts of pigs (1) increased with increasing survey strip width, and (2) decreased when live pigs as opposed to pig carcasses were counted. Similarly, Bayliss and Giles (1985) found that bias associated with helicopter counts of kangaroos increased with increasing aircraft height. Results of the double-count surveys undertaken as part of the current study would indicate that variation in bias would also likely have arisen from differences in habitat composition (particularly the amount of floodplain habitat) of the areas surveyed in each study.
Saunders (1988) suggested that recent helicopter shooting could increase visibility bias associated with counts of pigs from helicopters because pigs would modify their behaviour following harassment by helicopters, thus decreasing their sightability. The removal experiment in this study found no evidence that helicopter shooting decreased the sightability of pig groups.

Maximum percentage bait take

Saunders et al. (1993) found that bait uptake by pigs in a subalpine environment was significantly increased when bait was placed (1) at treelines, (2) on fire trails and (3) in areas where recent pig activity was evident. Further, they found a positive significant interactive effect of these three factors on the probability that bait would be taken, and that bait placement on fire trails interacted positively with season. Such complex interactions would seem to confound the comparison of bait take as an index of pig abundance between sites. Yet no significant site effect on the relationship between a measure of bait take (MPBT corrected for the effect of seasonal conditions) and pig density was found in the current study. A possible explanation is that in the current study bait trails were laid (1) at a similar density on each site, and (2) on the first occasion that baiting occurred, bait trails were laid strictly in locations where sign of recent pig activity was evident. Saunders et al. (1993) found that evidence of recent activity was most strongly related to the probability of bait acceptance by pigs. A similar response has been reported for bait uptake by wild pigs in the United States (Fox 1972, Fox and Pelton 1977).

Choquenot et al. (1993) investigated the relationship between bait trail consumption and pig density by monitoring the percentage of bait trails consumed for two populations of pigs which were intensively trapped. They indicated that the 20% of pigs which survived the trapping program did so because they would not consume bait, rather than any inability to find bait. They suggested that the percentage of pigs which would not consume bait was likely to be related to the availability of alternative sources of food, which would depend on prevailing seasonal conditions. As such, the proportion of a population which would survive
trapping or poisoning programs would depend to at least some degree on the abundance of alternative food (Choquenot et al. 1990, 1993). If seasonal conditions influence the proportion of pigs which will find or accept baits, variation in seasonal conditions will likely lead to variation in the point where a line describing the relationship between pig density and MPBT intersects the pig density axis, rather than the slope or shape of the relationship itself (Fig. 6.1).
References


