Population Dynamics of Eastern Grey Kangaroos in Temperate Grasslands

Don Fletcher BA

Institute of Applied Ecology
University of Canberra

A thesis submitted in fulfilment of the requirements of the degree of
Doctor of Philosophy in Applied Science at the University of Canberra

2006

ACKNOWLEDGMENTS

I am deeply appreciative of the support and guidance of my principal supervisor Prof. Jim Hone, throughout the project. His commitment to principles of scientific method in applied ecology, his knowledge of the literature, the breadth of his interests, and his patience, were inspiring. I also thank Stephen Sarre, my second supervisor, for his successful effort to complement what Jim provided, for constructive and friendly advice and criticism and for broadening my knowledge of the application of molecular biology to ecology.

My employer, Environment ACT, supported the project in various ways throughout, especially in tolerating my absence from the office when I was undertaking fieldwork or working at the University of Canberra. I particularly thank the manager of the research group at Environment ACT, Dr David Shorthouse, for dedicated and patient support, and for ably defending the project at the necessary times, and my colleague Murray Evans who carried an extra workload in 2002–03 in my absence. I also thank the former manager of the ACT Parks and Conservation Service, Tony Corrigan, for enlisting support at a crucial time when the project was commencing. The former Marsupial CRC, particularly its leader, John Rodger, supported the project handsomely with a cash grant without which it would not have commenced.

I want to thank the Applied Ecology Research Group (now the Institute of Applied Ecology) for friendly support. It has been an excellent research environment with a broad range of topics to learn about and a suitable range of activities, both academic and social, to encourage a friendly and worthwhile learning environment. The denizens of the postgrad room and environs at UC added much to my enjoyment of the project – especially Anna McDonald, Nicci Aitken, Kiki Dethmers, Michelle Walter, Alex Quinn, Megan McCann, Marion Hoehn, Wendy Dimond, Erika Alacs, and John Roe. Thank you for sharing your inevitable trials and tribulations, and of course enthusiasm and high spirits.

I thank Peter Bayliss for prompting and encouraging me to attempt postgraduate study. I am indebted to Peter for introducing me to the theory and practice of aerial survey methods, for facilitating the commencement of the study and for providing me with Caughley's (1976a) paper as an introduction to consumer-resource models. Most of all, it was Peter Bayliss, with input from Jim Hone and Steve McLeod, who designed a larger kangaroo research project from which I copied the main elements of the design reported.

I thank Steve McLeod and John Druhan for training with the walked line transect method and for demonstrating their method of vehicle-based line transect survey at night, of which my kangaroo counting method was an extension. I also want to thank John for a copy of his database for entering kangaroo survey data, and Steve for apt advice about managing the research project. Damien Woolcombe and Mark Dunford helped me when I had difficulties using the computer programs Access and Arc View. For helping me learn how to access scientific literature using the internet I am grateful to Pat Tandy, Tricia Kelly, Erika Alacs, and Anna McDonald.

The work crew at Tidbinbilla prepared the site where the temporary kangaroo yards for the grazedown were erected, and helped me remove the carpet and other debris at the end. After the yards were burnt in the 2003 bushfire, ACT Fencing and Metalwork allowed me to retain, for an extra year, the security fencing panels from which they were made, until grass returned and I could complete the grazedown.

Some parts of this project would have been impossible without the support of many volunteers. More than 200 names are listed in an appendix, but no doubt I have missed a few, for which I apologise. The dedicated support of those who returned time and again is especially appreciated. Even these are too many to list here but I particularly thank Peter Hann, Mel White and Angelina McRae for many hours of companionship and assistance.

Finally, but in first place, I thank my wife Kerry Moir for tolerating my absence, either physically or mentally, from many occasions when she wanted a more complete family, and my children for tolerating less interaction with their dad than may otherwise have occurred.

ABSTRACT

This thesis is about the dynamics of eastern grey kangaroo (*Macropus giganteus*) populations and their food supplies in temperate grasslands of south-eastern Australia. It is based on the study of three populations of eastern grey kangaroos inhabiting 'warm dry', 'cold dry', and 'warm wet' sites within the Southern Tablelands climatic region. After a pilot survey and methods trial in early 2001, the main period of study was from August 2001 to July 2003.

The study populations were found to have the highest densities of any kangaroo populations, 450 to 510 km^{-2}. Their density was the same at the end of the two year study period as at the beginning, in spite of a strong decline in herbage availability due to drought. The eastern grey kangaroo populations were limited according to the predation-sensitive food hypothesis. Fecundity, as the observed proportion of females with late pouch young in spring, was high, in spite of the high kangaroo density and restricted food availability. Age-specific fecundity of a kangaroo sample shot on one of the sites in 1997 to avert starvation was the highest reported for kangaroos. Thus, limitation acted through mortality rather than fecundity. Population growth rate was most sensitive to adult survival but the demographic rate that had the greatest effect in practice was mortality of juveniles, most likely sub-adults. The combination of high fecundity with high mortality of immatures would provide resilience to low levels of imposed mortality and to fertility control.

The normal pattern of spring pasture growth was not observed in the drought conditions and few of the recorded increments of growth were of the magnitude considered typical for sites on the southern and central tablelands. Temperature was necessary to predict pasture growth, as well as rainfall, over the previous two months. The best model of pasture growth (lowest AICc) included negative terms for herbage mass, rainfall over the previous two months, and temperature, and a positive term for the interaction between rainfall and temperature. It accounted for 13% more of the variation in the data than did the simpler model of the type used by Robertson (1987a), Caughley (1987) and Choquenot *et al.* (1998). However this was only 63% of total variation. Re-evaluation of the model based on measurements of pasture growth in more typical (non-drought) conditions is recommended. Grazing had a powerful influence on the biomass of pasture due to the high density of kangaroos. This is a marked difference to many other studies of the type which have been conducted in semi-arid environments where rainfall dominates.

The offtake of pasture by kangaroos, as estimated on the research sites by the cage method, was linear on herbage mass. It was of greater magnitude than the more exact estimate of the (curved) functional response from grazedowns in high–quality and low–quality pastures.

The widespread recognition of three forms of functional response is inadequate. Both the theoretical basis, and supporting data, have been published for domed, inaccessible residue, and power forms as well (Holling 1966; Noy-Meir 1975; Hassell *et al.* 1976, 1977; Short 1986; Sabelis 1992). Eastern grey kangaroos had approximately the same Type 2 functional response when consuming either a high quality artificial pasture (*Phalaris aquatica*), or dry native pasture (*Themeda australis*) in autumn. Their functional response rose more gradually than those published for red kangaroos and western grey kangaroos in the semi-arid rangelands, and did not satiate at the levels of pasture available. This gradual behaviour of the functional response contributes to continuous stability of the consumer-resource system, as opposed to discontinuous stability.

The numerical response was estimated using the ratio equation, assuming an intrinsic rate of increase for eastern grey kangaroos in temperate grasslands of 0.55. There is indirect evidence of effects of predation in the dynamics of the kangaroo populations. This is demonstrated by the positive relationship between r and kangaroo density. Such a relationship can be generated by predation. A desirable future task is to compile estimates of population growth rate and simultaneous estimates of pasture, in the absence of predation, where kangaroo population density is changing, so that the numerical response can be estimated empirically.

The management implications arising from this study are numerous and a full account would require a separate report. As one example, kangaroos in these temperate grasslands are on average smaller, eat less, are more numerous, and are more fecund, than would be predicted from other studies (e.g. Caughley *et al.* 1987). Thus the benefit of shooting each kangaroo, in terms of grass production, is less, or, in other words, more kangaroos have to be shot to achieve a certain level of impact reduction, and the population will recover more quickly, than would have been predicted prior to this study.

Secondly, of much importance to managers, the interactive model which can readily be assembled from the products of Chapters 4, 5 and 8, can be used to test a range of management options, and the effect of variation in weather conditions, such as increased or

decreased rainfall. For example, the model indicates that commercial harvesting (currently under trial in the region), at the maximum level allowed, results in a sustainable harvest of kangaroos, but does not increase the herbage mass, and only slightly reduces the frequency of crashes when herbage mass falls to low levels. (To demonstrate this with an ecological experiment would require an extremely large investment of research effort.) However, an alternative ‘national park damage mitigation’ formula, which holds kangaroo density to about 1 ha^{-1}, is predicted to increase herbage mass considerably and to reduce the frequency of crashes in herbage mass, but these effects would be achieved at the cost of having to shoot large numbers of kangaroos. Thus, aside from many specific details of kangaroo ecology, the knowledge gained in this study appears to have useful potential to illustrate to managers the dynamic properties of a resource-consumer system, the probabilistic nature of management outcomes, and the consequences of particular kangaroo management proposals.

TABLE OF CONTENTS

APPENDIXES

CHAPTER 1

GENERAL INTRODUCTION

All management decisions in ecology are based on models, even if those models are verbal or even less distinct 'gut feeling'. If it is decided not to use a mathematical model because the parameters cannot properly be estimated, the management decision will proceed regardless. (Hamish McCallum).

Female eastern grey kangaroo (centre) being courted by the male stroking her tail. Her young-at-foot (on right) would have permanently vacated her pouch a few weeks previously but will continue to suckle for another half-year. Five weeks after mating she is likely to give birth and then also to have a pouch young suckling from a separate teat.

CHAPTER CONTENTS

1 GENERAL INTRODUCTION

1.1 Why conduct this research?

This study aimed to increase knowledge of population dynamics of eastern grey kangaroos in temperate areas by estimating the pasture response, functional response and numerical response equations for Caughley's (1976a, 1987) interactive model, and evaluating the potential for the model to be applied to eastern grey kangaroo populations in temperate grasslands. There were two reasons for the choice of research topic, one political and one ecological.

1.1.1 Population dynamics, kangaroo management, and politics

The management of eastern grey kangaroos can be controversial. In the Australian Capital Territory (ACT) region there have been disagreements about kangaroo abundance, the extent to which kangaroos reduce rural production, the number of kangaroos that should be shot to relieve kangaroo impacts, how to manage the risk of motor vehicle accidents involving kangaroos, and the shooting of kangaroos in conservation areas (ACT Kangaroo Advisory Committee 1996, 1997). Following sustained expression of public concern and a moratorium in 1995 on licences to shoot kangaroos (ACT Kangaroo Advisory Committee 1996, p. 4), the ACT government adopted a policy of 'basing kangaroo management on sound scientific method' (ACT Kangaroo Advisory Committee 1997, pp. 3 – 4). The Kangaroo Advisory

Committee sought the type of research involved in this study (ACT Kangaroo Advisory Committee 1997, p. 12), and other research. Thus one motivation for this research was the desire of a group of politicians, resource managers, and scientists to improve the understanding of relationships between eastern grey kangaroo populations, pastures, and weather, in order to manage pasture-herbivore ecology in a more informed way. The number of eastern grey kangaroos subject to management action has been increasing in temperate south-eastern Australia, assuming the data for Victoria (Figure 1.1) is representative. The demand for such management programs to be scientifically based also seems likely to be increasing.

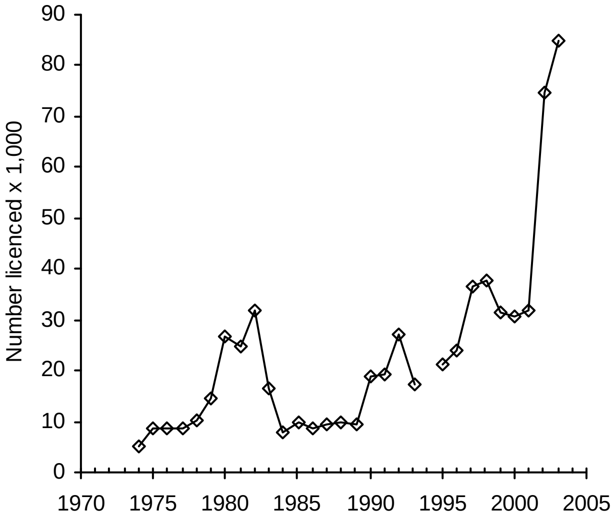


Figure 1.1: Number of kangaroos licenced to be shot in Victoria 1974 – 2003. These were all shot for damage mitigation, as Victoria allows no commercial harvest. Peaks occur in drought years but the overall pattern is increasing. Data from Ian Temby, Victorian Department of Primary Industries, personal communication, 2004.

1.1.2 An ecological perspective

The inspiration for the research described in this thesis was Graeme Caughley's study of red kangaroo (*Macropus rufus*) and western grey kangaroo (*Macropus fuliginosus*) populations in the semi-arid sheep rangelands (Caughley *et al.* 1987). As indicated above, the aim of my research was to estimate the pasture response, functional response and numerical response equations of Caughley's interactive model (Caughley 1976a, 1987) for eastern grey kangaroo populations in temperate grasslands. These equations are provided in Chapters 4, 5 and 8 of this thesis and correspond to the relationships of the same names estimated by Robertson (1987a), Short (1987) and Bayliss (1987) respectively.

The Caughley model, also called the interactive model, is a whole population, non-spatial, non-demographic, deterministic model, with stochastic elements arising from time effects and variable climate. It is described in Chapter 2. McCallum (2000), based on Caughley and Gunn (1996), describes what must be estimated. The pasture response is the growth rate of vegetation as a function of its own biomass and the relevant environmental parameters such as rain and temperature. The functional response of the herbivore is its eating rate as a function of vegetation availability. The numerical response of the herbivore is its population growth rate as a function of vegetation availability.

Most applications of the interactive model have been in the semi-arid rangelands (e.g. Choquenot 1994, 1998; McLeod 1996, 1997). The environment of the rangelands is simpler than the environment of temperate areas because mean monthly temperature in the rangelands has little or no effect on plant growth rate (Robertson 1987a). Rainfall dominates. Also, in the rangelands the wide variation between years in growth rates of both consumer populations and resource populations enables the equations named above to be estimated in less time and with greater confidence.

If the equations needed for an interactive model can be estimated in a temperate environment, and if the model adequately represents the dynamics of the temperate system, the model will provide a simple and cost-effective aid to the management of eastern grey kangaroo populations. In the same way that the Kinchega kangaroo study (Caughley *et al.* 1987) assisted the management of kangaroo species across the semi-arid zone (Shepherd and Caughley 1987), this research is intended ultimately to enable more informed assessment of alternative management strategies for eastern grey kangaroos in temperate grasslands. Rather than assuming the results of Caughley *et al.* (1987) can be extended to management of temperate kangaroo populations, a separate study is necessary because the differences between temperate and semi-arid environments are large (Table 1.1)

1.1.3 Research aims

The following specific research aims contribute to the achievement of the general aim stated in the first paragraph of this chapter. The methods used to achieve each of these aims are given in the chapters referred to in brackets.

1 To develop a simple empirical model which predicts pasture growth increments from weather. The model is to be derived from measurements of weather and pasture growth, at three sites which represent most of the range of pasture growth conditions in the southern tablelands weather region (Chapter 4);

2 To estimate the *per capita* functional response of eastern grey kangaroos consuming pastures characteristic of these sites (Chapter 5);

3 Take advantage of readily available data to (a) check the assumption underlying the estimation of the numerical response to food, that the kangaroo populations are food limited, and (b) investigate demographic processes to the extent possible with the data and time available (Chapter 6);

4 To estimate the density of the kangaroo populations found on the three sites, and evaluate the claim (Fruedenberger 1996; Nelson 1997; ACT Kangaroo Advisory Committee 1997) that the density of kangaroo populations on these ACT sites is the highest reported for any species of kangaroo (Chapter 7);

5 To estimate the numerical response of eastern grey kangaroo populations to food availability, using measurements of kangaroo density and pastures on the three sites (Chapter 8);and

6 Based on the implementation of aims 1 to 5, to evaluate the potential for Caughley's (1976a, 1987) interactive plant-herbivore model to be applied to eastern grey kangaroo populations in temperate grasslands (Chapter 9).

1.1.4 Research on kangaroos that is relevant to population dynamics in temperate areas

The four common species of kangaroos (eastern grey kangaroo, western grey kangaroo, red kangaroo, and euro *Macropus robustus*) are among the most intensively studied wildlife species in the world (Southwell 1989) and although much of the research on kangaroo population dynamics has been concentrated in the arid and semi-arid zones of the continent most of it is relevant to this study in some way. In particular, Caughley *et al*. (1987) has already been mentioned. Kangaroo population dynamics have been modelled in relation to rainfall by Cairns and Grigg (1993) and McCarthy (1996), and in relation to herbage availability by McLeod (1996, 1997) and Bayliss and Choquenot (2003).

Table 1.1: Differences between kangaroo populations, pastures and climates, in temperate and semi-arid environments. Semi-arid is exemplified by the Kinchega site (Caughley *et al.* 1987), and temperate by sites on the southern tablelands used for this study.

Kinchega National Park	Southern Tablelands
Plant growth not seasonal and not affected by monthly temperature.	Plant growth markedly seasonal due to temperature.
Rainfall highly variable between years (CV ~ 45%).	Rainfall relatively reliable (CV ~ 27 %).
Areas of kangaroo habitat extensive (> 1000 km^2).	Areas of kangaroo habitat localised (5–15 km^2).
Kangaroo density low (~ 0.4 ha^{-1}).	Kangaroo density high in localised areas (~ 4.8 ha^{-1}).
Kangaroo breeding aseasonal.	Kangaroo breeding strongly seasonal.

In addition to the interactive model (Caughley 1976a, 1987), the foundations for this study are the scores of papers that have been published about eastern grey kangaroos in temperate environments. Of particular note are numerous publications from Peter Jarman's team, mostly working at Wallaby Creek in north-eastern New South Wales (Jarman *et al.* 1987) and from Graeme Coulson and his students, mostly working in Victoria (e.g. Coulson 1979, 1989a; Coulson *et al.* 1999a). Of importance to the chapters about kangaroo density estimation and the numerical response are the development and testing of walked line transect survey methods for macropods by Colin Southwell and his co-workers (Southwell 1989, 1994; Southwell and Fletcher 1990; Southwell *et al.* 1995a, b, 1997; le Mar *et al.* 2001). Important to the chapters on population limitation and numerical response is the research by Peter Banks, who quantified the effect of fox predation on density, rate of increase, and foraging behaviour of eastern grey kangaroo populations (Banks *et al.* 2000; Banks 2001). Bayliss and Choquenot (2003) discerned the apparent cyclicity in the density estimates from Tidbinbilla (Chapter 3), and improved Caughley's (1976a, 1987) interactive model, making it more general by including density dependent interference in a biologically realistic manner, and advancing the contextual understanding of it, all of which are relevant to the numerical response chapter. However, all together, the published studies of eastern grey kangaroos in temperate Australia do not include information about population dynamics that approaches what is published for the arid zone kangaroo species, chiefly because estimates of population growth rate are uncommon among the temperate studies (Banks *et al.* 2000; and Coulson 2001 are exceptions) and those that exist are unaccompanied by contemporaneous measures of food availability.

1.2 Introduction to the ecology and management of eastern grey kangaroos

1.2.1 Eastern grey kangaroos

The biology of kangaroos has been described in numerous papers and several books, among which the following stand out: Frith and Calaby (1969); Caughley *et al.* (1987); Grigg *et al.* (1989); Dawson (1995); Hume (1999); and McCullough and McCullough (2000). Eastern grey kangaroos are probably the most numerous kangaroo species (Dawson 1995) and occur in all but two of the eight Australian states and self-governing territories (Poole 1995; Figure 1.2) ranging from tropical to cold-temperate latitudes, and from the coast and ranges, to semi-arid inland plains. The distribution of eastern grey kangaroos includes the main sheep and cattle producing areas on the continent and most of the human population, with the highest densities of all three found in the temperate parts of the range.

Eastern grey kangaroos have been described as K-selected species in contrast to the *r*-selected red kangaroo of the inland (Richardson 1975; Poole 1983; McCullough and McCullough 2000). Female eastern grey kangaroos seldom carry a dormant blastocyst, again differing from red kangaroos (Kirkpatrick 1965; Poole 1983) so there is a longer delay to replace any pouch young which may be lost. They breed in all months in the north of their range, with a summer peak (Kirkpatrick 1965), and are strongly seasonal breeders through the south-eastern half of their range (Pearse 1981; Poole 1983; Quin 1989; Figure 6.11).

In the temperate part of their range, eastern grey kangaroos are the largest indigenous mammals, both individually and in terms of biomass, and one of the most prominent. They graze selectively and modify the habitats of grassland birds and invertebrates (Neave and Tanton 1989; Neave 1991). They are preyed upon by dingoes (*Canis lupus*), wedge-tailed eagles (*Aquila audax*) and introduced red foxes (*Vulpes vulpes*) (Robertshaw and Harden 1989) and their carcasses provide food for a range of scavengers. In these ways they are likely to have an important ecosystem function. In some situations they are ‘ecosystem engineers’ as defined by Jones *et al.* (1997) and Wilby *et al.* (2001). For example, by maintaining uniformly short grass they exclude certain grassland bird species, or reduce their density (Neave and Tanton 1989) and their browsing of *Eucalyptus* and *Acacia* seedlings (Webb 2001) may help maintain grasslands against invasion of forest and woodland.

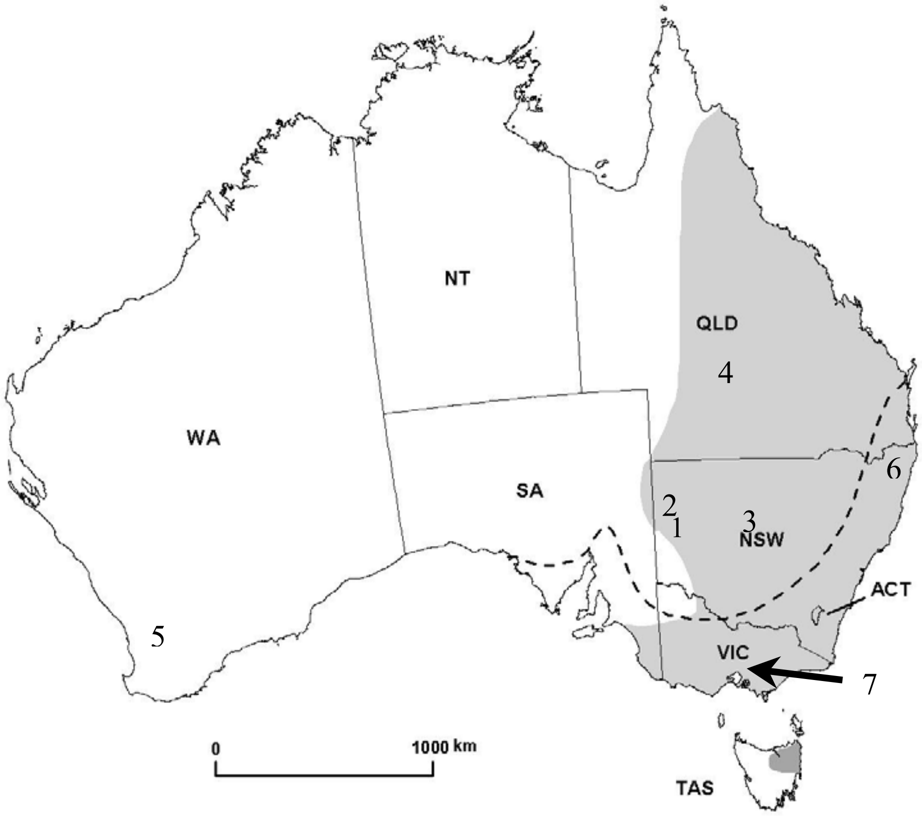


Figure 1.2: Locations of kangaroo research sites mentioned in the text (numbers), the distribution of eastern grey kangaroos (Poole 1995) indicated by shading, and the temperate zone indicated by the dashed line. The study sites were in the Australian Capital Territory (ACT) and adjacent New South Wales (NSW) (Figure 3.1 gives more detail on the study sites). Eastern grey kangaroos also occur in Queensland (QLD), Victoria (VIC), Tasmania (TAS), and South Australia (SA), but not the Northern Territory (NT), or Western Australia (WA). The dashed line marks the inland boundary of the temperate zone in eastern Australia, defined by Burbidge (1960). Numbers: 1 = Kinchega (Caughley *et al*. 1987); 2 = Fowlers Gap (Dawson 1995); 3 = Yathong (McCullough and McCullough 2000); 4 = Blackall (Pople 1996); 5 = various sites used by Arnold *et al*. (1991); 6 = Wallaby Creek (Jarman *et al*. 1987); 7 = Yan Yean (Coulson *et al*. 1999b). Population dynamics of kangaroos (but not eastern grey kangaroos) have been studied on sites 1 to 5.

1.2.2 Kangaroo management

Within a commercial zone on the inland plains of NSW and Queensland, where kangaroo density has been monitored for decades by strip counts from fixed-wing light aircraft (Cairns 1999; Gilroy 1999; Grigg *et al*. 1999; Pople and Grigg 1999), eastern grey kangaroos are harvested commercially for meat and skins, along with three other kangaroo species (NSW National Parks and Wildlife Service 2002). In 2002 the NSW government decoupled the commercial harvest from the damage mitigation process, i.e. commercial harvesting was justified in its own right as a sustainable and legitimate use of wildlife, rather than as a way to make use of a by-product of the damage mitigation process (NSW National Parks and Wildlife Service 2002). Four species of kangaroos are used by the commercial kangaroo industry, but the annual quotas for eastern grey kangaroos are the largest (Table 1.2). There is no commercial harvest in Victoria or the ACT.

Table 1.2: Quota of kangaroos permitted by Australian governments to be shot for commercial use since 2000. From Department of Environment and Heritage (2003).

	Eastern grey kangaroo (millions)	Red kangaroo (millions)	Western grey kangaroo (millions)	Euro / Wallaroo (millions)
2000	2.1	2.3	0.5	0.5
2001	2.1	2.3	0.5	0.5
2002	3.2	2.6	0.5	0.6
2003	3.3	2.3	0.5	0.4
2004	2.0	1.5	0.4	0.4
2005	1.6	1.4	0.4	0.5
Mean	2.4	2.1	0.5	0.5

Shooting to reduce kangaroo impacts on grazing properties is managed separately. In the ACT, NSW, Queensland, Tasmania, and Victoria, rural landholders apply to state or territory governments for licences to shoot eastern grey kangaroos on the basis that uncontrolled kangaroo grazing causes hardship for their primary production (Eveleigh 1995; ACT Kangaroo Advisory Committee 1996, NSW National Parks and Wildlife Service 2002).

Table 1.3: Number of eastern grey kangaroos licenced to be shot each year from 2000 to 2003 for damage mitigation in south eastern Australia. The NSW and ACT figures include only eastern grey kangaroos shot for damage mitigation, i.e. the NSW commercial harvest is not included, nor NSW species other than eastern grey kangaroos. The Victorian figures are for all species but are mainly eastern grey kangaroos, and do not include kangaroos shot in conservation areas or 15,000 kangaroos shot on a military site in 2002. Data from Department of Environment and Conservation (NSW), Department of Primary Industries (Victoria), and Environment ACT.

	2000	2001	2002	2003
Victoria	30,574	31,739	74,834	84,976
NSW	25,410	27,499	52,454	67,632
ACT	4,020	3,258	3,732	3,745
TOTAL	60,004	62,496	131,020	156,353

Products from these kangaroos are not admitted to the commercial trade; the carcasses are left in the paddock, buried, or fed to farm dogs. The official term ‘damage mitigation’ is used to describe this type of management, but it is in fact pest control by another name, more similar in intent to the management of feral pigs than to sustainable harvesting of kangaroos. It is widely believed by state government officials and graziers to whom I have spoken, that in contrast to the commercial shooting, the damage mitigation licencing statistics (Table 1.3) underestimate the number of kangaroos that are really shot for this purpose, because some landholders do not obtain licences and others exceed their licences.

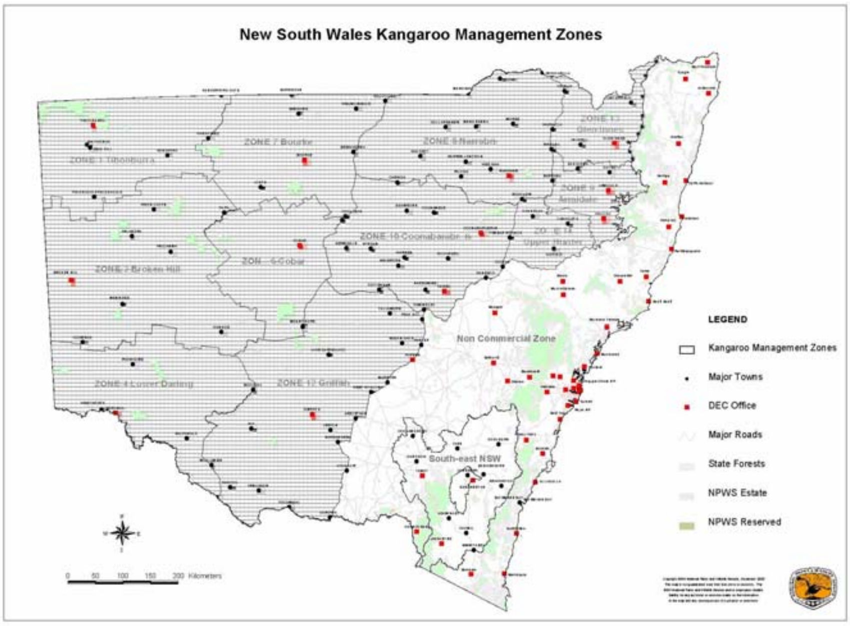


Figure 1.3: Kangaroo management zones in NSW. Shading identifies the commercial kangaroo zone in western New South Wales as it was prior to this study. The additional 'island' of commercial zone in the south east of the state, was announced as a 4-year trial during this study. The 'non-commercial' or 'damage-mitigation' zone is that part of the state outside the commercial zone. Map courtesy of NSW Department of Environment and Conservation.

Until 2004, the temperate distribution of eastern grey kangaroos (Figure 1.2) coincided approximately with the long-standing non-commercial zone (Figure 1.3) and lay outside the area which can be surveyed by fixed-wing light aircraft. However during the course of this study the NSW government announced the commencement of a four-year trial for commercial harvesting in temperate areas of southern NSW (surrounding the sites used in this study) and harvesting commenced in March 2004 (NSW Department of Environment and Conservation 2003).

In Tasmania a different situation applies to the 'forester' subspecies *M. g. tasmaniensis*. A small 'vulnerable' population of eastern grey kangaroos (less than 20,000) has shown 'disturbing' signs of decline (Poole 1995). It now occupies only 10% of its pre-European range (Hocking and Driessen 1996), following ‘massive’ decline in density between the 1880s and 1950s (Tanner and Hocking 2001). The kangaroos occur mainly on farmland and are associated with a range of agricultural impacts (Tanner and Hocking 2001). Substantial conservation efforts have been made, including reintroductions to parts of their former range but damage mitigation licences are also issued. The main objective is not sustained yield for a commercial harvest, nor is it primarily damage mitigation, but management of a vulnerable and taxonomically distinct population.

1.3 Predation on eastern grey kangaroos

Kangaroo predation was potentially a confounding factor in this investigation, preferably to be eliminated, minimised, or measured and accounted for. Predation of the Macropodoidea is reviewed by Robertshaw and Harden (1989) who identified the main predators of eastern grey kangaroos, other than humans, as dingoes *(Canis lupus dingo)*, introduced European red foxes (*Vulpes vulpes*), and wedge-tailed eagles (*Aquila audax*). All three of these predators were present on the study sites.

1.3.1 Wedge-tailed eagles

Wedge-tailed eagles were continually present on all three sites and I often saw them feeding on dead kangaroos. The Googong and Gudgenby sites were each within the range of two nesting pairs of wedge-tailed eagles (Esteban Fuentes, personal communication 2003). Wedge-tailed eagles were often seen at Tidbinbilla.

Wedge-tailed eagles prey primarily on rabbits and other mammals of similar size, large birds, macropods and reptiles (Marchant and Higgins 1993). Wedge-tailed eagles have often been reported to be predators of eastern grey kangaroos and other kangaroo species (e.g. Leopold and Wolfe 1970; Brooker and Ridpath 1980; Robertshaw and Harden 1989) although eyewitness accounts of predation are rare. Skeletal remains of kangaroos too young to leave the pouch voluntarily (joeys) have been found at eagle nests and are considered to be evidence of predation on pouch young, supported by observations of eagles harassing kangaroo mothers until they eject the pouch young. Wedge-tailed eagles were observed harassing kangaroos at Gudgenby in September 2003, although fresh carcasses of kangaroos were abundant nearby at the time (Amanda Carey, ranger, personal communication, 2003). Cooperative hunting of eastern grey kangaroos has been observed on at least two occasions on military sites near Canberra in which an eagle on the ground ‘provoked’ a group of female kangaroos with young-at-foot while another eagle dived on young kangaroos which became isolated (Michael Parker, Boeing Security, personal communication 2004). However predation of pouch young or young-at-foot would be unlikely to affect kangaroo density on the study sites as these food-limited eastern grey kangaroo populations are insensitive to mortality of immature kangaroos (Chapter 6).

Predation of adult kangaroos would be more important in terms of its potential to alter kangaroo density (Chapter 6). Accounts of wedge-tailed eagle predation of adult kangaroos are reported by Geary (1932), Ealey (1960 p. 24), and Brooker and Ridpath (1980). Woodland (1988) reports unsuccessful cooperative hunting of an adult kangaroo. Successful hunting of an adult female kangaroo was observed during the period of this study at Orroral valley, which is adjacent to, and similar to, the Gudgenby site (Esteban Fuentes personal communication 2003) and an attack on an adult female kangaroo was also observed at Googong (Anton Maher, ranger, personal communication 2002). In contrast, Sharp *et al.* (2002) tracked the diet of wedge-tailed eagles through a sustained decline in rabbit density caused by the introduction of rabbit calicivirus disease without reporting evidence of kangaroo predation or an increase in the proportion of macropod in the diet. Sharp *et al.* (2002) considered the main factor influencing the proportion of kangaroo in the diet to be the presence or absence of kangaroo shooters in the area.

Despite this evidence and their diurnal habits, wedge-tailed eagles are rarely observed hunting kangaroos. More than 100 of the kangaroo carcasses I examined during the study showed signs of their feeding, but only four showed signs I could detect of having possibly been killed, rather than scavenged, by eagles (Chapter 6). It is unlikely that predation by wedge-tailed eagles would have any detectable effect on kangaroo density on the three sites, based on the low density of wedge-tailed eagles relative to kangaroos, and limited evidence of killing.

1.3.2 Foxes

The introduced European red fox (hereafter ‘the fox’) is an opportunistic predator and scavenger (Newsome and Coman 1989; Saunders *et al.* 1995), whose adaptibility is reflected in its success in having invaded most continents, making it the most widely distributed carnivorous mammal (Jarman 1986). Newsome *et al.* (1997) reviewed the literature on fox predation. They included a summary (their Table 2, p. 24) of 15 Australian fox diet studies.

Adding seven studies published subsequently or omitted by Newsome *et al*. (1997), which identify fox samples separately from other predators and which subdivide the prey sufficiently to identify the contribution of kangaroos (Table 1.4), gives a pool of 22 Australian fox diet studies.

Table 1.4: Additional fox diet studies not included in Newsome *et al*. (1997) and percentage frequency of kangaroo in diet samples.

Report	Location and/or habitat	% frequency of kangaroo	No. and type of sample
Croft and Hone (1978)	NSW, probably mainly rural areas	0.9	811 stomachs
Lunney *et al*. (1996)	Deep gorges NE NSW	0.0	144 scats
Banks (1997); Banks *et al*. 2000)	Two valleys near the Gudgenby site	45.0	482 scats
Bubela *et al*. (1998)	Alpine and sub-alpine	0.0	272 scats
Risbey *et al*. (1999)	Shark Bay, WA	0.0	47 stomachs
Wilson and Wolridge (2000)	Otway Ranges, Vic.	9.0	143 scats
Molsher *et al*. (2000)	rural Central NSW	37.6	263 stomachs

Kangaroo, most often eastern grey kangaroo, was a component in the diet of foxes in 14 of the 22 studies; generally a minor component but ranging from less than 1% to 45% of samples, excluding the result of Martenz (1971). Martenz (1971) reported an occurrence of red kangaroo in 69.1% of samples, but presumed this was due to scavenging of waste left by kangaroo shooters. Kangaroos are rare or absent from the study areas of Lunney *et al*. (1996), Bubela *et al*. (1998) and Risbey *et al*. (1999) in Table 1.4. But kangaroo tends to occur more frequently in the diet on sites where kangaroos are abundant, as expected for an opportunistic predator or scavenger. In two valleys near the Gudgenby site, eastern grey kangaroo occurred in fox scats almost as frequently as rabbits did (Banks 1997) and in central rural NSW eastern grey kangaroo occurred more frequently in fox stomachs than any other item, including rabbits, although at lower volume than rabbit or sheep (Molsher *et al*. 2000). On the Central Tablelands of NSW fox counts were significantly correlated with counts of kangaroos but not counts of other likely prey species, namely rabbits (*Oryctolagus cuniculus*), hares (*Lepus capensis*) and brushtail possums (*Trichosurus vulpecula*) (Berghout 2000 p. 132). The pattern across these studies is consistent with the description of the fox as an opportunist (Newsome and Coman 1989; Saunders *et al*. 1995).

Foxes are considered predators of small macropods (Kinnear 1988,1998; Burbidge and McKenzie 1989; Robertshaw and Harden 1989) but have been considered to be only scavengers of kangaroos (e.g. Martenz 1971; Coman 1973; Lunney *et al.* 1990) and their potential impact on the population dynamics of kangaroos has been discounted (Robertshaw and Harden 1989). However more recently fox predation of juveniles was invoked by Arnold *et al.* (1991) as a possible explanation for limited growth of a population of western grey kangaroos. In valleys near the Gudgenby site, monthly application of fox baits was demonstrated to alter the foraging behaviour of eastern grey kangaroos (Banks 2001), and the recruitment of sub-adults (Banks *et al.* 2000) so that the two sites where foxes were poisoned experienced higher exponential rates of population growth (annual $r = 0.47$ and 0.55) than unpoisoned sites (annual $r = 0.08$ and – 0.14).

Therefore, as a part of this study, to reduce the potential influence of fox predation on the eastern grey kangaroo populations, fox baiting was carried out on all sites. However as shown in Section 3.4.1, the fox baiting was not conducted on all of the study sites at the consistent monthly frequency applied by Banks (1997). It is possible that the monthly frequency of bait replacement is important. Greentree *et al.* (2000) conducted a two-year experiment with three levels of fox baiting to protect lambs. Fox control significantly reduced the maximum percentage of lamb carcasses killed by foxes from 10.25% (no fox control) to 6.50% (baiting once per year) or 3.75% (baiting three times per year) but baiting had no significant effect on fox abundance or lamb production.

1.3.3 Dingoes

Dingo predation has been inferred to have reduced kangaroo density in several studies, including ones by Caughley *et al.* (1980), Shepherd (1981), Robertshaw and Harden (1989), Thompson (1992), and Pople *et al.* (2000). Robertshaw and Harden (1989) hypothesized that some small populations of eastern grey kangaroos had been eliminated by dingo predation and Thompson (1992) found dingo predation reduced kangaroo populations to such low levels, the reduction appeared to have been to the detriment of the dingo population.

Savolainen *et al.* (2004) used mitochondrial DNA from 211 dingo-like animals collected widely across the Australian continent, in comparison to a global database of *Canis lupus* samples, to confirm that dingoes have a distinct and ancient origin in Asia, separate from the origin of domestic dogs in Australia. According to the nomenclature recommended by

Fleming *et al.* (2001, p. 12), the population of wild dogs in the region of the study sites comprises a mix of 'pure' dingoes *Canis lupus dingo* and so-called 'hybrids', or so-called 'feral dogs', referring to intraspecific breeding between *Canis lupus dingo* and the domestic dog subspecies *Canis lupus familiaris*. Hereafter I refer to the odd-coloured wild dogs of the region (Figure 1.4) as 'dingoes' because that term is more compatible with DNA evidence (Alan Wilton, UNSW, personal communications 2002 – 2004), and their behaviour (i.e. howling rather than barking, preying on adult kangaroos, and hunting alone and in packs).

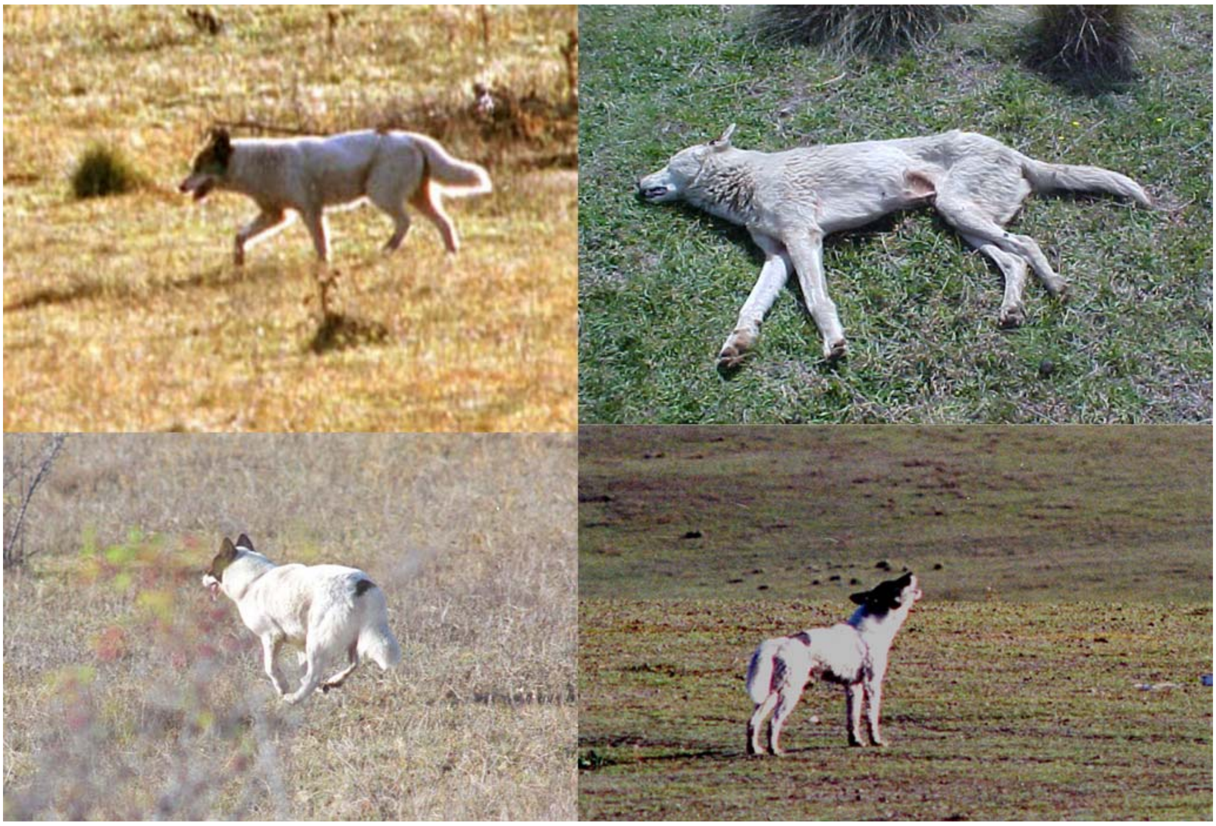


Figure 1.4: Dingoes photographed at the Gudgenby site during visits for pasture surveys. On appearance these wild dogs seem to most people incompatible with the term 'dingo' but that is the term used here because it is more compatible with the evidence – see text. Four individuals are illustrated of the nine recognised at Gudgenby during the study period.

At Gudgenby, evidence of dingoes such as scats, tracks or chewed carcasses, was seen on the majority of visits. Evidence of scavenging or predation by a dingo was present on 64 of the kangaroo carcasses at Gudgenby. I heard dingoes howling on many of the winter nights when I was present, and occasionally at other seasons, but the dingoes themselves were seen infrequently. In two years of fieldwork I made 22 observations of dingoes, a total of 44 individual animal sightings. By noting, and where possible photographing, their features, and comparing information with other observers in the area, particularly Anne Henshaw of Gudgenby Homestead, it was established that at least nine individuals were present. During the study two of the known individuals were found incapacitated and were humanely killed. On one evening four dingoes were observed attacking a large male kangaroo, and a kangaroo carcass was found nearby the next morning.

At Tidbinbilla no evidence of dingo scavenging or predation were found, and no tracks or scats. Few sightings were recorded in spite of much more intensive observation there than at Gudgenby due to a large number of resident staff who cooperated by providing me with their sightings. During the study period, howling was heard by resident staff on a few occasions, and there were four sightings by staff and one by me, comprising two individual dingoes. An intense bushfire in January 2003 burnt all of Tidbinbilla Nature Reserve, including the study site, and changed the dingo sighting situation. Just as kangaroo density at Tidbinbilla was much reduced by the fire (Chapter 7), dingoes also seemed less abundant, although observer effort was much reduced due to the houses having been destroyed. Also, after the fire, the area baited for dingoes by the ACT Parks and Conservation Service was increased further into the reserve. It seems unlikely that dingo predation at Tidbinbilla would have affected kangaroo density, based on the low density of dingoes relative to kangaroos, and the absence of evidence of dingo kills.

At Googong, no dingoes were present, nor any other non-human predator larger than foxes. Chapter 6 examines the possibility that dingo predation limited the population of eastern grey kangaroos at Gudgenby.

Having introduced the research topic and the study animal in this chapter, in the next chapter I introduce some of the population models that have been developed to represent the dynamics of consumer populations.

CHAPTER 2

CONSUMER - RESOURCE MODELS

Every observation has to be for or against some value to be of service (Charles Darwin, on the importance of having a hypothesis to evaluate before making scientific observations)

Rendezvous Creek valley, part of the Gudgenby site, with eastern grey kangaroos in the middle distance and pasture appearing evenly eaten down.

CHAPTER CONTENTS

2 CONSUMER-RESOURCE MODELS

2.1 Conceptual approaches to explain population growth rates

2.1.1 Historical developments

Primitive farmers may have recognised that population growth accelerates at low density but is restrained by environmental limits at high density, but the first known written record of this is from 1588 by Botero (cited by Cole 1958). Hutchinson (1978, p 8) credits Graunt with similar insight in 1662 in regard to human populations. Later writings of Malthus (1803) on the subject have become famous. These are the earliest known written models of logistic-like population dynamics. Sibly *et al.* (2003) summarise the historical development.

The earliest known mathematical model of logistic population growth (growth rate declining linearly with density, Eqn 2.1, Fig 2.1) was provided by Pierre-Francois Verlhulst, who also coined the term ‘logistic’ to describe it (Andrewartha and Birch 1954 p. 347; Hutchinson 1978 p. 20; Krebs 2001). The logistic equation was also derived independently in 1920 by Pearl and Reed (Andrewartha and Birch 1954).

Although the contemplation of population growth rate may have ancient origins, and population growth rates first attracted the attention of mathematicians more than 150 years ago, population growth rate has been widely appreciated as having a central place in ecology only following the computer technology advances of the late 20th century (Caswell 2001; Sibly *et al.* 2003).

2.1.2 Single species models

Principles of thermodynamics require an increase in consumer biomass to be attained at the expense of biomass at a lower trophic level, i.e. resource biomass, which normally is subject to independent influences such as weather. Therefore for most consumer populations in natural conditions, the application of single species models is unrealistic. In addition, the resource biomass (e.g. prey, vegetation) that is potentially available to a consumer in any time interval will be a function of both the rate of resource renewal and the rate of resource consumption (depletion) in previous time intervals. Many studies have shown resource growth rates to be a function of resource level (e.g. Crawley 1983). For example plants grow faster at intermediate biomass than when grazed down or ungrazed, therefore the resource renewal rate is dependent on the depletion rate. But the use of a single species model implies that consumption has no effect on the rate of renewal of the resource (Caughley 1976a; Caughley and Lawton 1981). That appears to be a strong criticism, yet in spite of the conceptual limitations, single species models (e.g. exponential growth and logistic growth) have been used widely, and remain useful as a convenient shorthand, or as a short–term approximation. For example, Eberhardt (1987) showed that published time–series data on density of 16 species of large mammal fitted an exponential model, and Caley and Morley (2002) showed that the dynamics of some rabbit populations were explained most adequately as exponential growth that differs in rate between winter and summer seasons.

Logistic growth (Equation 2.1) is a more appropriate general case than simple exponential growth because it incorporates density dependence, thereby representing the common observation that nothing increases forever. However the view of logistic growth as the outcome of density acting on population growth rate (a single species model) is a misinterpretation (Andrewartha and Birch 1954 pp. 347 – 398) and was criticised by Caughley (1976a p. 203) as missing the point of what logistic growth is all about. Instead a logistic model represents population growth in peculiar conditions where the resource is supplied at a fixed rate irrespective of its consumption, such as a constant rate of food supply into an experimental aquarium. Caughley (1976a) showed that the absence from the logistic equation of a term for the rate of food supply is because it has cancelled out as a consequence of this peculiarity:

$$dN/dt = r_{max} N(1- N/K) \qquad \text{Eqn 2.1}$$

where N = number of organisms; t = time; r_{max} = intrinsic population growth rate; and K = carrying capacity or maximum population level. The mathematics of delayed logistic equations (Equation 2.2) enable a variety of observed conditions to be reproduced empirically, such as cycles, equilibrium, and extinction (May 1973, 1981, Figure 2.1).

$$dN(t)/dt = r_{max} N_t (1 - N_{t-T}/K) \qquad \text{Eqn 2.2}$$

where T is the length of the delay

The discrete time version of the delayed logistic is

$$N_{t+1} = N_{t-T} + N_{t-T} * r_{max} * (1 - N_{t-T}/K) * \Delta T \qquad \text{Eqn 2.3}$$

where $\Delta T = N_{t+1} - N_t$.

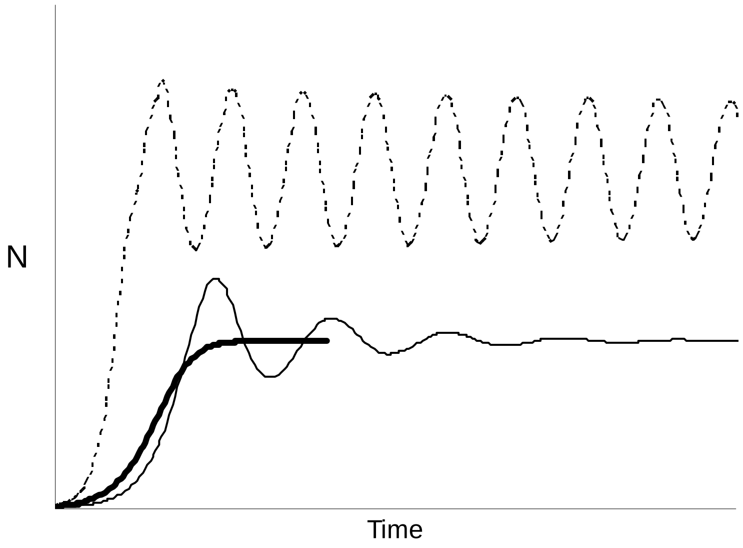


Figure 2.1: Delayed logistic equations can represent a range of patterns observed in the real world, such as cycles (dashed line), equilibrium (thick line), extinction, and eruption followed by dampening oscillations (thin line).

Krebs (2001 p162 – 168) reviews the logistic model, concluding that while it remains useful as a simple empirical description of how populations tend to grow initially in a favourable environment, it must be rejected as a universal law of population growth. Even laboratory insect colonies in constant conditions may not stabilise around the upper asymptote and natural populations rarely do.

Caughley (1976a, 1977a; Caughley and Lawton 1981; Caughley *et al.* 1987) argued that herbivore models must explicitly include the interaction between the consumer and the resource. An important limitation of single species approaches, and both density-dependent and demographic paradigms, is that in the absence of evidence supporting a ‘pre-ordained’ density for each species wherever it occurs, they lack the necessary information for generalisation to times or places where biological productivity or the level of critical resources is different to the environment in which they were developed. In particular, this includes the vast semi-arid regions of the world and other places where resource availability fluctuates stochastically, where consumer populations are not likely to be able to remain at equilibrium, and where cyclic populations are unknown.

2.1.3 Modern paradigms

Modern ecologists have adopted three main approaches to study and explain the magnitude and variation of population growth rates. First, the most commonly adopted conceptual approach, or paradigm, relates population growth rate to population density (Caughley and Sinclair 1994; Krebs 2001) thus conforming to the density paradigm (Krebs 1995, 2002). Logistic growth, in which rate of change of consumers is a negative linear function of density, can be considered an example (Houston 1982; Sinclair *et al.* 1985; Eberhard 1987; Sibly *et al.* 2000, but see Caughley's 1976a dissenting view, set out below). Secondly, the demographic paradigm relates population growth rate to demographic rates such as fecundity and mortality (Sibly and Hone 2003, and references therein). Both of these conceptual approaches, density and demographic, explain population growth rates within one trophic level. A third approach explicitly involves more than one trophic level, by relating population growth rate to an ecological factor such as food availability, thus conforming to the 'mechanistic paradigm' (Caughley and Sinclair 1994; Krebs 1995, 2002). This is the least commonly adopted conceptual approach but it is the one underlying this study.

These three paradigms have rarely been integrated. Sibly *et al.* (2003) and Hone and Sibly (2003) in combination list six studies that combine two approaches and only two which combine three approaches, i.e. Taylor (1994) and White and Garrott (1999).

A less widely adopted division of population ecology into paradigms was provided by den Boer and Reddingius (1996). They too identified a mechanistic paradigm (p. 3), but defined it as being characterised by the application of mathematical equations to biology, mainly referring to the work of Lotka (1925) and Volterra (1926), and especially equations originally developed in physics or chemistry. den Boer and Reddingius (1996) identified two paradigms in population ecology, the 'systems paradigm' (comprising the merging of the mechanistic paradigm and the 'engineering' or 'regulation' paradigm) and the 'natural history paradigm'. The former is 'basically using a modelling approach' (p. 294) while the latter, preferred by the authors, uses history and descriptive comparison between similar species or locations as its primary methods. In spite of the title ‘Regulation and Stabilization Paradigms in Population Ecology’ the 340 page text has little to say about the study of population growth rates. For example, it includes none of the work of the thirteen authors contributing to the references listed in the preceding two paragraphs, except Krebs (1970), a paper that reports a search for behavioural or genetic correlates of vole population fluctuations.

Unlike the separation between ‘paradigms’, the underlying biological processes are widely accepted. Availability of resources such as food, and access by consumer organisms to them, determines the rate of biomass conversion between trophic levels. Combined with physiological attrition (Owen-Smith 2002a, b), and losses due to agents of mortality such as hunting, weather and starvation, the biomass conversion rate is reflected in consumer demographic rates (fecundity, mortality etc). The combination of demographic rates determines the population growth rate, whether expressed in terms of biomass or numbers. In many cases the population growth rate of consumers is a negative function of their density, i.e. growth is density dependent.

The division of ecologists between paradigms may be ending. Choquenot (1998, his Figure 10) proposes that a continuum exists between constant environments where food availability is dominated by herbivore consumption, and stochastic environments where food availability is determined by environmental variation. At the constant environment extreme, single species models such as the logistic or delayed logistic would represent herbivore dynamic accurately. At the opposite extreme interactive models would be essential, and are the general case (Bayliss and Choquenot 2003). Single species models are a particular case.

2.1.4 Practical applications

For an applied ecologist with a limited budget, the difference between alternative conceptual approaches (paradigms) may translate to a question of which ecosystem processes it is most useful to measure. If the conclusions and management actions arising from the research are to be generalised beyond the research sites to other places or times, the most useful investigation is likely to be of the putative mechanisms influencing population growth rate (Williams *et al.* 2001 p. 30; Krebs 2002, 2003).

Conforming to the mechanistic paradigm does not signify that an ecologist has rejected the hypothesis that population growth rate is density dependent. It is simply that the researcher believes it would be of limited assistance merely to establish that as a fact. It would be more useful to establish which factor (e.g. food shortage) is causing density dependent population growth (Sinclair *et al*. 1985). But in many cases that knowledge might have been predicted correctly in advance from field observation and a knowledge of relevant literature. For example, 90% of studies of large herbivore populations have found them to be food limited (Sinclair 1996). Of greater practical value are quantitative estimates of the relationship between consumer population growth rates and food supply, (as well as any other influential environmental factors) and estimates of the rates of consumption and renewal of the food and other critical resources. This is the mechanistic approach. It embraces the concepts of extrinsic and intrinsic food limitation (Andrewartha and Birch 1954; Choquenot 1994), by incorporating both. In terms of Choquenot's (1998) continuum referred to above, intrinsic food limitation is more important in stable environments, and is associated with intraspecific competition regulating density close to an equilibrium. Conversely, extrinsic food limitation is dominant in stochastic environments, where the term 'centripetality' (Caughley 1987) is a more apt description than 'equilibrium' for a system which tends to return from extremes to which it is constantly pushed by the weather.

Just as adoption of the mechanistic approach does not imply rejection of the possibility of density dependence (referred to above), neither does it imply a rejection of the hypothesis that density itself may be the cause of density dependence, acting through spacing behaviour, or other social or physiological mechanisms (Chitty 1952). However the importance and plausibility of the social mechanism will be low if most of the variation in demographic rates or population growth rate of wild populations can be explained by environmental factors (i.e. mechanistically) as often has occurred (e.g. Sinclair 1977; Houston 1982; Sinclair *et al.* 1985; Caughley *et al.* 1987; Sinclair 1989; Pech *et al.* 1992; Sinclair 1996; Choquenot 1998; Gaillard *et al.* 1998; Banks *et al.* 1998, 2000; Clutton Brock and Coulson 2003; Hone and Sibly 2003).

2.1.5 More than one trophic level - interactive models

Both Lotka (1925) and Volterra (1926) are credited (May 1981) with simultaneously developing one of the simplest interactive models of consumer–resource dynamics using differential equations to describe a simple system of a predator and its prey:

$$dN/dt = a\,N - \alpha\,N\,P \qquad \text{Eqn 2.3}$$

$$dP/dt = -bP + \beta\,N\,P \qquad \text{Eqn 2.4}$$

where dN/dt = population growth rate of prey, and aN is the propensity of the prey for (geometric) growth, which is reduced by αNP the functional response of the predator (prey consumption rate), and dP/dt = population growth rate of predators, and -bP is the intrinsic death rate of the predators, opposed by βNP the predator fecundity.

The result is a structurally unstable system sensitive to starting parameter values, readily displaced by disturbance, and prone to oscillations (May 1981). A fundamental criticism is that the resource or prey population has boundless growth aN. However this can be overcome by replacing aN with a logistic term so that predator-free growth is density dependent. A series of modifications to make the design more realistic (and complex) is given by May (1973, 1981). Interactive predator-prey models were also developed by Rosenzweig and Macarthur (1963).

In the mid 1970s, grazing systems began to attract the attention of numerical ecologists who had previously concentrated on predator-prey systems. Noy-Meir (1975) drew on a body of predator-prey theory developed in the 1960s and early 1970s (see references in Noy-Meir 1975) to apply the principle of the Lotka-Volterra predator-prey equations to vegetation and herbivores, using the ‘graphical analysis’ techniques of Rosenzweig and Macarthur (1963) in order to examine the equilibrium conditions and the stability properties of grazing systems. At about the same time Caughley (1976a, b) used the improvements developed by May (1973 his Eqn 4.4) to the Lotka-Volterra predator-prey equations to model herbivore populations and their food plants, showing that the patterns generated were broadly consistent with observed real populations, such as the increase and collapse to extinction of reindeer on St Matthew Island.

A comprehensive classification of consumer-resource relationships, based on Caughley and Lawton (1981), is represented in Figure 2.2.

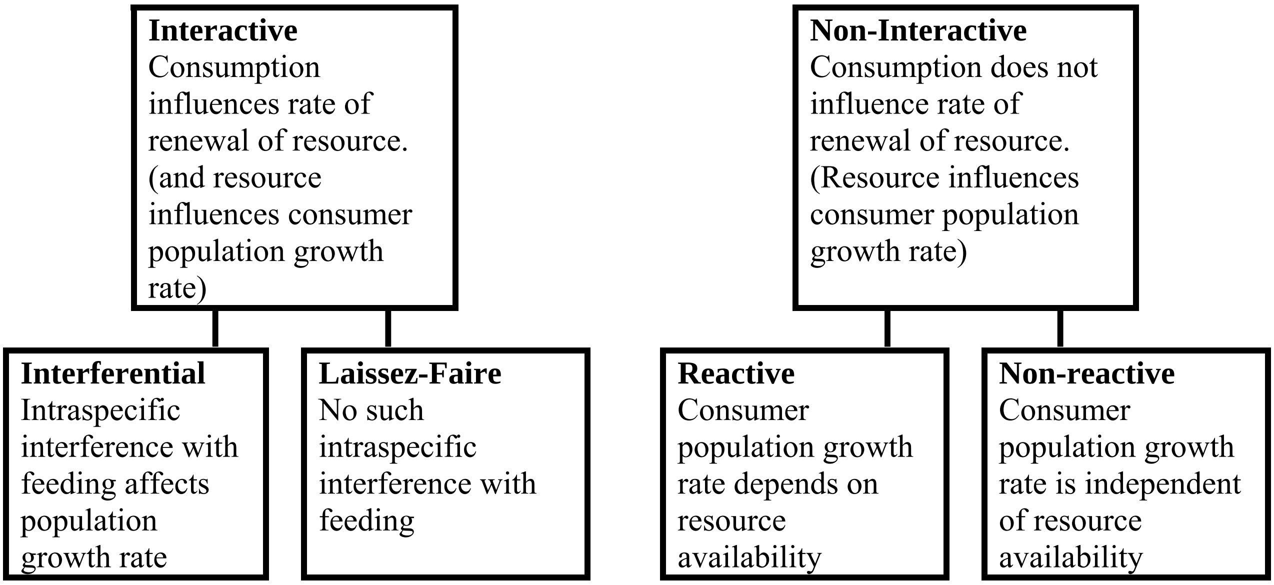


Figure 2.2: Classification of consumer-resource systems, based on Caughley and Lawton (1981).

Caughley's (1976a, his Eqns 5a and b) model represents plant growth as:
Vegetation growth rate = growth rate of vegetation - consumption (or intake) rate by herbivores, with the consumption rate as a function of herbivore density and vegetation availability, i.e.:

$$dV/dt = G(V) - I(N, V), \qquad \text{Eqn 2.5}$$

In particular:

$$dV/dt = r_1 V (1 - V/K) - c_1 N (1 - e^{-d_1 V}) \qquad \text{Eqn 2.6}$$

The parameters are defined in Table 2.1.

Here plant growth is represented as a logistic function, a relationship well supported by many studies (Crawley 1983). Rate of consumption by herbivores is an inverted exponential or Ivlev function representing a Holling's (1965, 1966) type 2 functional response (See Chapter 5 for description of functional responses and alternative mathematical forms.)

The other part of Caughley's (1976a) model represents the growth rate of the consumer population (herbivores in this case) as:

Herbivore population growth rate = density x rate of increase in terms of food (vegetation) availability, i.e.

$$dN/dt = F(V, H) \qquad \text{Eqn 2.7}$$

In particular:

$$dN/dt = N[\ -a + c_2(1 - e^{-d_2 V})] \qquad \text{Eqn 2.8}$$

Again an Ivlev form is preferred. The parameters are defined in Table 2.1.

Table 2.1: Meaning of parameters in Equations 2.6 and 2.8, from Caughley (1976a), and Caughley and Lawton (1981).

Symbol	Meaning
r_1	The intrinsic rate of increase of the vegetation
K	Plant biomass carrying capacity
c_1	Maximum rate of food intake by one herbivore
d_1	Grazing efficiency of the herbivore, or the rate at which satiation is approached with increasing V
a	Maximum rate of decline of herbivores, when the vegetation is zero
c_2	Rate at which that decline is ameliorated at high vegetation density
d_2	Demographic efficiency of the herbivore, its ability to multiply when vegetation is sparse

Caughley and Lawton (1981) further developed this analysis including an examination of the equilibrium conditions for the model and its potential for oscillation or extinction. Minor typographic errors confuse interpretation of this significant work, including a mistake in their Equation 7.13 in which H should be replaced with V*. An error in the caption of Figure 7.4 describes the vegetation equilibrium as ‘the curve’ and the herbivore equilibrium as the straight line, whereas the reverse is the case. Barlow (1985) pointed out that interference competition reduces the intake rate and should therefore be made to act through the functional response, rather than directly affecting the numerical response. Eberhardt *et al.* (2003) point out the model implies breeding occurs in 20 even steps per year and under more realistic arrangements the time required for the system to equilibrate blows out from about 70 years in the original model to more than 600 years. Eberhardt (1988) also discusses whether the parameter values are indeed as realistic as stated by Caughley (1976a). Owen-Smith (2002a) also mentions concerns about this without specifying them. These reservations do not affect the foundation of the model which represents a milestone in the development of the field and which is still cited as the basis for development of recent models, e.g. by Owen-Smith (2002a) and Eberhardt *et al*. (2003).

Simple mathematical models are useful as the basis for management recommendations, and the ready availability of computers has accompanied a proliferation of such models. However according to Caughley and Gunn (1996) 'testing those models against reality through the rigour of scientific method is in short supply'. For example, Abrams and Ginzburg (2000) commented that of 63 papers debating a controversy about functional responses, only one included a measurement of a functional response.

2.2 Evaluating the interactive model - the Kinchega kangaroo study

In a masterful piece of field ecology, Graeme Caughley and his co-workers (Caughley *et al*. 1987) studied the ecology of red kangaroos and western grey kangaroos in and near Kinchega National Park, which is near Menindee in the sheep rangelands of semi-arid western New South Wales. From 1980 to 1984, through a cycle of drought and plenty typical of the rangelands, they measured the production of vegetation in response to changes in the weather; tracked the density of each kangaroo species through a drought-induced crash and subsequent recovery; determined kangaroo movements and use of habitat; estimated functional responses of all the main herbivore species; and investigated the diets, body condition, reproduction and mortality of the two herbivore species. It was essentially the research project recommended at the end of Caughley's (1976a) paper with additional investigation of movements, body condition, reproduction and mortality. The ecological components were assembled in the form of an interactive model (Caughley 1987, Figure 2.3) of the general type published in Caughley's earlier papers.

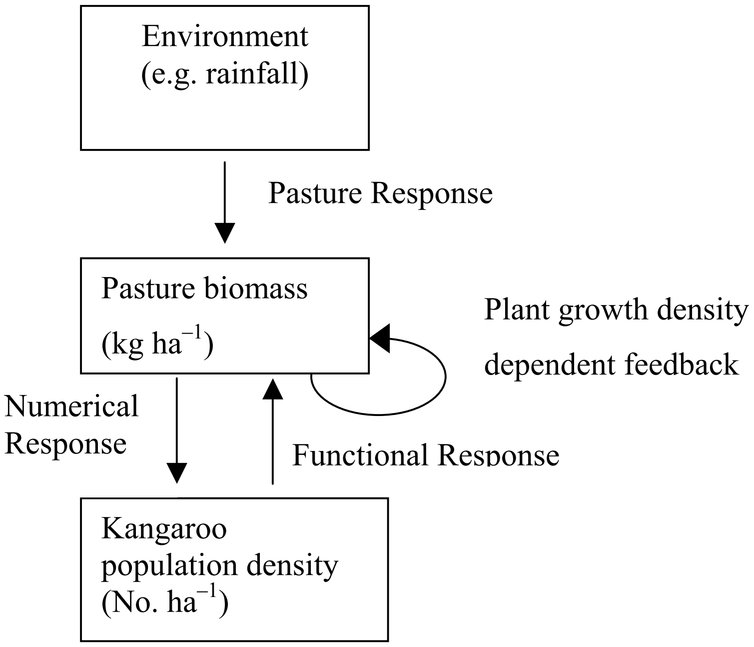


Figure 2.3: Structure of the interactive model used by Caughley (1987) to represent the variation in pasture biomass and kangaroo density at Kinchega National Park.

The Kinchega environment was driven by stochastic rainfall with a coefficient of variation of 45%, and with no correlation between years and no seasonality. Monthly mean temperature had no effect on plant growth. Pasture biomass varied in irregular cycles of high frequency and amplitude, however kangaroo density varied more slowly (Figure 2.4) reflecting the lower population growth rate of kangaroos compared to pasture, and less negative rate of decline in the absence of resources. Caughley (1987) used the term ‘centripetality’ to describe the tendency of the system to return toward its equilibrium, even though it could not remain there. The model of this system assumed an equilibrium of 250 kg ha^{-1} of pasture and 0.68 kangaroos ha^{-1} when rainfall was fixed at its mean value. A series of model simulations showed that despite the dominant effect of variable rainfall, the relatively minor feedback of the functional response was necessary to prevent kangaroo density increasing without limit.

Caughley’s (1987) model has been extended to other species in the rangelands. Choquenot (1998), modelled the dynamics of wild pigs (*Sus scrofa*) in riparian environments within the semi-arid zone using functional and numerical responses he estimated for the pigs in conjunction with Caughley’s (1987) pasture response. The effect of kangaroos on the system was simulated using Caughley’s kangaroo numerical response from Kinchega. McLeod

(1997) used the model to evaluate whether carrying capacity is a useful concept in that environment and Davis *et al.* (2003) used the model to quantify the effect of environmental variability, which effectively reduces the growth rate of the herbivore. Choquenot *et al.* (1998) were probably the first to successfully use data collected in the field to parameterise an interactive model for a temperate environment, that is, for rabbits (*Oryctolagus cuniculus*) and sheep (*Ovis aries*) on the central tablelands of New South Wales. Bayliss and Choquenot (2003) repeated that success by modelling introduced possums (*Trichosurus vulpecula*) that fed on the native trees in New Zealand. Pech *et al.* (1999) also took the interactive model outside the semi-arid rangelands, to model mouse plagues in a Mediterranean climate. Of all these, only the model of Pech *et al.* (1999) has been evaluated with data additional to that used in model development.

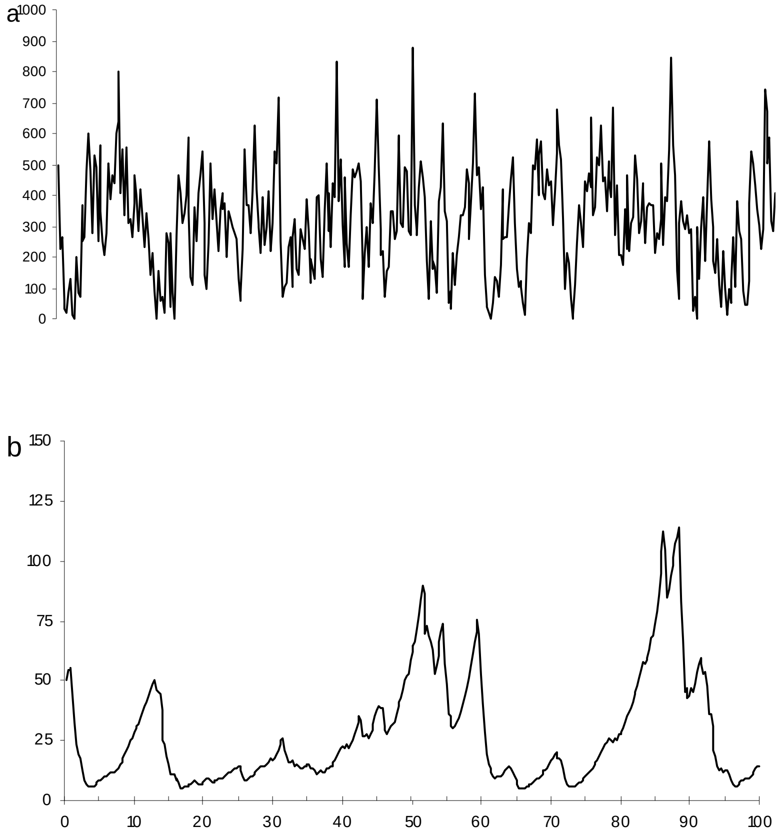


Figure 2.4: Typical output from a single 100-year simulation using Caughley’s (1987) model for kangaroos at Kinchega in far western New South Wales. Time in years is on the x axis; (a) herbage mass (kg ha^{-1}); and (b) kangaroo density (kangaroos km^{-2}) resulting from (a).

2.3 The GMM model

A major landmark may have been created in the field of population dynamics comparable to Caughley's (1976a) paper. This was Norman Owen-Smith's (2002a, b) elaboration of what he calls the GMM model (for growth, metabolism, mortality), which was published part way through this study. It is based on Caughley's (1976a) interactive herbivore model but goes well beyond it in some ways. Whereas Caughley (1976a) exemplifies the mechanistic paradigm, Owen-Smith (2002 a, b) has combined the mechanistic and demographic paradigms by explicitly modelling the effect of resources on demographic rates, such as mortality rates. The GMM model uses a so-called metaphysiological approach based on the concept that mass gained at the herbivore trophic level is a function of both growth, and losses through mortality and metabolic inefficiency. Similar to Caughley's (1976a) paper, Owen-Smith's parameters tend to be drawn widely from the literature rather than being empirical estimates based on the study of one ecosystem such as the kangaroos at Kinchega (Caughley *et al*. 1987) or the pigs along the Paroo River (Choquenot 1998). Thus the book (Owen-Smith 2002a) and the paper (Owen-Smith 2002b) provide a set of frameworks of conceptually sound modelling approaches equivalent to Caughley (1976a) rather than a demonstration equivalent to Caughley *et al*. (1987) or Choquenot (1998). Owen-Smith (2002a) is said to eschew the modelling of whole ecosystems (Stenseth and Mysterud 2003).

One of several valuable advances included in GMM appears to be the explicit modelling of mortality as a non-linear function of nutrient gain. On the other hand I found Owen-Smith's (2002a) models difficult to reproduce compared to those of Caughley (1976a, 1987) and Caughley and Lawton (1981). Some of his conceptual approaches depend on types of data whose importance may not previously have been widely appreciated. Herbivore intake is represented in brief feeding bursts, and the time allocation between feeding and not feeding is crucial, as is the definition of these states. Representing intake rates over longer time intervals, e.g. per day rather than per minute, seems a better and simpler approach, less prone to estimation error. Also, measuring grazing intake in brief bursts is associated with use of 'feeding arenas', an estimation method which is criticised in my chapter on functional response (Chapter 5).

Owen-Smith's (2002a) use of biomass to represent herbivores, rather than population is intuitively appealing because (a) it is more consistent with the representation of the vegetation, and (b) it might allow seasonal changes in body condition of the herbivores to be represented. However it seems likely to introduce at least as many sources of error as it removes. It remains to be seen how influential the GMM approach becomes.

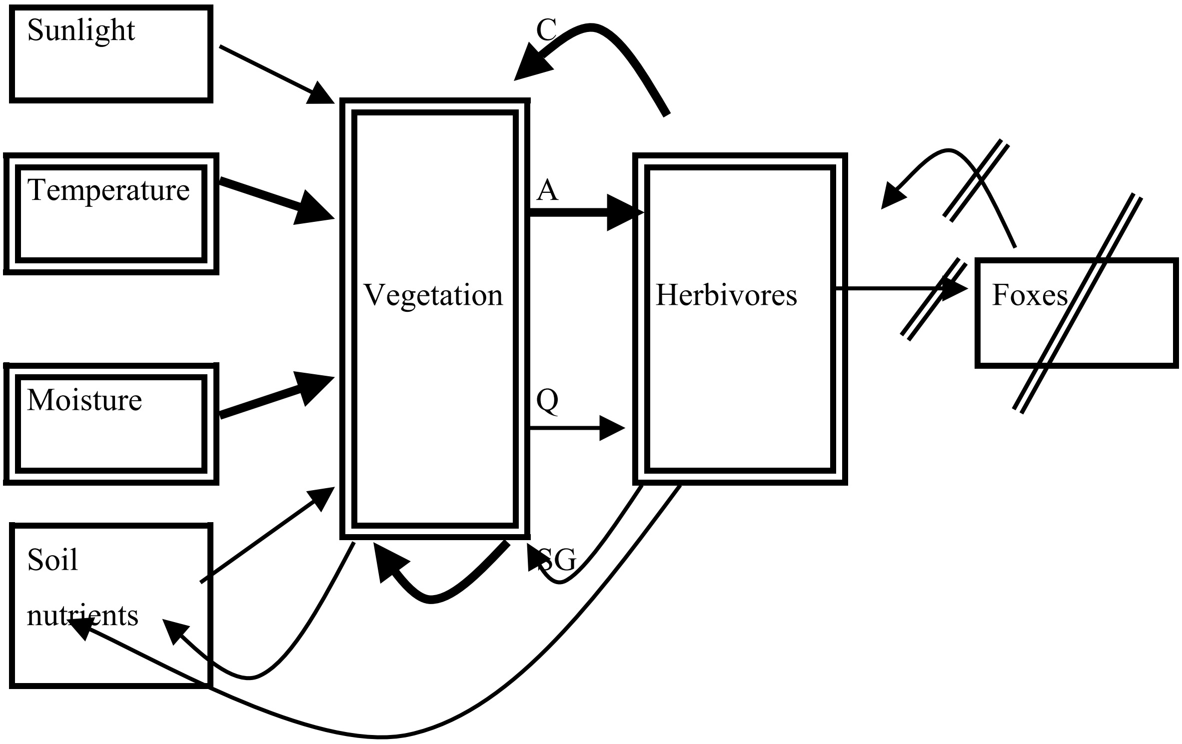


Figure 2.5: A schematic summary of an interactive herbivore-vegetation system. Modified from Fig 1.2 in Owen-Smith (2002a) which, in turn, is an elaboration of Caughleys (1976a, 1987) representation (See Figure 2.3). Bold arrows and doubled boxes indicate processes and attributes estimated in this study. See text for further explanation.

Figure 2.5 is the interactive model in a more complex representation than Figure 2.3 and is based on Owen-Smith's (2002a) Figure 1.2. My study estimated the relationships represented by the bold arrows, which required measurement of items in the doubled boxes. Some of the trophic relationships can be separated into aspects that were measured and ones that were not. The effect on the kangaroo population of changes in the availability of kangaroo food (relationship A) was estimated, but there was no analysis of change in food quality (relationship Q). Similarly, the consumptive effect of kangaroos on vegetation (the 'functional' or 'intake' response, C) was estimated, but not the slower-acting effect of selective grazing on species composition, (relationship SG). The crossed out effect of foxes on kangaroos represents the attempt to reduce this influence by controlling foxes. However at the Gudgenby site, dingo predation was not evidently affected by the fox baiting (Chapter 6).

This chapter provided an introduction to the theoretical context of consumer-resource models. The next seven chapters are concerned in some way with empirical estimation of the parameters needed for one of these models (Figure 2.3). The first of these chapters (Chapter 3) begins with an explanation of the research design and goes on to describe the study sites, including the populations of vertebrate herbivores and predators that they support.

CHAPTER 3

THE STUDY SITES

An eastern grey kangaroo in the shade of a tree at the Googong site, near one of approximately 150 pasture assessment points (marked by post) with a grazing exclosure cage nearby (white mesh cylinder).

CHAPTER CONTENTS

3 THE STUDY SITES

3.1 Selection of sites for the research design

3.1.1 A mensurative experiment

This study was not a ‘manipulative experiment’ but a ‘mensurative experiment’, adopting the classification of Krebs (1999, p. 341), due to the nature of the research questions, resource constraints and political constraints. The Kinchega kangaroo study (Caughley *et al.* 1987) was also a mensurative experiment. A comparable example of a manipulative experiment is a study of the interdependence of density of feral pigs and density of pasture by Choquenot (1998) who held pig density at three different levels (x 2 replicates) on different sites. In my study, three sites were selected to: (a) encompass a range of different pasture growth conditions found in the southern tablelands of NSW so as to provide a better basis for generalising to a range of sites in the region; (b) have independent kangaroo populations; and (c) be relatively free from unwanted influences such as kangaroo shooting, or grazing by other vertebrate species. The selected sites were Googong, Gudgenby and Tidbinbilla (Figure 3.1).

A difference in pasture growth between the three sites was assumed from the difference in the long-term average values for rainfall and temperature (Section 3.2.2) and published evidence of the expected effect of this on pasture growth (e.g. Vere *et al*. 2001). Realistically, three sites can not fully represent all temperate grasslands, nor can they be completely independent in the context of this type of study. They share common weather systems, so they all experienced the 2002 - 2003 drought which affected most of Australia. Such limitations are probably inevitable with this type of research, and imply the need for appropriate caution when extrapolating to different circumstances, as mentioned under Discussion in Chapter 4. Such limitations could be reduced most effectively by greater replication, not of sites, but of investigations, and by longer periods of recording from the same sites. Notwithstanding these remarks, there is the potential to obtain valuable insights from the research design as it stands, and to improve decisions about management of eastern grey kangaroos.

After a pilot survey and methods trial from April to July 2001, the main study was conducted from August 2001 to July 2003. In Chapter 6 I also analyse data recorded in 1997 from a sample of shot kangaroos from the previously unshot population at Tidbinbilla.

3.2 Description of the sites

My Googong site was a part of Googong Reservoir Foreshores, my Gudgenby site was within Namadgi National Park, and my Tidbinbilla site was part of Tidbinbilla Nature Reserve.

3.2.1 Geology, geomorphology and soils

The Gudgenby and Tidbinbilla sites are the grassy floors of sub-alpine valleys. The Googong site is the cleared foreshore of a reservoir that now floods the valley floor.

The Gudgenby site includes part of the catchment of three sub-alpine creek systems (Rendezvous, Middle, and Bogong) and Bogong Swamp, which is the source of the Gudgenby River. It includes substantial creek flats. Compared to the other study sites it has gentler slopes, includes swampy areas, and the open slopes occupy a greater range of combinations of aspect and slope. At Googong the reservoir covers the former areas of low slope. At Tidbinbilla, the steeper south facing areas of the valley floor are closed shrubland, which does not provide feeding areas for kangaroos, and was not included in the pasture assessments. In effect, the Tidbinbilla site is more north-facing than the others, although there is a northerly bias at Gudgenby also, i.e. a saw-tooth landform.

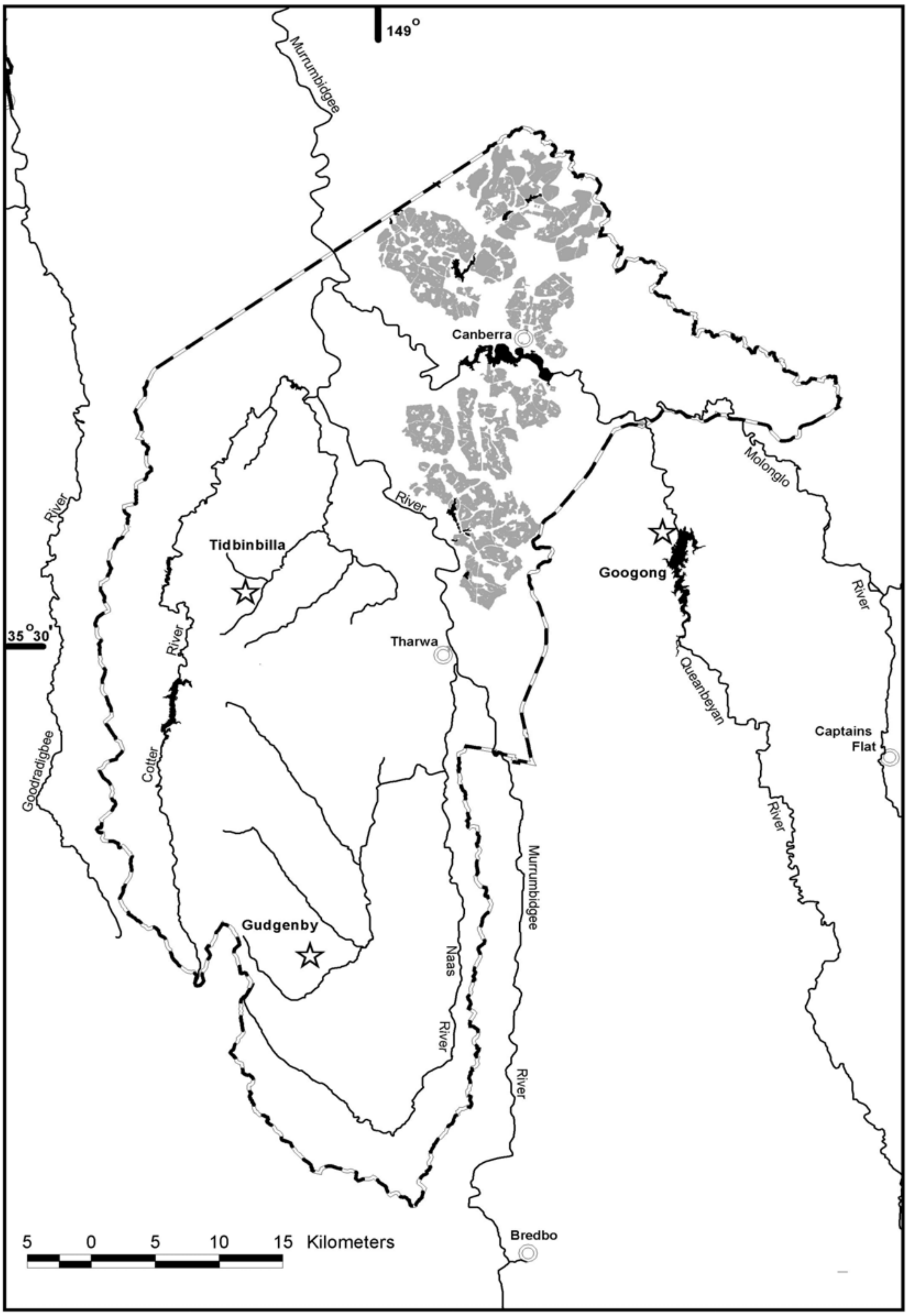


Figure 3.1: Locations of the three study sites, i.e. Googong, Gudgenby and Tidbinbilla, (stars) in relation to the border of the Australian Capital Territory (dashed line) which can also be seen on Figure 1.2. The grey shading marks the Canberra suburban area. The Brindabella Range, which is associated with locally higher rainfall, lies between the Goodradigbee and Cotter Rivers to the west of the study sites.

Soils at the Gudgenby and Tidbinbilla sites are similar. They occupy similar catenary positions on the same Silurian granite geology (Owen and Wyborn 1979). Grey-brown podzolics predominate with small areas of yellow podzolics at Tidbinbilla and in the Rendezvous Creek catchment. There are some red podzolics at Tidbinbilla (personal observation) and small areas of alpine humus soil on creek flats and areas of impeded drainage in both sites (Ingwersen 2001). Exposed rock is common, mainly in the form of granite tors. Googong is characterised by shallow, acidic lithosols and steeper slopes with much exposed rock, mainly Ordovician metasediments (Jenkins 2000).

3.2.2 Climate

Tidbinbilla receives 1½ times the rainfall of Googong and is only slightly colder (Table 3.1). Consequently in summer the pastures in the Tidbinbilla rural district are often green when pastures at Googong are yellow and dried out. The mean annual rainfall at Gudgenby is intermediate to the other sites. The lower annual mean temperature at Gudgenby means there are at least three times as many frosts (Table 3.1), and a shorter growing season, compared to the other two sites. Snow persists on the pasture at Gudgenby for a few days in most years, but this has happened rarely at Tidbinbilla and is unknown at Googong. The occurrence of short-term weather events also differs. For example, an intense storm in March 2003 did not affect Tidbinbilla or Gudgenby but at Googong it caused spectacular flooding and scoured the pasture (Section 3.5.2).

The Bureau of Meteorology maintains a long-term record of rainfall (133 years) collected at the Queanbeyan Bowling Club approximately ten kilometres north west of the Googong site, as well as a 65 year record from the Canberra station, at the airport. The coefficient of variation (CV) between years is 27% in both cases (Table 3.1). On the study sites, records have been kept for 52 years at Gudgenby (CV = 27%), 35 years at Tidbinbilla (CV = 29%) and less than ten years at Googong (CV = 20%). These temperate sites experience much more predictable rainfall than the sites studied by Caughley *et al.* (1987) in the semi-arid, sheep-rangelands at Kinchega where the CV between years was 47 % (Robertson *et al.* 1987) or 45% (Caughley 1987). Yet at CV = 27%, the variation between years is still sufficient to strongly alter pasture growth between years (Vere *et al.* 2001; Clark *et al.* 2003).

The three sites span a wide range of pasture growing conditions (within their temperate regional context) as indicated by differences in the long-term mean values for rainfall and temperature (Table 3.1, Figure 3.2). These differences can be attributed mainly to two factors, the differences in elevation of the sites, and their relative proximity to the Brindabella Range. Googong is in a rain shadow (Jenkins 2000).

Table 3.1: Elevation, long-term average rainfall, annual mean daytime temperature and number of frost days at the three study sites compared to regional weather stations at Canberra and Queanbeyan, which have longer records. The table also includes the coefficient of variation of rainfall between years (CV) and the number of years recorded. The mean daytime temperature was calculated from daily maximum and minimum temperatures using the formula given by Moore *et al.* (1997). Frost days were defined as minimum temperature < 0° C. There are many unexplained gaps in the record of minimum temperature in winter months at Googong, and the number of frost days here is my estimate. Rainfall and temperature data were supplied by the Bureau of Meteorology, in August 2004. NR = not recorded

Site Name	Elevation (m)	Annual Precipitation (mm)			Mean Day. Temp. (° C)		Mean No. frost days per year
		Mean	CV (%)	No. years	Mean	No. years	
Canberra	580	624	27	65	12.5	65	61
Queanbeyan	580	588	27	133	NR	NR	NR
Googong	670	624	20	10	13.0	9	~33
Gudgenby	1000	769	27	52	9.7	20	116
Tidbinbilla	750	973	29	35	11.8	18	38

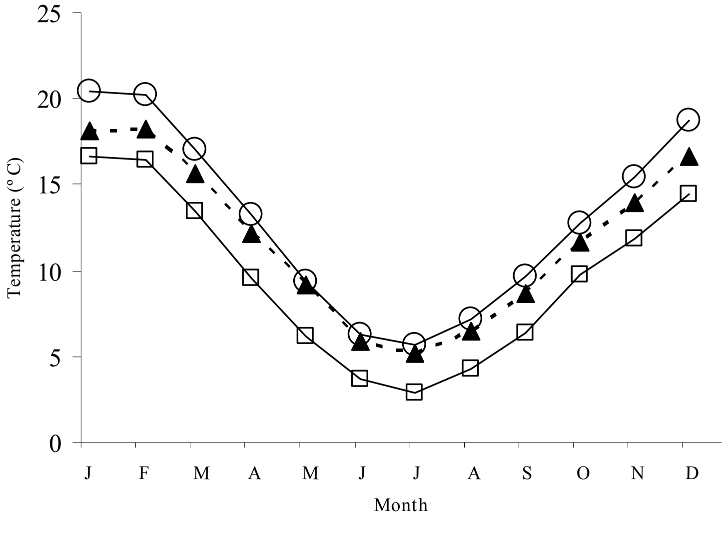


Figure 3.2: Monthly mean daytime temperature at the study sites. ○ = Googong; □ = Gudgenby; ▲ = Tidbinbilla. Calculated from long-term monthly mean maximum and minimum temperatures provided by the Bureau of Meteorology, using an equation given by Moore *et al.* (1997).

3.2.3 Vegetation

The pastures on all three study sites are mainly ‘high quality native pastures’ using the classification of Vere *et al*. (2001) with some areas of ‘low quality native pasture’, some ‘introduced legume pasture’ especially at Gudgenby, and small patches of ‘introduced perennial pasture’ in poor condition. Continuing the classification of Vere *et al*. (2001), Gudgenby and Tidbinbilla fall into their Granite High Rainfall group and Googong into the Sedimentary Medium Rainfall and Acidic Sedimentary Medium Rainfall groups. On all sites, the north facing pastures are dominated by kangaroo grass (*Themeda australis*) and the flat areas by river tussock (*Poa labillardieri*).

The pasture is mainly a product of previous clearing. The remaining overstorey at Googong comprises patches of mealy bundy – broad-leaved peppermint (*Eucalyptus. nortoni* – *E. dives*) woodland, remnants of yellow box – red gum (*E. melliodora* – *E. blakelyi*) open woodland and traces of a mixed species open woodland, including isolated trees or small clumps of candlebark (*E. rubida*), red stringybark (*E. macrorhyncha*) and manna gum (*E. mannifera*), as well as saplings of these species resulting from plantings by the site managers. At Gudgenby, few trees remain, although stumps and other wood indicate the site was almost entirely wooded before it was cleared. The remaining trees include broad-leaved peppermint (*E. dives*), candlebark (*E. rubida*), snow gums (*E. pauciflora*), black sallee (*E. stellulata*), and ribbon gum (*E. viminalis*). The remnant overstorey species on the Tidbinbilla site have been classified by Ingwersen (1985) into three associations dominated by narrow leaved peppermint (*E. robertsonii radiata*), broad-leaved peppermint, ribbon gum (*E. viminalis*), and mealy bundy. Thus there was probably considerable overlap in the original Eucalyptus species on the three sites, bearing in mind that the Googong reservoir would have covered the colder, riparian parts of the local terrain where ribbon gum, black sally and snow gum may have occurred. However yellow box and red gum are known only at the Googong site. Following clearing of the original woodland and forest, the south facing slopes and some other areas at Tidbinbilla have been invaded by closed shrubland dominated mainly by *Kunzea philicoides*, *Hakea sericea* and *Banksia marginata.* Small areas of closed shrubland are also present at Googong and Gudgenby, mostly *Kunzea philicoides*.

3.2.4 Other herbivore species

The eastern grey kangaroo is the only vertebrate herbivore species whose populations are capable of having a measurable effect on pasture biomass on the sites. Other local macropod species (red-necked wallabies *Macropus rufogriseus*, wallaroos *M. robustus* and swamp wallabies *Wallabia bicolor*) are at low density and tend to inhabit the fringing woodlands, rocky hill slopes or shrubby forests of the region, rather than the grasslands. The grass biomass removed from the sites by these three species would be insignificant in comparison to the larger eastern grey kangaroos, of which 9,326 groups were recorded in all of my density estimation surveys on all sites. In comparison, solitary wallaroos and swamp wallabies were each seen twice, and 64 small groups of red-necked wallabies.

There are generally no commercial grazing stock on the sites although trivial exceptions occurred occasionally on all sites. One incursion was substantial and significantly affected the availability of pasture for kangaroos. 70 pregnant cows and four bulls grazed for ten weeks at Tidbinbilla after a bushfire in January 2003 (Section 3.5.1). Prior to their arrival, there had been an atypical abundance of pasture due to the death of almost half of the Tidbinbilla kangaroos in the bushfire, but by the time the cattle were removed, the Tidbinbilla pasture had been reduced to the lowest herbage mass recorded on any site during the study (Section 4.3, Figure 4.8).

Rabbit density was low on all sites throughout the study. At Googong and Tidbinbilla, rabbit density appeared to vary little and spotlight counts by the site managers on standard transects remained below 2 rabbits sighted per transect kilometer (mean of 2-3 counts). This is a fraction of the peak values previously recorded on these sites, namely 6.7 and 57.1 rabbits km^{-1} respectively (Bill Woodruff, Environment ACT, personal communication). Rabbit density was highest at Gudgenby and appeared to increase throughout the study. In April 2003 the site managers recorded 11 rabbits km^{-1} on a spotlight count (mean of 2 counts). At the end of my fieldwork, in July 2003, I estimated a density of 1.2 rabbits ha^{-1} at Gudgenby using the line transect method. My surveys started one hour after sunset on three calm moonless nights when most rabbits would have been out feeding (Kolb 1992; Williams *et al*. 1995). Making ‘worst case’ assumptions that half the rabbits were still below ground, that all rabbits weigh 2.5 kg, and using Short’s (1985) measurement of maximum pasture consumption by rabbits of 80 g kg$^{-0.75}$ d^{-1}, the herbage mass removed at Gudgenby would be approximately 0.38 kg ha^{-1}, which is insignificant in the context of this study.

As well as eastern grey kangaroos and rabbits, feral pigs also consume pasture. Feral pigs probably were not present on the Googong site during the study. They were detected a few times at Tidbinbilla and promptly eliminated by the site managers. At Gudgenby I observed feral pigs, or fresh rooting by pigs, on many of my visits. However their density was low. In the mid 1980s, before an annual poisoning program was commenced by the managers of Namadgi National Park, feral pigs were more abundant, and their density in a large area of the Park, including the Gudgenby site, was estimated at 1-2 km^{-2} (Hone 2002). A feral pig density index was commenced in 1985 (Hone 2002). During my study the index was less than one sixth of what it was before poisoning had commenced (Hone 2006). Therefore the amount of pasture consumed by feral pigs on the study sites is likely to have been insignificant compared to kangaroos, which were at a density of 450 - 510 km^{-2} (Chapter 7).

3.2.5 Site boundaries, and area of each site

The boundary of each study site was selected so as to minimise kangaroo movement onto and off the defined site. This was done by using as boundaries, features such as the junction between low-angle grassland and steep forested valley sides, or kangaroo-resistant fences, and at Googong, the water reservoir.

Throughout their lives eastern grey kangaroos are relatively sedentary (Johnson 1989) compared to red kangaroos (Priddel 1987). A partly concurrent study of eastern grey kangaroo habitat use and movements on the Googong and Tidbinbilla sites found the eastern grey kangaroos on these sites were sedentary in all seasons (minimum convex polygon mean size 0.43 km^2 ± 0.06 SE and 0.61 km^2 ± 0.08 respectively; Viggers and Hearn 2005). Kangaroos were not radio tracked at Gudgenby but my observations suggest there is no more movement of eastern grey kangaroos on and off the site there than at Tidbinbilla. Thus it is likely there was little net movement of kangaroos on and off the study sites.

On the Gudgenby site, where the kangaroos were easiest to observe, I noticed that the kangaroos tended to remain in the grassy areas in all weather conditions, and eastern grey kangaroos are encountered infrequently in the steep forested terrain bounding the Gudgenby and Tidbinbilla sites. Some eastern grey kangaroos are known to shelter in woodlands or forests, but at night even these will invariably feed in grassy clearings (Dawson 1995) as the diet of eastern grey kangaroos is 99% grass (Jarman and Phillips 1989). A study of habitat use by adult female eastern grey kangaroos (Moore *et al*. 2002) recorded large variation in most parameters investigated except that grassy areas were selected strongly at all hours of day.

The sites varied in size, as a consequence of setting their boundaries so as to minimise kangaroo immigration and emigration to and from the study populations. The areas were 528 ha at Googong, 1384 ha at Gudgenby and 477 ha at Tidbinbilla.

Figure 3.3: Eastern grey kangaroos at Tidbinbilla. A pasture assessment location (post and white exclosure cage) is visible. The study site was on the valley floor. Steep forested areas in the background were excluded.

3.3 History of eastern grey kangaroo populations on the sites

All three sites had been grazed commercially for 50 – 150 years until withdrawn in recent decades for conservation or water supply purposes. Each site supported an unmanaged population of eastern grey kangaroos, which was at high density.

Kangaroos were scarce in the ACT region in the 1940s and 1950s (Schumack 1977; ACT Kangaroo Advisory Committee 1996, p. 9). This included the study sites. The first employees in the Tidbinbilla Nature Reserve lived there for three months in 1963 before seeing a kangaroo (Mick McMahon, former employee, personal communication; ACT Kangaroo Advisory Committee 1996) and salt blocks were put out to attract kangaroos in the years before the reserve was opened to the public (ACT government official file: Tidbinbilla Fauna Reserve Advisory Committee – 1966).

The increase from low to current high kangaroo densities was recorded best at Googong. Spotlight counts of rabbits also recorded eastern grey kangaroos as a by-product. Counts started in 1980, stopped after six years, then resumed in 1996. Commercial grazing was withdrawn progressively from the site during the mid 1980s. The pattern of kangaroo density (Figure 3.4) appears to be a herbivore eruption. Kangaroo density increased more rapidly from 1996 to 2000 after sheep and cattle grazing had ended. It had an exponential population growth rate of $r = 0.26$ ($R^2 = 0.911$), which is substantially lower than the intrinsic rate of increase (Chapter 8). It is not known why the increase at Googong was not faster, unless it was diminished by illegal shooting, which still occurs there to a small degree.

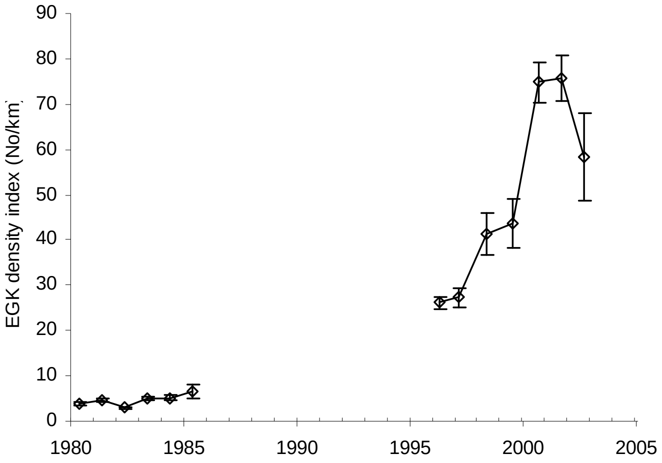


Figure 3.4: Index of density of eastern grey kangaroo population (EGK) at Googong (± SE) from rabbit spotlight count. Values are means of ~12 monthly counts before 1986, and after 1996 values are means of three near-consecutive nights. (Data from Bill Woodruff, Environment ACT, personal communication).

Eastern grey kangaroo density must also have increased at Tidbinbilla during the thirteen years after the first employees were stationed there. After the thirteen year interval, from 1976 to 1986 the managers were shooting eastern grey kangaroos (EGK) to reduce their grazing effect. A density index commenced in 1976 was too late to record most of the increase phase (Figure 3.5), but shows density varying around a mean of 35 EGK km^{-1}, until the monitoring ended in 1991.

Based on the Tidbinbilla data, there has been a suggestion that the dynamics of temperate kangaroo populations may be different in kind from those reported for other temperate herbivores. Bayliss and Choquenot (2002) argued that population instability is an inherent characteristic of kangaroos, even in stable environments. (The CV of rainfall at Tidbinbilla is

27% (Table 3.1) so it is not stable, but it is less variable than the semi-arid rangelands from where Bayliss and Choquenot (2002) drew their main comparative set of data.)

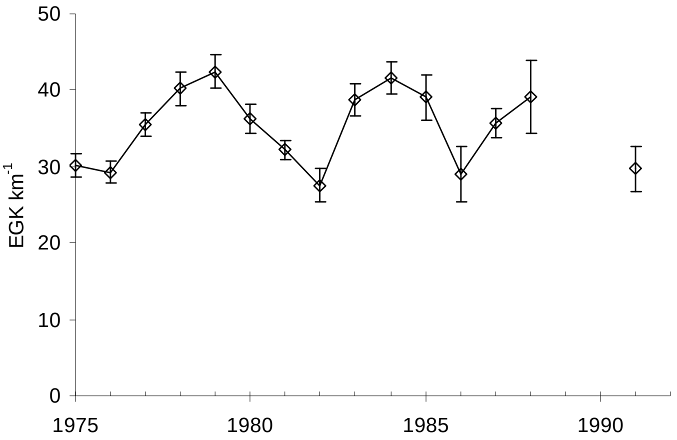


Figure 3.5: Density index of eastern grey kangaroos at Tidbinbilla Nature Reserve from 1975 to 1991. Annual mean (± SE) of spotlight counts on fixed transects. Source data copied from a logbook and other papers in the office at Tidbinbilla Nature Reserve.

Bayliss and Choquenot (2002) pointed out the appearance of a stable limit cycle in the Tidbinbilla data (Figure 3.5). If confirmed, cyclicity would demand revision of some of the published theory. For example May (1973), Crawley (1983) and Sinclair (1996) believe that cycles would be likely to be discerned from background variation only for species capable of population growth rates much higher than those of which kangaroos are capable. Caughley's (1976b) hypothesis about a stable limit cycle for elephants and trees, based on tree-ring data, is a contrary claim. The explanation of the Tidbinbilla pattern may be that the cycles are real (and the theory needs revision), or it may lie with any of five other possible explanations hypothesized by Bayliss and Choquenot (2002), or the 'cycles' may be dampening oscillations of the sort predicted theoretically for large and medium sized herbivores by the herbivore eruption hypothesis (Leopold 1943; Caughley 1970, 1976a; May 1981; Caughley and Lawton 1981; McCullough 1997; Forsyth and Caley 2006) and arguably observed in real populations (Caughley 1970, 1976a; Leader-Williams 1988; Saether *et al.* 2002; Festa-Bianchet *et al.* 2003). The increase in the Tidbinbilla kangaroo population from 1963 to 1976 may have eaten out the food supply, causing the kangaroo population to crash, and the pasture-herbivore system to reverberate during the 1976 – 1992 period recorded in Figure 3.5. The herbivore eruption possibility was not discussed by Bayliss and Choquenot (2002).

At Gudgenby, as at Tidbinbilla, there is no quantitative record of the increase phase, only anecdotal information. Just as kangaroo density must have increased at Tidbinbilla in the

1960s and 1970s, and at Googong in the 1980s and 1990s, it presumably increased to modern levels at Gudgenby during the 1980s and 1990s, following similar land use change from agriculture to national park. Similar anecdotal information also applies to the neighbouring upper Naas valley, the former 'Boboyan' station. However in that case the anecdotes are supported by kangaroo faecal pellet counts (ACT Parks and Conservation Service 1995). The counts were low in the 1980s when the valley was still under stock grazing and higher in 1993 to 1995 when repeated by Banks (1997, 2001).

3.4 Site management

There was no deliberate manipulation of kangaroo density by the managers of any of the three sites, nor any supplementary feeding during the present study. Occasionally, small numbers of eastern grey kangaroos were shot illegally at Googong.

3.4.1 Fox baiting

Fox control was to be commenced on all study sites by employees of the ACT Parks and Conservation Service prior to the commencement of the study. Foxoff® baits containing 2 mg of 1080 were buried on average every 400 m along all roads, except within 500 m of dwellings. In the first month after the baiting commenced on each site, bait sites were inspected every few days and any baits taken were replaced. Thereafter, all baits were renewed at monthly intervals. Baiting at Googong proceeded to that plan. Also at Gudgenby except that it was neglected for half a year from April 2002. At Tidbinbilla baiting did not commence until January 2002, and it stopped ten months later.

I observed multiple fox carcasses on each site, especially in the weeks after the commencement of baiting, and occasionally thereafter, 17 in all. Over two years, the number of live foxes I saw in daytime was two at Googong, four at Gudgenby and 17 at Tidbinbilla. Baiting records obtained from the ACT Parks and Conservation Service show the proportion of baits removed on each site quickly rose to a peak during the first month of more intensive baiting then declined to a relatively low level (Figure 3.7).

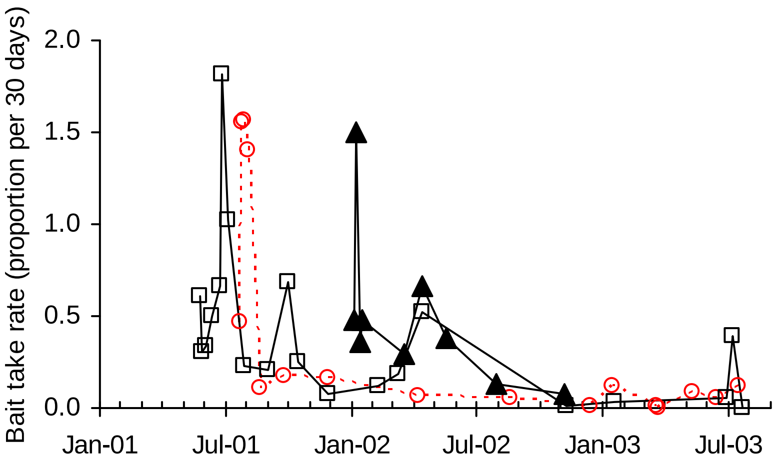


Figure 3.7: Monthly removal rate of poisoned fox baits. ○ = Googong (n=32 baits); □ = Gudgenby (n=33 baits); ▲ = Tidbinbilla (n=42 baits). Calculated as 30 x Number of baits taken / (Baits available x Days available).

3.4.2 Rabbit control

The site managers had also agreed to control rabbits on the sites during the study. At the commencement of the investigation, rabbit density indexes maintained by the site managers were low and showed rabbit density to be a small percentage of the maximum values previously recorded on each site. Rabbit control was carried at Googong and Tidbinbilla in 2003 using a four-wheel drive tractor to destroy warrens by ripping, but no rabbit control was carried out at Gudgenby. See 'Other herbivore species' above for rabbit density estimates.

3.5 Unpredicted disturbances

3.5.1 The bushfire of January 2003

A large bushfire burnt through the ACT region on 17th and 18th January 2003. The burnt area continued to expand spasmodically over the following weeks. The Googong site was unaffected. The main effects on this study took place at the Tidbinbilla site, although most of the field equipment was rapidly removed from Gudgenby ahead of the fire front, and replaced later, and some loss and damage occurred during removal. The Gudgenby site was the only large island of unburnt land within the perimeter of what became known as 'the Brindabella fire complex'. Compared to typical bushfires, this one was unusual in the low proportion of area left unburned. Of the 55 km^2 Tidbinbilla Nature Reserve (including the Tidbinbilla study site) 100% was burnt at high intensity. (Official ACT Government records state that 99% of the Reserve was burnt, but are incorrect.)

Most of the study equipment that had been destroyed or damaged at Tidbinbilla and Gudgenby (weather stations and exclosure cages) was quickly replaced or repaired, so data losses were slight. The effects on the data are dealt with under the relevant chapters. An exception was temporary grazedown yards at Tidbinbilla, which were not repaired for about a year (Chapter 5). A substantial proportion of the eastern grey kangaroos at the Tidbinbilla site were killed (Chapter 7) and every living eastern grey kangaroo I saw there a week after the fire was behaving as if it had burnt feet. The burnt pasture commenced regrowing almost immediately (Chapter 4).

In contrast, only 110 ha (7 %) of the grassland at Gudgenby was burnt, at the perimeter of my study site, although the surrounding *Eucalyptus* forest seemed to have all burnt. In spite of careful inspection at Gudgenby, I found no fresh kangaroo carcasses there during the six weeks after the fire, from any cause, nor did I see any kangaroo with burnt feet, and have inferred that the 2003 bush fire caused no reduction in density of eastern grey kangaroos at Gudgenby.

3.5.2 The hail storm of March 2003

An intense hail storm passed across the southern part of the Googong site on 16 March 2003. The weather station at the northern end of the site recorded 25.7 mm of rainfall overnight but I suspect more fell to the south. Wire netting stock fences in good condition were washed over, kangaroos were killed, creeks and road drains were scoured out, dams were breached, and a large number of logs, and masses of other flotsam, were washed well out into Googong reservoir. Thick beds of ice remained for days protected from the sun under a blanket of grass litter and animal droppings where they had accumulated in places such as against fences and on the shoreline of overflowing farm dams (Figure 3.8). Scouring by surface flow removed dead grass, eroded soil, and significantly reduced the vegetation ground cover. This is discussed in Chapter 4.

Figure 3.8: Banks of ice >30 cm deep (arrow) survived for several days in a few places at Googong after the storm in March 2003. They occurred where water currents had deposited drifts of hail stones under a layer of grass litter, faecal pellets and other flotsam.

Having introduced the study topic (Chapter 1), some of the theoretical background (Chapter 2), and described the study sites (this chapter), the presentation of results of the study begins in the next chapter with the measurements of the pasture and the weather.

CHAPTER 4

THE PASTURE

The best explanation is as simple as possible, but no simpler (Albert Einstein)

Mobile grazing exclosure cages were repositioned on each bimonthly visit, to enable pasture growth and herbivore offtake to be estimated.

CHAPTER CONTENTS

4 THE PASTURE

4.1 Introduction

This chapter estimates the pasture response for the study sites, an equation expressing pasture growth in relation to pasture biomass and weather. Because this thesis evaluates Caughley's (1987) interactive kangaroo-pasture model for application to a seasonal, temperate environment (Chapter 1) this chapter repeatedly refers to the pasture chapter (Robertson

1987a) of the book in which Caughley's interactive kangaroo grazing model is presented (Caughley *et al.* 1987). The results begin with weather and pasture data for my study sites during and before my two year period of pasture measurements, which ended in July 2003. Data on groundcover are also presented (which are not used in the pasture response model) because they are relevant to kangaroo management.

If the simple empirical approach adopted here to model the pasture response generates useful strategic insights, it will be a substantial cost saving compared to the work that would be necessary to parameterize more complex alternative models. In the spirit of this approach, I have deliberately restricted the input parameters to rainfall and temperature, which are widely measured, readily available and well understood, rather than, for example, evapotranspiration or evaporation, which are measured less and calculated in varied ways.

The interactive plant-herbivore model in Australia has so far been applied mainly in the semi-arid interior of the continent (Caughley *et al.* 1987; Choquenot 1998; McLeod 1996, 1997; Pech and Hood 1998; Davis *et al.* 2003). The semi-arid is a region characterised by fluctuation between extremes of drought and plenty. Rainfall drives plant growth and, therefore, the growth of herbivore populations (Robertson 1987a, 1987b, 1988; McCarthy 1996; Freudenberger *et al.* 1999). At the Kinchega site where Caughley's (1987) interactive kangaroo model was parameterized, mean monthly temperature had no influence on pasture growth. Rainfall during the previous year explained 71% of the variation in herbage mass measured over three-month intervals (Robertson 1987a, p. 55). There was no seasonality (Robertson 1987b) and rainfall was random between years with a CV of 45% (Caughley 1987) or 47% (Robertson *et al.* 1987). Likewise, in a seven year study of sheep grazing in semi-arid woodlands, Freudenberger *et al.* (1999) found annual rainfall accounted for 60% of the variation in live weight gain, and 79% of the variation in wool growth. In the semi-arid environment, few parameters are needed to empirically model pasture growth as a basis for modelling fluctuations in density of herbivores (Caughley 1987; McLeod 1997; Choquenot 1998) or herbivores and predators (Pech and Hood 1998). The pasture response in Caughley's (1987) Kinchega model contains only one rainfall parameter to account for weather effects, and a quadratic expression to provide density dependent pasture growth (Robertson 1987a).

Choquenot *et al.* (1998) made an interactive model of rabbit and sheep production based on data they collected in an environment much more relevant to my study, the temperate central tablelands of NSW. Using the same pasture response model as Robertson (1987a) (but parameterized for the temperate-zone data) Choquenot *et al.* (1998) explained 83% of the variation in their pasture biomass data. Like the models mentioned in the paragraph above, their model includes only parameters for rainfall and logistic growth. Surprisingly, they found it unnecessary to add a temperature parameter. Their success in a very similar environment provides great encouragement for the approach outlined for this study, that of evaluating a simple empirical model using a small number of weather inputs.

In contrast to the models mentioned previously for semi-arid Australia and the model of Choquenot *et al.* (1998), empirical models of plant growth in temperate regions generally, or for the entire Australian continent (not limited to the semi-arid), have generally invoked multiple weather parameters e.g. including temperature and evaporation as well as rainfall (Fitzpatrick and Nix 1970). Mechanistic models have included large numbers of parameters and complex interactions, resulting in sophisticated computer programs, such as GrassGro (Moore *et al.* 1997) which model the dynamics of a restricted group of exotic grasses, as a basis for predicting the production of domesticated stock. The algorithms and parameter values used in the program are given by Moore *et al.* (1997).

Notwithstanding that there was no seasonality in pasture growth at the Kinchega site (Robertson 1988), and temperature was not a factor in the temperate pasture model of Choquenot *et al.* (1998), seasonal patterns of pasture growth and herbivore production are a distinctive feature of temperate sites generally, and my study sites particularly. The annual cycle of production of several types of pasture has been quantified for the NSW central and southern tablelands region (including the study sites) by Vere *et al.* (2001) based on consensus of a group of NSW Agriculture's pasture specialists (Figure 4.1). Rainfall in the region is relatively evenly distributed across seasons and the large variation in monthly pasture growth illustrated in Figure 4.1 is attributable mainly to temperature (and other forms of solar influence, such as radiation and daylength), and to interactions between temperature and moisture availability. The median or mean production values of Vere *et al.* (2001) are unaccompanied by estimates of variance. This study provided an opportunity to assess the extent to which real pastures either conformed to the strongly seasonal (temperature-based) pattern illustrated by Vere *et al.* (2001) for the central and southern tablelands, or to the aseasonal, rainfall-dominated model of Choquenot *et al.* (1998), also originating from the central tablelands.

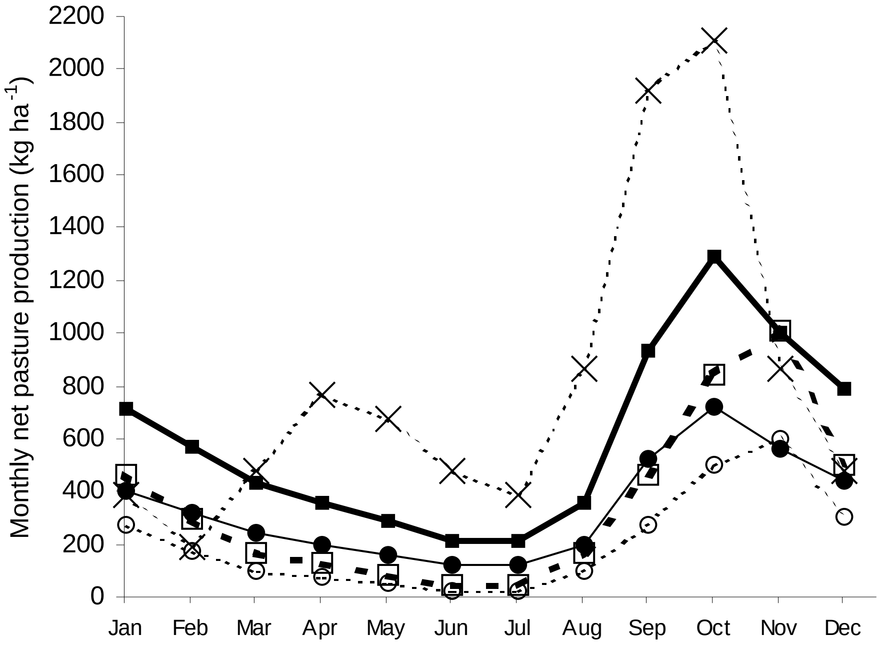


Figure 4.1: Net pasture production predicted by Vere *et al.* (2001) for the central and southern tablelands of NSW. Values shown are for the pasture, soil and rainfall categories that correspond to the study sites; —■— High quality native pasture (HQ) on granitic soil with high (>700 mm) rainfall (GHR); — □ — Low quality native pasture (LQ) on GHR; — ● — LQ on acidic soil of sedimentary origin with medium (550 – 700 mm) rainfall (ASMR); - - ○ - - LQ on ASMR; - - X - - introduced perennial grasses on GHR, patchily represented on study sites. Prepared from data given by Vere *et al.* (2001, Table 1).

The search for a simple model to represent pasture growth on my sites, and the evaluation of Robertson's (1987a) model are the same process, that of evaluating a range of alternative models against the data. Table 4.1 lists five models for evaluation. The ideas that generated them focus on growth being either density dependent, a function of weather, or some combination of density dependence and weather, as follows.

4.1.1 Density dependence, and alternatives

Pasture growth has often been considered density dependent, resulting in approximately logistic growth (Caughley 1976a, 1981a, 1987; Crawley 1983; Barlow 1987; Roughgarden 1997; Owen Smith 2002a). The Gompertz equation, which approaches the upper limit more gradually than the logistic, is preferred for some plant growth data, or the Chanter equation, which incorporates both Gompertz and logistic, (Thornley and Johnson 1990, pp 74 – 88). The relationship of ΔV (growth increment) and V (herbage mass) is parabolic with the logistic equation but positively skewed or undercompensating with the Gompertz. (The same pattern is produced by the theta logistic equation when θ is less than one.) Other authors have preferred equations in which the pattern is negatively skewed, or overcompensating, the relationship produced when θ is greater than 1 (Maynard-Smith and Slatkin 1973). However Crawley (1983, p. 108) indicates overcompensation to be unlikely in continuously grazed swards, as applies to my study sites. In order to restrict the number of models to be evaluated, of those mentioned I tested only the logistic. Historically, an alternative to density dependent growth is density-independent growth. The latter was explored by Andrewartha and Birch (1954) using weather variables as determinants of population growth. Miller's (1979) empirical growth model for heather shoots is an example. A density independent model is included among those I evaluated (Table 4.1).

4.1.2 Climate

The long-term mean values for rainfall and temperature on the study sites and at regional weather stations, were presented in Chapter 3. Aspects relevant to this chapter include: (a) the much lower CV of rainfall between years compared with the Kinchega site of Robertson (1987a) and Caughley (1987), i.e. 27% in the region of the study sites compared with 45% near Kinchega (Caughley 1987); and (b) the substantial differences between the three study sites in the amounts of annual rainfall they receive, their mean temperatures, and number of frost days (Table 3.1) resulting in a shorter growing season on average at Gudgenby, and warmer, dryer conditions at Googong.

4.1.3 Temperature

It is a reasonable expectation that to transfer a pasture growth model from semi-arid regions to seasonal temperate ones, may require the addition of parameter(s) for temperature. The effect of temperature on pasture growth is dome shaped, with gradual reduction in growth rates as temperatures increase or decrease outside an optimum range (Fitzpatrick and Nix 1970, Moore *et al*. 1997). Miller (1979) reported a linear effect of temperature for production of heather shoots in Scotland, possibly reflecting the influence of a cold climate in which temperature falls below, but rarely exceeds, the optimum.

4.1.4 Rainfall and interaction of temperature and rainfall

The relationship of pasture growth to rainfall may be linear both in semi-arid areas (e.g. Robertson 1987a) and temperate ones (e.g. Miller 1979; Clutton-Brock and Albon 1989, their Fig 4.2).

There may be an interaction between rainfall and temperature. This represents the common observation in temperate areas that high soil moisture levels in winter often result in little growth, but in summer they result in higher growth.

Table 4.1: Candidate pasture growth models for evaluation, and reason chosen. GV = initial green herbage mass (kg ha^{-1}); R = rainfall (mm); T = temperature (^{o}C); RT = interaction between rain and temperature (i.e. R x T); b_1, b_2, etc = parameters to be estimated. The response variable (ΔGV) is the change in green herbage mass over 60 days.

Number and Name of model Mathematical representation	Why model was identified for evaluation
(1) Logistic on GV (no effect of weather) $\Delta GV = b_1 + b_2GV + b_3GV^2$	Density dependent growth. Exploratory use, for comparison with 2 and 3.
(2) Weather only (no effect of herbage mass) $\Delta GV = b_1 + b_2R + b_3T + b_4RT$	Density independent growth. Miller (1979) found production of heather shoots to be a function of R and T, with no effect of herbage mass. This model tests whether that may also apply to heavily grazed pasture where a large residual tissue mass (underground) responds to favourable weather by producing shoots.
(3) Logistic + rain $\Delta GV = b_1 + b_2GV + b_3GV^2 + b_4R$	The model of Robertson (1987a) within Caughley's (1987) interactive kangaroo model, also used for temperate sites by Choquenot *et al.* (1998).
(4) Logistic + R + RT $\Delta GV = b_1 + b_2GV + b_3GV^2 + b_4R + b_5RT$	Robertson's (1987a) model plus an interaction of temperature with rainfall.
(5) Logistic + R + T + RT $\Delta GV = b_1 + b_2GV + b_3GV^2 + b_4R + b_5T + b_6RT$	Robertson's (1987a) model plus temperature and an interaction of temperature with rainfall.

4.1.5 Generation of models for testing

Restraint is required in combining the variables into candidate models to be confronted with the 29 values from this study for the vegetation growth increment, ΔV. In particular an overfitted model with an excessive number of parameters may provide a statistically superior fit to a particular dataset at the cost of generality (Burnham and Anderson 2002; Ginzburg and Jensen 2004). This project is about testing whether simple empirical models can be applied (Chapter 1), not about developing a mechanistic explanation of the process, therefore the selected models (Table 4.1) have three to six parameters although reasons could readily be found for larger numbers of parameters in more complex models.

4.2 Methods

4.2.1 Weather record

I installed automatic weather stations at Tidbinbilla (Measurement Engineering Australia, Standard Weather Station) and Gudgenby (Environdata Mk II). Daily weather data from an automatic station at Googong was supplied by Ecowise Environmental. Parameters were recorded at 30 minute intervals and combined to give daily totals. Daily values were summed (rainfall) or averaged (temperature) to provide 1, 2, 3, 6, 12, and 24-month values used as the explanatory variables in regressions of pasture growth (see below). Long-term weather records were purchased from the Bureau of Meteorology.

Gaps occurred in all three weather records due to lightning strikes, a bushfire, a mechanical breakdown, and unknown factors at Googong. Weather data are also required for a period before the pasture measurements began because pasture growth may be responding to prior conditions such as rainfall accumulated over 6 months or longer. However for logistical reasons I had got weather stations working and installed at about the same time as I commenced pasture measurements. To fill all these gaps, data were purchased from the Silo Patched Point service (NRM 1998, Jeffrey *et al*. 2001) for Tidbinbilla and Gudgenby, and from the Silo Data Drill service (NRM 1998, Jeffrey *et al*. 2001) for Googong.

4.2.2 Pasture sampling design

Appendix 2 provides details of the pasture sampling design. It explains why I sampled bimonthly. It details how I decided in advance the number of pasture sampling locations. It explains the stratified –random design used to distribute sampling locations across the sites, and it gives the formula used to allocate sampling effort between strata.

4.2.3 Exclosure cages

Near each pasture sampling marker (Appendix 2) I pegged a 0.3 m^2 grazing exclosure cylinder (or 'cage') made from plastic trellis mesh. This enabled the pasture to be assessed in the manner of Robertson (1987a, 1987b, 1988) and other grazing studies (e.g. Cayley and Bird 1996; Choquenot *et al.* 1998; t'Mannetje and Jones 2000). On each sampling visit to each site, the pasture outside the cage was assessed non-destructively within a 0.25 m^2 circular quadrat positioned on a randomly chosen spot within a few metres of the post. The exclosure cage was then moved onto that place and the pasture was measured where the cage had been removed. The difference between the means of measurements inside and outside the cages on any occasion gave the pasture offtake by medium and large herbivores over the time since the previous measurement; and the difference between times gave pasture growth or dieback.

Thus growth was obtained from repeated measures in the same quadrats (at the time of caging, then two months later). Growth is one of the most difficult pasture parameters to measure (t'Mannetje 2000) and the reduction in error due to repeated (non-destructive) measures of the same sites improves the accuracy of its estimation. The non-destructive measuring techniques are described below.

In common with many other grazing studies, I did not set up an experiment to quantify the effect of the cage itself on the pasture growth estimates. In view of the comments I make below in Section 4.4.6, in future studies of the type, pasture growth estimates should preferably be adjusted for this influence.

4.2.4 Non-destructive estimation of herbage mass

Claims by researchers to have measured pasture biomass usually refer only to what agronomists call 'yield' (material clipped for weighing) also known as 'herbage mass', the term used hereafter. Herbage mass was estimated using the comparative yield method (Haydock and Shaw 1975; Friedel and Bastin 1988; Waite 1994; Cayley and Bird 1996; t'Mannetje and Jones 2000) and disc meter method (Bransby *et al.* 1977; Earle and McGowan 1979; Michell 1982; Cayley and Bird 1996; Li *et al.* 1998; t'Mannetje and Jones 2000). Both were calibrated on each sampling occasion at each site, against plots in which the pasture was cut, dried for 24 hrs at 80° C, and weighed. The disc meter is more rapid and appears more objective than comparative yield but also seems potentially to suffer from differences in the resistance to compression of different species and different growth stages of plants. I considered it possible that the disc meter method may have a relative advantage over comparative yield for the estimation of pasture growth, which involves comparison of successive measurements at the same point, while comparative yield may be superior for the measurement of herbivore offtake which involve comparison of measures on different sets of quadrats. To maximise the value of the disc meter for the estimation of pasture growth or dieback, a small steel peg was left inside the exclosure cage marking where the point of the disc meter had been placed, so the measurement after eight weeks protection from grazing was in the same spot. Li *et al.* (1998) stated that disc meters outperform 'visual estimates' (presumably including the comparative yield method) especially on grazed pasture. Disc meters are also referred to in the literature as 'rising plate', 'falling plate', 'weighted disc', 'drop disc' and 'pasture' meters (t'Mannetje 2000). They are considered convenient and useful on shorter types of pastures although less accurate on stemmy material (t'Mannetje 2000). A difficulty noted on some sampling visits was that a higher than usual proportion of disc meter readings were inconsistent or changeable (e.g. could decline suddenly) due to the prevalence of stemmy material in the pasture, such as flower-stalks. This applied mainly to the measurement of ungrazed pasture, especially in March both years at Googong, in March 2002 at Tidbinbilla and in July 2003 at Tidbinbilla and Gudgenby.

To convert the comparative yield ratings (0 – 5 scale) to herbage mass in kg ha^{-1}, linear regressions through the origin were applied to all 33 sets of data from clipped plots. Likewise to convert the arbitrary disc meter readings, except a power function was used in place of a straight line for five of the 33 sets of clipped plots. The coefficient of determination (R^2) for the comparative yield regressions ranged from 0.88 to 0.97 with a mean of 0.93. The coefficient of determination (R^2) for the disc meter regressions ranged from 0.70 to 0.94 with a mean of 0.86.

The routine bimonthly estimation of herbage mass was interrupted in January 2003. When work had been completed at Googong and Gudgenby and was commencing at Tidbinbilla, the pasture and the plastic exclosure cages at Tidbinbilla were burnt (Section 3.5, Figures 4.10 and 4.12). The cages and the weather station were speedily removed from the Gudgenby site, in the expectation that it would also be burnt, but it survived. Both sites received new or replaced exclosure cages in February 2003. A normal pasture assessment was completed in March 2003 at Googong and Gudgenby but some of the pasture assessment locations at Tidbinbilla were not visited in March, so this was resumed fully in May 2003. Other extraneous factors also impinged on the pastures during the study. The Tidbinbilla site was heavily grazed by cattle in the autumn and early winter following the fire, and herbage mass was reduced to the lowest level experienced during the study period. An unusually intense storm in March 2003 scoured the pasture at Googong, removing dead plant material and reducing ground cover (Section 3.5).

4.2.5 Estimating the proportion of living pasture

Previous similar studies (Caughley *et al.* 1987; Maas 1997; Choquenot 1998; Choquenot *et al.* 1998) have estimated only total herbage mass ('biomass'), presumably because of the extra time and difficulty required to separately estimate the proportion of green (living) plant material. According to t'Mannetje (2000), knowing the total dry matter yield of pasture is often of little use unless it is further qualified, particularly in regard to the proportion of green material present, due to the importance of this for animal production (Cowan and O'Grady 1976; t'Mannetje and Ebersohn 1980; t'Mannetje 2000). Temperate pastures vary seasonally and between sites in the relative proportions of green material and dead material they contain, and to facilitate valid comparison between seasons and sites, in agricultural practice it is usual to disregard the dead material and report only the availability of the green component. Therefore in this study the proportion of living material in each plot was estimated visually on a ten point scale, based on plots that were cut and sorted into living and dead components before drying and weighing.

4.2.6 Ground cover

Ground cover of plant material was estimated visually on a ten point scale both before and after caging. Murphy and Lodge (2002) showed that the visual estimation method produces accurate and consistent results even when used by relatively inexperienced observers. Helm and Mead (2004) reported that variation between observers was the largest source of variability with this and four other methods of estimating cover of each species in a forest understory. All cover estimates in this study (approx 9,000) were made by one person. To maintain consistency over time, reference diagrams were used corresponding to the cutpoints between the categories on the 10-point scale.

The main application intended for the ground-cover measurement was to assess potential for erosion. Therefore not only vascular plants but also cryptograms, fungi and algae were included as cover, although they are not food for eastern grey kangaroos and did not contribute significantly to clipped herbage mass.

4.2.7 Data analysis

The main analysis was to develop a pasture growth model. It occurred in three main stages. Following data transformations, multiple linear regression was used to select a set of candidate explanatory variables for inclusion in the five alternative models of pasture growth listed in Table 4.1. In the third and final step, non-linear least-squares regression (Statistica 6.1, StatSoft Inc 2004) was used to fit these five models to the increments of pasture growth (ΔGV, defined below), with selection between models based on minimum value of the Akaike Information Criterion corrected for small samples (AICc). The AICc was calculated from the residual sum of squares using the method given by Burnham and Anderson (2002, p. 63). For convenience, the result for each model is generally expressed as ΔAICc, which is the difference between the AICc for that model and the AICc for the best model. By definition the best model has ΔAICc = 0.0. Models with ΔAICc less than 2.0 are considered by Burnham and Anderson (2002) to have reasonable support from the data.

The response variables in analyses were the absolute change in total herbage mass (ΔV) and in green herbage mass (ΔGV). Both variables were in units of kg ha^{-1} between pasture measurements, and were standardised for a 60-day interval ending at the median date of each pasture measurement session at each site.

Potential explanatory variables prepared for analysis of pasture growth included: herbage mass (V), the square of herbage mass (V^2), green herbage mass (GV) and the square of green herbage mass (GV^2), site, day of the year, and day of the year minus 173 (to correspond to southern hemisphere seasonal patterns, following Moore *et al*. 1997). The following weather parameters were also prepared: rainfall accumulated for the two, three, six, 12, and 24 ‘months’ previous to the median pasture assessment dates, where ‘month’ means the 30 day period prior to the sampling date, mean daytime temperature (calculated by the formula given in Moore *et al*. 1997) for the previous two, three, and six months, a thermal growth index for the same periods, and terms for interactions between rainfall and temperature over two and three months. See below for explanation of the thermal index and of the transformation applied to rainfall data.

The thermal index appears similar to Figure 1.6 of Fitpatrick and Nix (1970) but was calculated in a similar way to the temperature limiting factor of Moore *et al*. (1997 Eqn 28). Moore *et al*. (1997) use a daily time step and lagged temperature, but the lag was unnecessary in view of the longer time intervals used in my study. The parameters given by Moore *et al*. (1997) for *Phalaris aquatica* were replaced with the ones given in the caption of Figure 4.2 for the mixed-species, C4-dominated pastures on my sites. The optimum temperature and lower limit to pasture growth set by the resulting index (Figure 4.2) are the same as or close to those given for temperate grasses by Fitzpatrick and Nix (1970) but above 30°C my index provides faster growth than theirs. This made no difference to the results because such high temperatures were not recorded during my study.

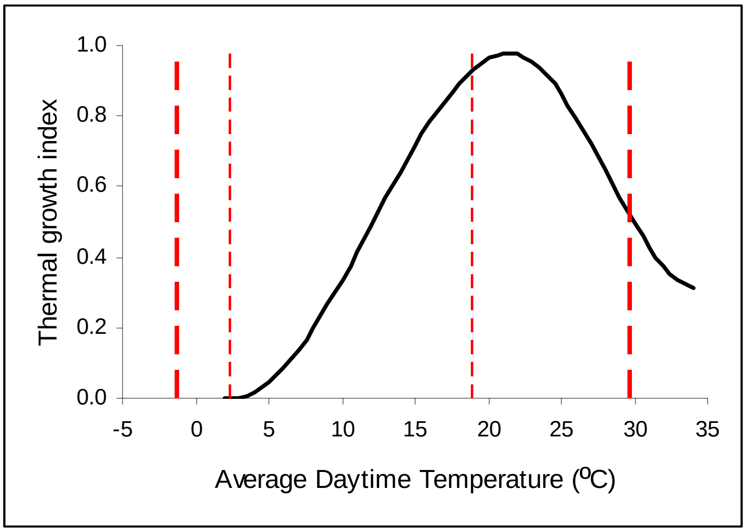


Figure 4.2: Thermal growth index calculated for this study based on Moore *et al*. (1997, Eqn 28). Optimum temperature 22°C, lower temperature for 5% of maximum growth 5.5°C; lower temperature for 95% of maximum growth 21°C; upper temperature for 95% of maximum growth 23°C. The outer pair of dashed vertical lines mark the highest and lowest mean daytime temperatures recorded in the study, and the inner pair mark the highest and lowest monthly averages of mean daytime temperatures.

In exploratory regressions of bimonthly incremental change in herbage mass (ΔV) and green herbage mass (ΔGV), each thermal index performed only marginally better, or worse, than the temperature counterpart from which it had been derived (Table 4.2). Therefore, in the interests of simplicity, temperature was used for model fitting, rather than the thermal index.

Table 4.2: Results from individual regressions of pasture growth against thermal indexes compared with results from individual regressions of pasture growth against average daytime temperature over the same period. ADT = average daytime temperature; TI = thermal index. None are significant.

	R^2	SE	t	p
2 month ADT	0.059	49	1.28	0.211
2 month TI	0.060	828	1.29	0.209
3 month ADT	0.061	53	1.30	0.206
3 month TI	0.063	893	1.32	0.198
6 month ADT	0.004	65	0.31	0.762
6 month TI	0.002	1139	0.25	0.804

Rainfall distribution typically has a positive skew and can often be transformed appropriately as its cube root, e.g. Pech and Hood (1998). That this generalisation applies to rainfall in the region of the study sites is demonstrated by a large local rainfall dataset collected at Queanbeyan for the Bureau of Meteorology. The probability that the transformed rainfall did not differ from normal was greater than 0.257 by Kolmogorov-Smirnov test (Figure 4.3). As I intended to use rainfall in non-linear regression models and to estimate AICc from the residual sum of squares, a cube root transformation was applied to the rainfall records from the three study sites.

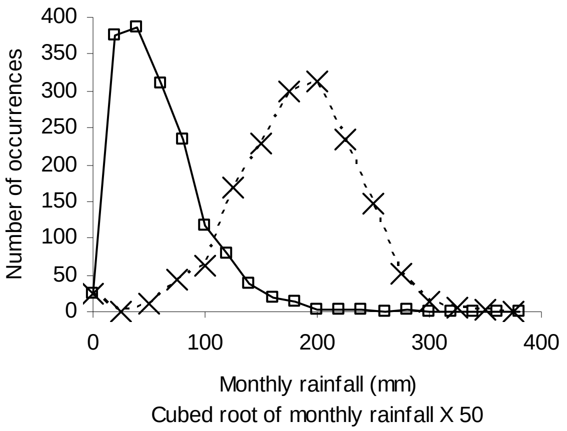


Figure 4.3: Effect of transforming rainfall data —□— = Frequency of monthly rainfall at Queanbeyan (1870 – 2004); - - X - - = frequency of cubed root of monthly rainfall X 50 (n=1607).

4.3 Results

4.3.1 Weather

Monthly rainfall, and mean daytime temperature on the study sites from January 2000 to July 2003 (prior to and including the study period) are presented in Figure 4.4, together with long-term monthly averages for comparison. As demonstrated in Table 4.3 and illustrated by Figure 4.4, rainfall during the study was below average on all sites.

Intense rainfall on all sites in February 2002 boosted the total rainfall recorded during the study period, and resulted in a strong spurt of pasture growth, the only one of its magnitude recorded, but the proportional influence of the rainfall on pasture growth may have been diminished due to run-off. The damaging storm at Googong in March 2003 (Section 3.5) is not clearly evident in Figure 4.4 because the main storm passed south of my rain gauge, and because it was the intensity as well as the amount of rain which determined the damage. The damage caused and the height of flood debris indicates an additional amount of greater than 50 mm may have fallen on part of the Googong site, however most of the unmeasured rain would have run off quickly, and had little influence on pasture growth.

Table 4.3: Rainfall (mm) recorded on each site during the two year study period compared with the long-term mean and lower 95% confidence limit.

	Googong	Gudgenby	Tidbinbilla
2-year rainfall in study period to July 2003 (mm)	837	1235	1281
Lower 95% conf. value of mean 2-year rainfall to July from all previous records	1188	1469	1814
Mean 2-year rainfall to July from all previous records	1253	1569	1922
Number of 2-year records	10	42	35

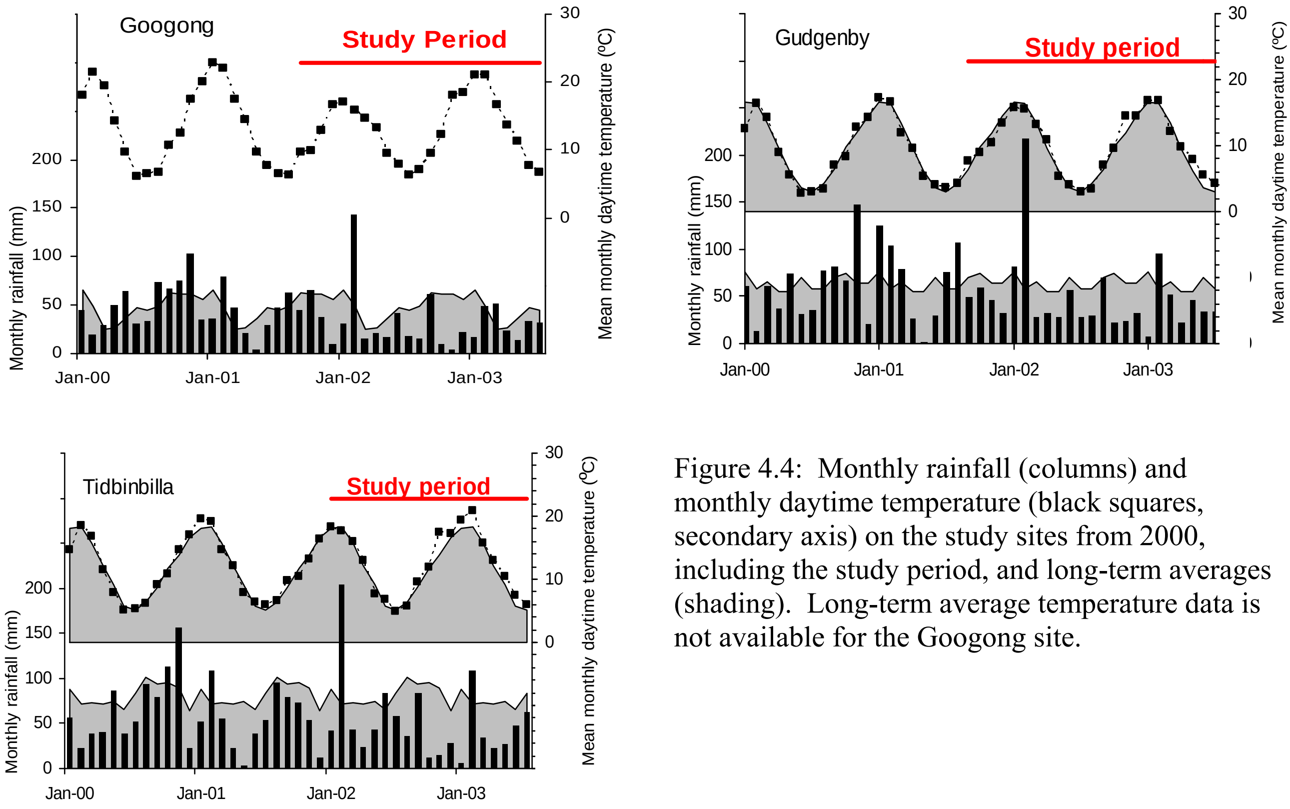


Figure 4.4: Monthly rainfall (columns) and monthly daytime temperature (black squares, secondary axis) on the study sites from 2000, including the study period, and long-term averages (shading). Long-term average temperature data is not available for the Googong site.

4.3.2 Comparison of two methods of measuring herbage mass

The two methods of estimating herbage mass, the disc meter and comparative yield, resulted in similar estimates (r = 0.89; df = 65; p. <0.001) of green herbage mass (Figure 4.5). The disc meter was more precise; with mean CV over all surveys and sites of 36% (range 4 – 152) as compared to 113% (range 44 – 321) for the comparative yield method. The disc meter tended to produce higher estimates of herbage mass than the comparative yield method, both in the ungrazed pasture with more flowering stems (Equation 4.1; SE = 334; F = 111; df = 1, 32; p < 0.001; $R^2 = 0.776$), and the grazed pasture (Equation 4.2; SE = 254; F = 101; df = 1, 31; p < 0.001; $R^2 = 0.765$). The coefficients of equations 4.1 and 4.2 are not significantly different (t = 0.71; df = 1, 31; p = 0.6) therefore the two sets of data were combined, resulting in Equation 4.3 (SE = 294; F = 241; df = 1, 65; p<0.001; $R^2 = 0.788$) (Figure 4.6). This highly significant relationship implies that with one or both methods there must have been differences in the measurement process between the reference quadrats (used to calibrate both methods) and the survey quadrats. It is possible that relatively higher estimates may have been obtained with the disc meter because the extra attention given the reference plots when setting them up, and repeated visits to them, may have resulted in the crushing of stemmy material to a greater extent than in survey quadrats.

$$CY = 0.792\ DM - 7 \quad \text{(for ungrazed pasture)} \qquad \text{Eqn 4.1}$$

$$CY = 0.852\ DM - 26 \quad \text{(for grazed pasture)} \qquad \text{Eqn 4.2}$$

$$CY = 0.803\ DM - 4 \quad \text{(for both grazed and ungrazed pasture)} \qquad \text{Eqn 4.3}$$

where CY = total herbage mass (kg ha^{-1}) by comparative yield; DM = total herbage mass (kg ha^{-1}) by disc meter. The slope coefficient of Equation 4.3 is significant (t test; t = 15.54, df = 65, p<0.001) but not the intercept (t test; t = 0.053, df = 65, p>0.5).

In view of these results, the comparative yield estimates are used throughout.

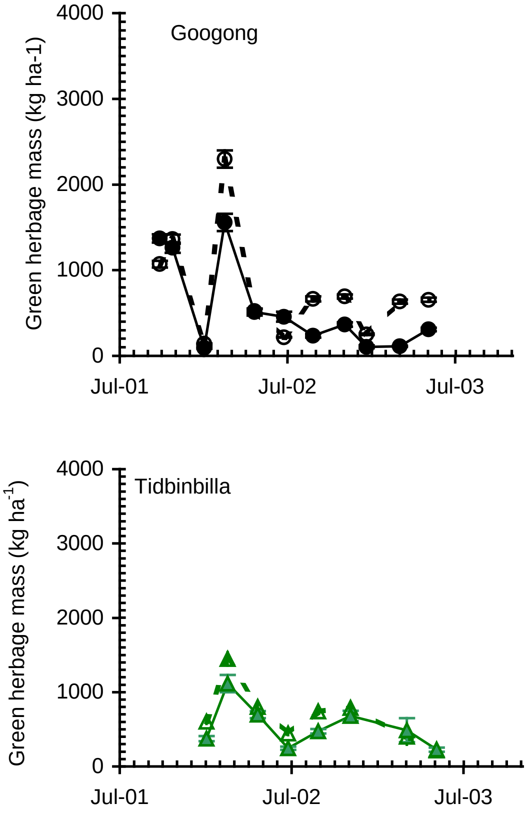


Figure 4.5: Results from two different methods of estimating green herbage mass GV (kg ha^{-1} ± SE); dashed line and hollow symbols = disc meter; continuous line and solid symbols = comparative yield. Error bars are obscured by symbols in some cases.

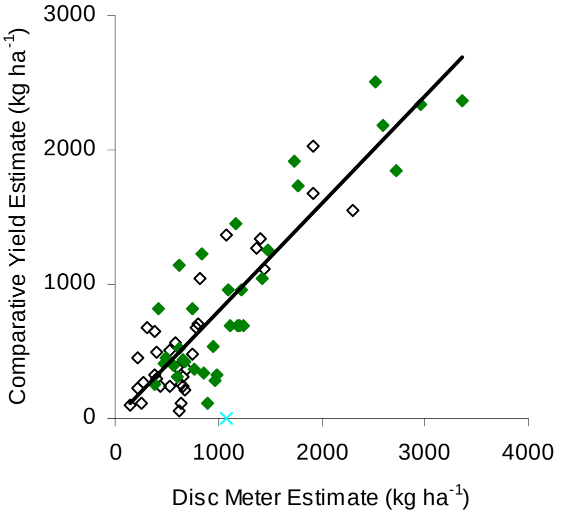


Figure 4.6: The relationship between estimates of green herbage mass GV by comparative yield and by disc meter; ◊ = estimate in grazed pasture; ♦ = estimate in ungrazed pasture. The fitted relationship is Eqn 4.3.

4.3.3 *Herbage mass*

Herbage mass and green herbage mass estimates ranged widely (Figure 4.7) but on average were about an order of magnitude higher than in the Kinchega study.

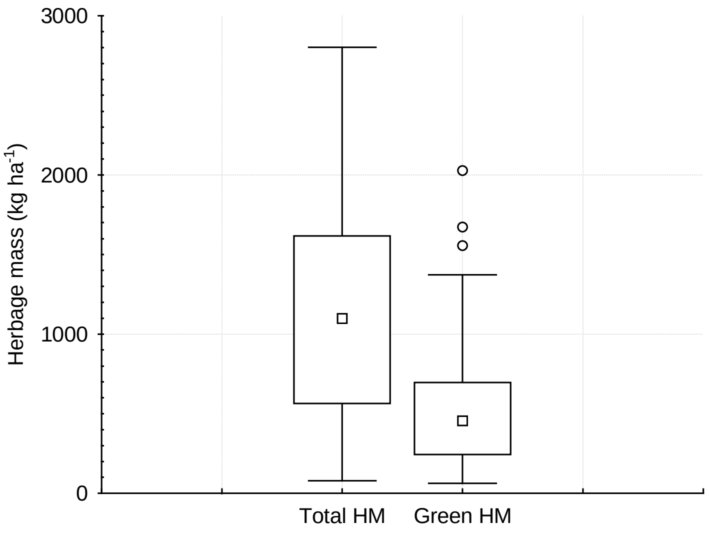


Figure 4.7: Median, interquartile range, and range of total herbage mass (V) and green herbage mass (GV) (kg ha^{-1}) in all surveys on all sites.

As the drought advanced through 2002 and 2003, periods of increase in total herbage mass (V) and green herbage mass (GV) were generally short lived, e.g. in spring (Figures 4.8 and 4.10), and regressions of both total and green herbage mass over time had a negative slope on all sites. The slopes were all significant except for green herbage mass at Tidbinbilla (Table 4.4).

Table 4.4: Parameters, standard errors, F statistics, and p values for linear regressions of total herbage mass (V, kg ha^{-1}) over time, and green herbage mass (GV, kg ha^{-1}) over time.

Site	Slope (± SE)	Intercept (± SE)	F	df	p	R^2
	Total herbage mass (kg ha^{-1})					
Googong	–0.299 (0.061)	623 (69)	23.78	1, 10	<0.001	0.704
Gudgenby	–0.245 (0.027)	695 (44)	79.87	1, 10	<0.001	0.889
Tidbinbilla	–0.289 (0.045)	612 (52)	41.87	1, 7	<0.001	0.857
	Green herbage mass (kg ha^{-1})					
Googong	–0.277 (0.095)	487 (72)	8.47	1, 10	0.016	0.458
Gudgenby	–0.300 (0.059)	582 (57)	26.17	1, 10	<0.001	0.724
Tidbinbilla	–0.36 (0.19)	495 (107)	3.53	1, 7	0.102	0.335

The proportion of green (living) pasture varied widely between surveys, and evidently is liable to change more rapidly than does total herbage mass (Figure 4.8 compared with Figure 4.9). The lowest greenness estimate, at Googong in January 2001, resulted from the sudden death of abundant pasture in hot dry weather. The freshly killed pasture is evident in the illustration on the title page of Chapter 3. The highest greenness estimate was that of the re-growth following the bushfire at Tidbinbilla, measured in March 2003. However the greenness estimates at Tidbinbilla soon declined (Figure 4.9) as forbs and leaves of some grasses began to die in the dry conditions.

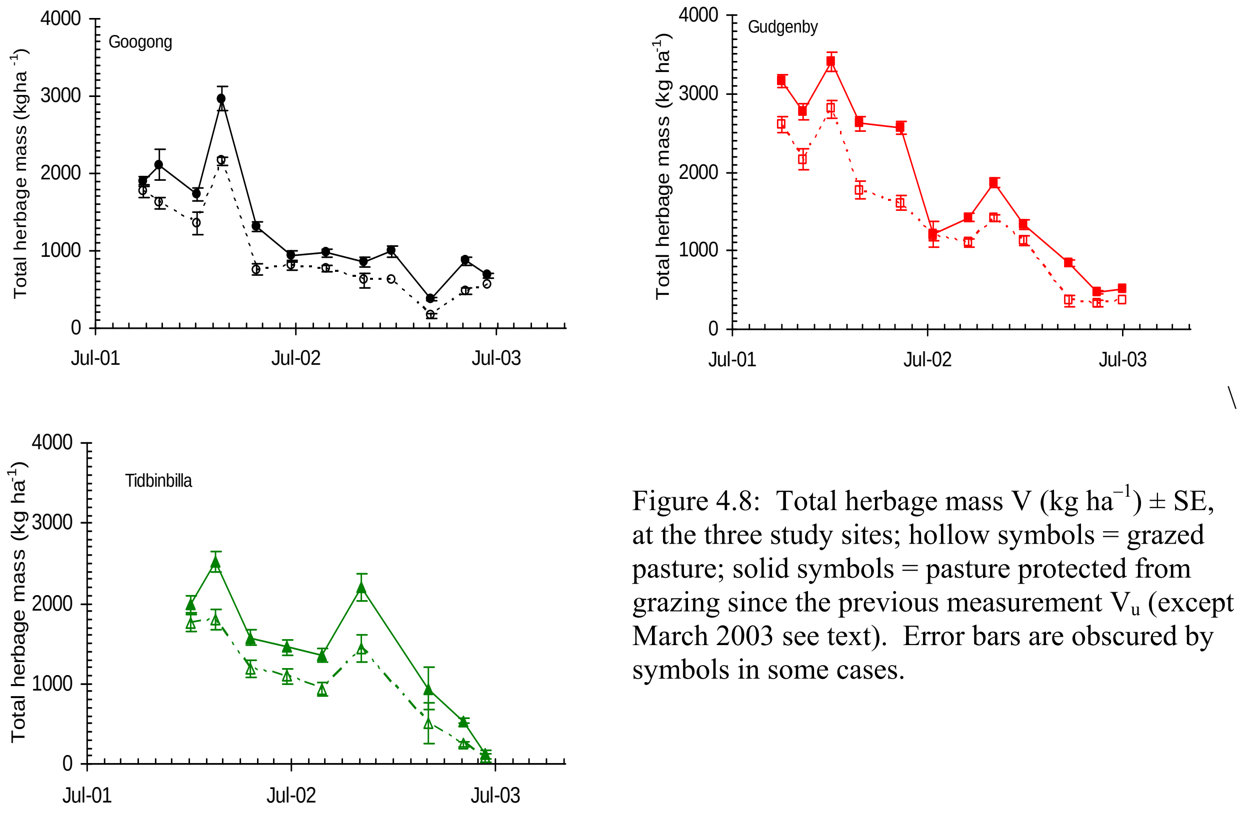


Figure 4.8: Total herbage mass V (kg ha^{-1}) ± SE, at the three study sites; hollow symbols = grazed pasture; solid symbols = pasture protected from grazing since the previous measurement V_u (except March 2003 see text). Error bars are obscured by symbols in some cases.

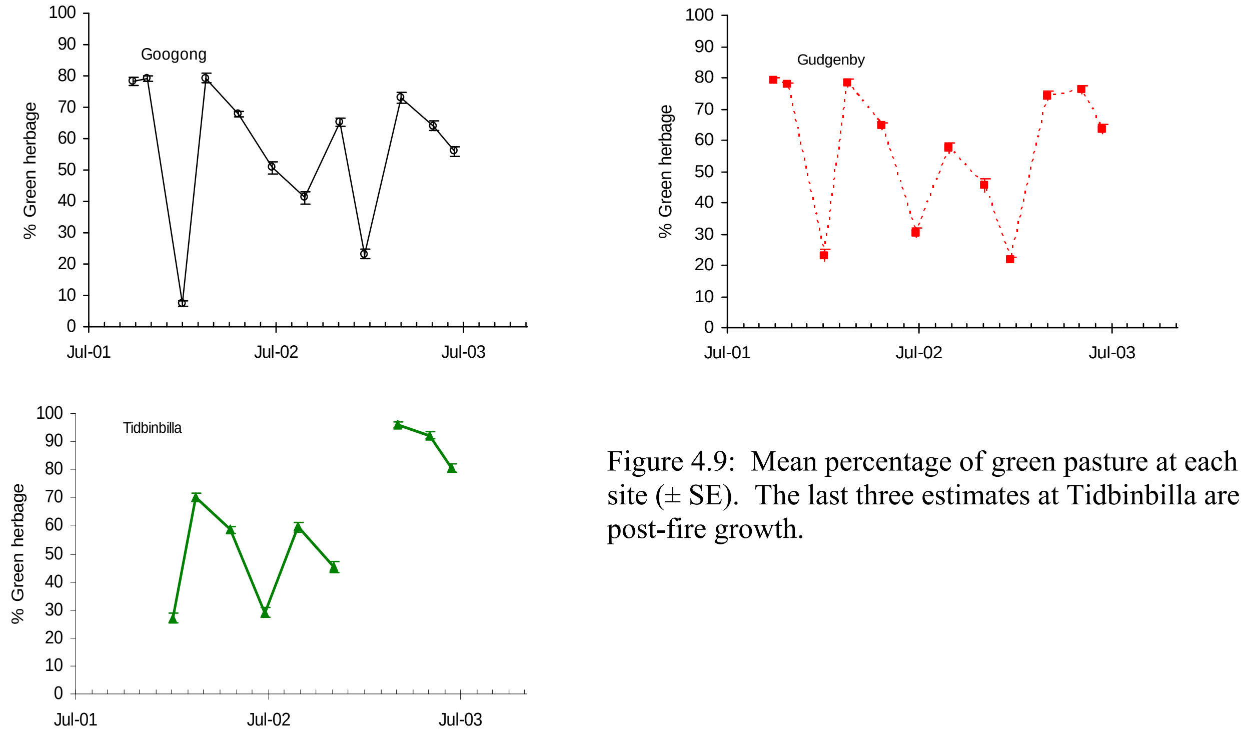


Figure 4.9: Mean percentage of green pasture at each site (± SE). The last three estimates at Tidbinbilla are post-fire growth.

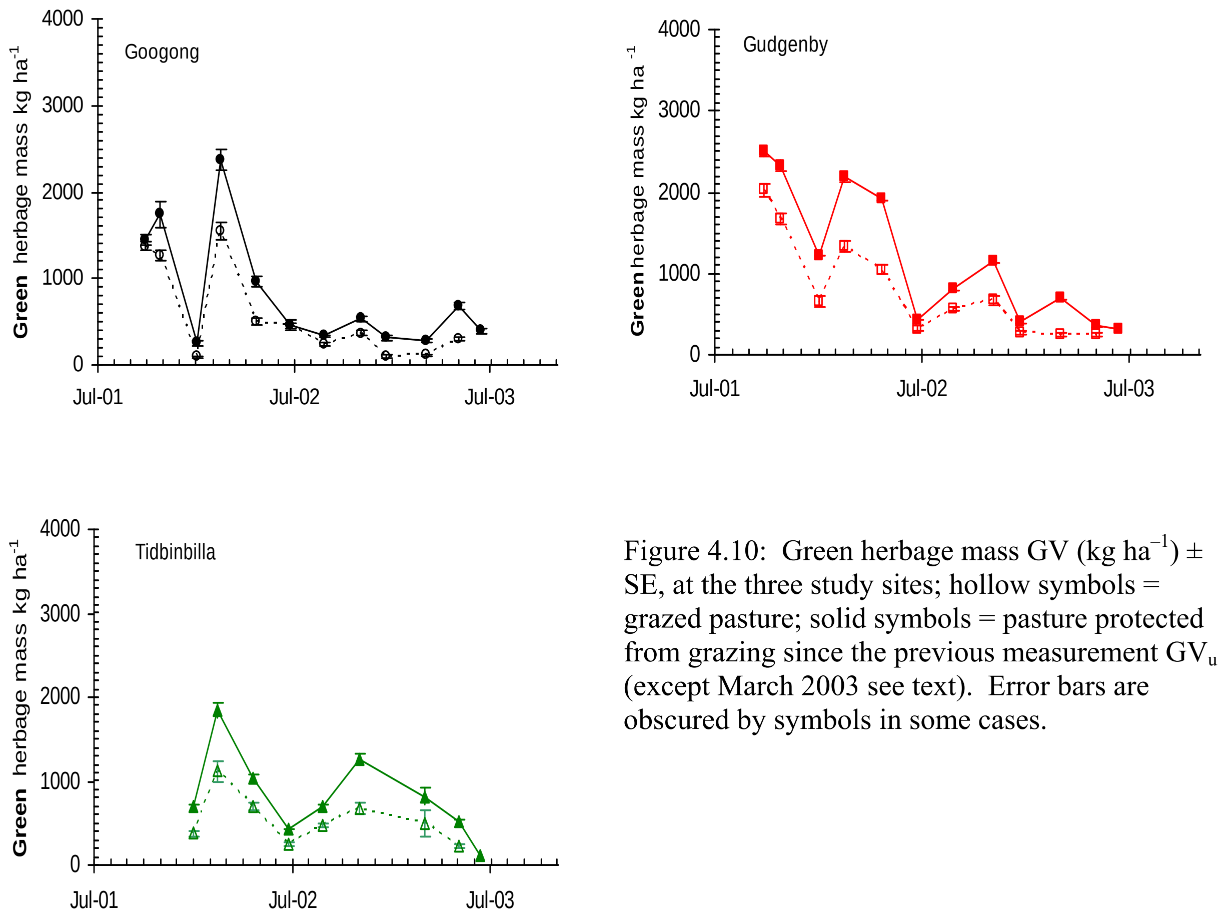


Figure 4.10: Green herbage mass GV (kg ha^{-1}) ± SE, at the three study sites; hollow symbols = grazed pasture; solid symbols = pasture protected from grazing since the previous measurement GV$_u$ (except March 2003 see text). Error bars are obscured by symbols in some cases.

4.3.4 Influence of rainfall on herbage mass

The influence of rainfall is evident from the regressions of herbage mass in the ungrazed plots (V$_u$) over rainfall in the previous 2, 3, 6, 12 and 24 months (Table 4.5, Figure 4.11). The regressions are all significant except for V$_u$ against rain over 2 months. Rainfall over the previous 12 months was most closely associated with total herbage mass (V$_u$, kg ha^{-1} Figure 4.11a), accounting for 45% of the variation. Rainfall alone has no greater explanatory power when green herbage mass (GV$_u$, kg ha^{-1}) is used as the response variable (rather than total herbage mass), 45% of the variation being accounted for by rainfall over 3 months (Figure 4.11b). Linear equations have been used at this point (see non-linear models below), although the effect of rainfall on herbage mass would be expected to become asymptotic at high rainfall.

Table 4.5: Parameters, standard errors, F statistics, and p values for linear regressions of ungrazed total herbage mass (V_u, kg ha^{-1}) and ungrazed green herbage mass (GV_u, kg ha^{-1}) over the cubed root of rainfall accumulated over preceding time periods from 2 to 24 months.

Period of rainfall accumulation (mths)	Slope (± SE)	Intercept (± SE)	F	df	p	R^2
	Total herbage mass (V_u, kg ha^{-1})					
2	324 (161)	115 (717)	4.06	1,31	0.05265	0.12
3	585 (190)	–1385 (956)	9.50	1,31	0.00428	0.23
6	689 (180)	–2913 (1170)	14.59	1,31	0.00060	0.32
12	766 (151)	–4831 (1263)	25.60	1,31	0.00002	0.45
24	666 (178)	–5716 (1941)	14.00	1,31	0.00075	0.31
	Green herbage mass (GV_u, kg ha^{-1})					
2	424 (116)	–897 (515)	13.50	1,31	0.00090	0.30
3	655 (130)	–2307 (655)	25.28	1,31	0.00002	0.45
6	504 (152)	–2294 (986)	10.99	1,31	0.00234	0.26
12	516 (137)	–3335 (1142)	14.23	1,31	0.00069	0.31
24	469 (152)	–4150 (1653)	9.58	1,31	0.00414	0.24

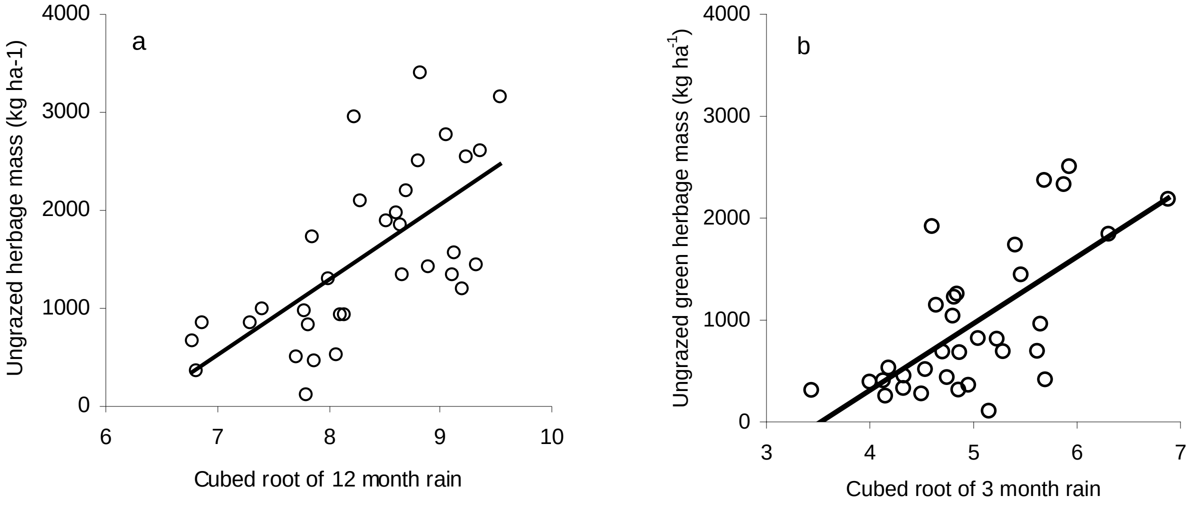


Figure 4.11: Regression of (a) V_u, ungrazed total herbage mass (kg ha^{-1}) and (b) GV_u, ungrazed green herbage mass (kg ha^{-1}) on the cubed root of rainfall (mm) for the 12 months (V_u) and 3 months (GV_u) before each estimate. Data pooled from all sites. Parameters of fitted equations are given in Table 4.5.

4.3.5 Effect of weather on pasture growth and dieback

The increments of growth and dieback in the green herbage mass, i.e. ΔGV, (Figure 4.12) are of generally greater magnitude at Googong, and in the first half of the study period. It is self-evident why increments of plant growth would diminish as a drought sets in. The reduction in the increments of dieback is likely to be simply a consequence of the reduced mass of herbage available. Dead herbage mass also declined through the study (Figure 4.13). Little dead herbage was left in the pasture by 2003, especially at Tidbinbilla where the pasture comprised mainly regrowth following the bushfire in January 2003.

The pasture dies in response to both hot dry periods, and frost periods. For example the difference between total herbage mass and green herbage mass at Googong in January 2002 (Figures 4.8 and 4.10) reflects the death of an abundant pasture due to the former, and the difference between the figures for Tidbinbilla in July 2002 probably reflects the latter.

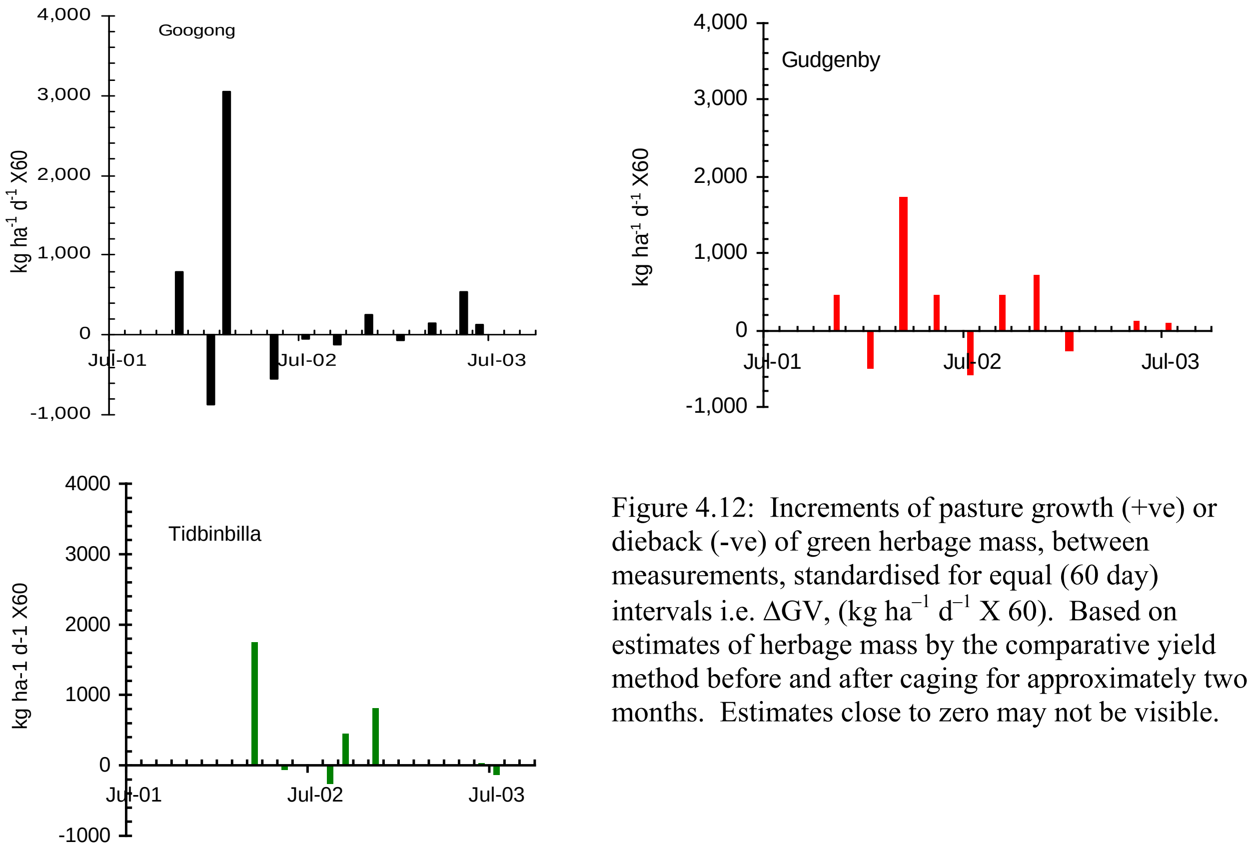


Figure 4.12: Increments of pasture growth (+ve) or dieback (-ve) of green herbage mass, between measurements, standardised for equal (60 day) intervals i.e. ΔGV, (kg ha^{-1} d^{-1} X 60). Based on estimates of herbage mass by the comparative yield method before and after caging for approximately two months. Estimates close to zero may not be visible.

The bimonthly increments of growth (and dieback) were correlated between sites (Table 4.6) but they did not correlate with the values illustrated in Figure 4.1 for average or typical pasture production patterns on such sites (Table 4.7).

Table 4.6: Correlations between sites of bimonthly increments of pasture growth and dieback.

Sites	Correlation Coeff	t	df	p	R^2
Googong: Gudgenby	0.80	3.81	8	<0.01	0.64
Googong: Tidbinbilla	0.85	3.62	5	<0.01	0.72
Gudgenby: Tidbinbilla	0.93	5.76	5	<0.005	0.87

Table 4.7: Correlations between bimonthly pasture growth increments recorded during the study, and predictions of Vere *et al*. (2001) for the native pastures of the types on the study sites. The abbreviations are from the source document, namely: HQ= high quality native pasture; LQ= low quality native pasture; ASMR= acidic soil on sedimentary geology with medium rainfall (550 – 700 mm); GHR= granitic soil with high rainfall (greater than 700 mm).

Comparison	Correlation Coeff	t	df	p	R^2
Googong: HQ-ASMR	0.15	0.45	9	ns >0.1	0.022
Googong: LQ-ASMR	0.14	0.44	9	ns >0.1	0.021
Gudgenby: HQ GHR	0.19	0.53	8	ns >0.1	0.034
Gudgenby: LQ GHR	0.16	0.44	8	ns >0.1	0.024
Tidbinbilla: HQ GHR	0.54	1.42	5	ns >0.1	0.287
Tidbinbilla: LQ GHR	0.47	1.18	5	ns >0.1	0.219

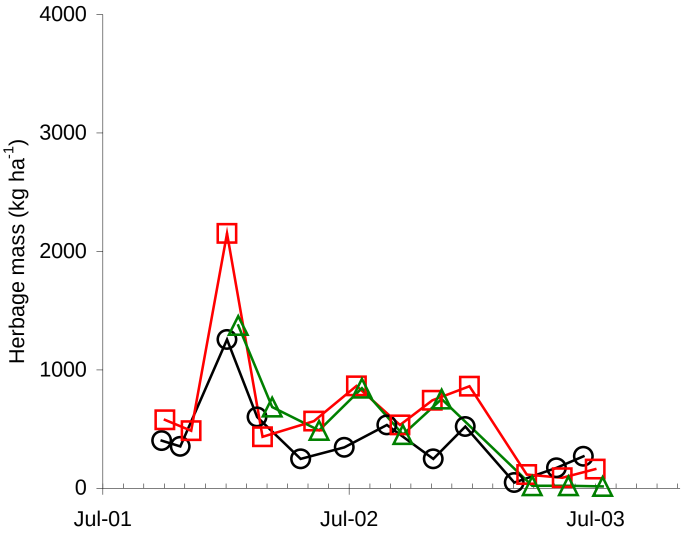


Figure 4.13: Mass of dead herbage (kg ha^{-1}) —○— Googong**;** —□— Gudgenby; — Δ — Tidbinbilla.

Results of linear regressions were presented previously that evaluated the relationship between rainfall and total herbage mass (V) or green herbage mass (GV) (Table 4.5, Figure 4.11). Linear relationships with weather are now reported with the increments of pasture growth ΔGV (kg ha^{-1}), as the response variable. These are the linear regressions of ΔGV (kg ha^{-1}) used as an initial ‘coarse filter’ to cull the candidate variables to be used in the subsequent evaluations of non-linear models of pasture growth. The candidate variables were compared in three groups: (a) rainfall variables (rainfall accumulated for the previous 2, 3, 6, 12, and 24 months, transformed as the cube root); (b) temperature variables plus interactions between rain and temperature; and (c) vegetation variables (V, V^2, GV, GV^2). Two day-of-year-variables were also included in group (a). The results are presented in Table 4.8. Bold type indicates the variables retained for use in the evaluation of candidate pasture growth models. Where more than one related variable was significant (e.g. temperature for the previous 2 months and 3 months), the one having the lowest p-value was retained.

Table 4.8: Regression terms from multiple regression of ΔGV (kg ha^{-1}) in three groups as described in text. D_o_y = day of year; mth=month; R=rainfall; T= temperature; V= total herbage mass (kg ha^{-1}); GV= green herbage mass (kg ha^{-1}).

Group (a) rainfall variables plus day-of-year variables. SE=600; F=4.17; df=7, 20; p=0.006; R^2=0.59.

	Parameter	Std.Err.	t(20)	p-level	Significant?
Intercept	2244	2311	0.97	0.343	ns
Day of year	–0.3	1.4	–0.25	0.809	ns
D_o_y_–173	3.8	2.4	1.61	0.123	ns
$^{3}\surd$ 2mth R	681	221	3.08	**0.006**	sig
$^{3}\surd$ 3mth R	314	287	1.09	0.288	ns
$^{3}\surd$ 6mth R	–284	349	–0.81	0.426	ns
$^{3}\surd$ 12mth R	965	574	1.68	0.108	ns
$^{3}\surd$ 24mth R	–1183	623	–1.90	0.072	ns

Group (b) temperature variables and interactions between rain and temperature. SE=507; F=6.97; df=7, 20; p<0. 001; R^2=0.71.

	Parameter	Std.Err.	t(20)	p-level	Significant?
Intercept	162	882	0.18	0.856	ns
2mth_T	–887	297	–2.99	**0.007**	sig.
3mth_T	907	378	2.40	0.026	sig.
6mth_T	–279	165	–1.69	0.107	ns
12mth_T	202	94	2.15	0.044	sig.
R X T 2mth	35	12	2.84	**0.010**	sig.
R X T 3mth	25	17	1.46	0.161	ns
R X T 6mth	–30	18	–1.69	0.106	ns

Group (c) pasture variables. SE=551; F=8.80; df=4, 23; p<0. 001; R^2=0.60.

	Parameter	Std.Err.	t(23)	p-level	Significant?
Intercept	365	350	1.04	0.308	ns
V	1.57	0.66	2.39	0.025	sig
V^2	–0.00014	0.00022	–0.62	0.540	ns
GV	–3.66	0.92	–3.96	**0.001**	sig
GV^2	0.00104	0.00045	2.32	**0.030**	sig

My Refs: mult reg results.xls which gets results from Revised mult regn IV.stw. Data sheet = Pstr Rspns using CY data fr Pasture Data Bms Calc 4 B reduced.sta in non-linear gwth fcns directory. Statistica Results Workbook= Revised mult regn IV.stw

Table 4.9: Individual linear regression statistics for ΔGV against parameters selected from Tables 4.6 to 4.8. Legend as for source tables.

Parameter	Slope (± SE)	Intercept (± SE)	F	df	p	R^2
$^3\sqrt{}$ 2mth R (mm)	546(136)	–2018 (593)	16.07	1, 26	**0.0005**	0.382
2mth_T (°C)	59 (34)	–364 (418)	2.94	1, 26	0.0983	0.102
R x T 2mth	22.2 (5.1)	–772 (275)	18.90	1, 26	**0.0002**	0.421
GV	–0.4782	626	2.88	1, 26	0.1014	0.100
GV^2	–0.0002	445	1.68	1, 26	0.2059	0.061

Table 4.10: ΔAICc values, regression statistics and parameter values for the models from Table 4.1 fitted to the pasture and weather data. GV = green herbage mass (kg ha^{-1}); R = 2–month rainfall$^{1/3}$ (mm); T = mean day temperature for 2 months (° C) ; RT = interaction R x T; b_1, b_2, etc = parameters. sig=significant (0.05); ns=not significant. The equation with the lowest ΔAICc value is outlined.

Model No and name as per Table 4.1			Parameters					
Equation **Ranked by ΔAICc**	Model Fit		Estimates		SE	t	p-level	Sig?
(1) Logistic (no weather)	AICc	343	b_1	996	380	2.62	0.01	sig.
$\Delta GV = b_1 + b_2GV + b_3GV^2$	ΔAICc	43	b_2	–1.8	1.1	–1.64	0.11	ns.
	F	2.95	b_3	0.00070	0.00056	1.25	0.22	ns.
5	df	3, 25						
	p	0.05						
	R^2	0.15						
(2) Weather only (no effect of herbage)	AICc	319	b_1	1217	2599	0.47	0.64	ns.
	ΔAICc	19	b_2	–348	583	–0.60	0.56	ns.
$\Delta GV = b_1 + b_2R + b_3T + b_4 RT$	F	9.23	b_3	–208	173	–1.20	0.24	ns.
	df	4, 24	b_4	61	38	1.59	0.13	ns.
3	p	0.0001						
	R^2	0.55						
(3) Logistic + R	AICc	321	b_1	–1298	632	–2.05	0.05	ns.
$\Delta GV = b_1 + b_2GV + b_3GV^2 + b_4R$	ΔAICc	22	b_2	–1.66	0.85	–1.96	0.06	ns.
	F	7.85	b_3	0.00067	0.00044	1.53	0.14	ns.
4	df	4, 24	b_4	524	127	4.11	<0.001	sig.
	p	0.0003						
	R^2	0.50						
(4) Logistic + R + RxT	AICc	307	b_1	–1270	577	–2.20	0.04	sig.
$\Delta GV = b_1 + b_2GV + b_3GV^2 + b_4R + b_5RT$	ΔAICc	9	b_2	–1.36	0.79	–1.73	0.10	ns.
	F	8.71	b_3	0.00054	0.00041	1.33	0.20	ns.
2	df	5, 23	b_4	342	138	2.47	0.02	sig.
	p	0.0001	b_5	13.1	5.4	2.42	0.02	sig.
	R^2	0.60						
(5) Logistic + R + T + RxT	AICc	299	b_1	1881	2493	0.75	0.46	ns.
$\Delta GV = b_1 + b_2GV + b_3GV^2 + b_4R + b_5T + b_6RT$	ΔAICc	0	b_2	–1.44	0.78	–1.85	0.08	ns.
	F	7.75	b_3	0.00059	0.00040	1.47	0.15	ns.
	df	6, 22	b_4	–354	553	–0.64	0.53	ns.
1	p	0.0001	b_5	–213	164	–1.30	0.21	ns.
	R^2	0.63	b_6	60	36	1.65	0.11	ns.

The results of non-linear regressions of the candidate models of pasture growth are presented in Table 4.10. The model with lowest ΔAICc is Model 5, the most complex of the models tested, with 6 parameters. The shape of the relationship between ΔGV and GV described by Model 5 is a reversal of the concave-down shape that is typical of logistic and Gompertz growth. In other words the modelled increments of growth were larger at lower herbage mass. The same is true of the other models containing logistic growth. In equations that are logistic on GV, the squared term would normally evaluate to a negative sign but in all cases here it is positive. Thus the name 'logistic' is not appropriate using the parameter values required by this data.

In contrast, Model 2 which has only terms for weather, shows that increments of pasture growth conformed to a predictable pattern for a temperate site in regard to the rainfall and temperature parameters (Figure 4.14). Little growth occurred in dry conditions irrespective of temperature, and at low temperature, growth was not strongly increased by additional rain. But when there was sufficient warmth, pasture growth responded strongly to additional rain. When less than 36mm of rain fell over the two months, the pasture died back. There is no indication from Model 2 of the descending arm of the thermal index illustrated in Figure 4.4,

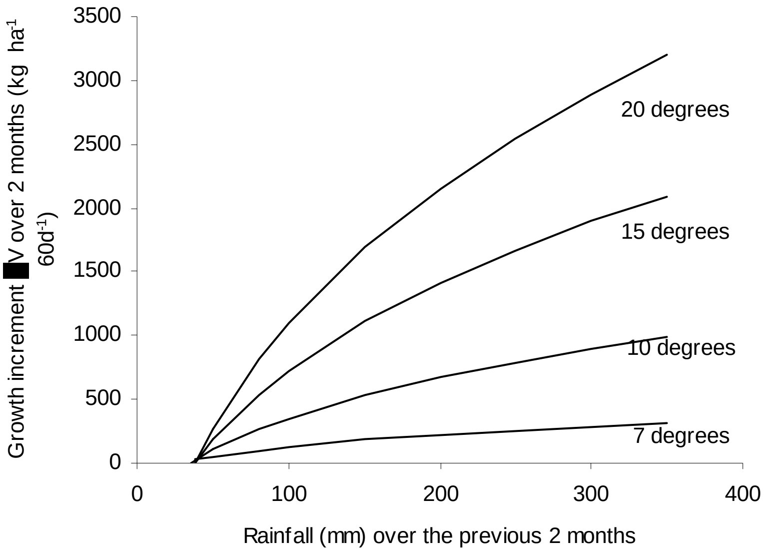


Figure 4.14: Model 2 of Table 4.10. Increments of pasture growth over two months (ΔV, kg ha^{-1} $60d^{-1}$) as a function of rainfall over the preceding two months, and average day temperature over the same period.

that is to say conditions recorded in this study were on most occasions not hot enough for the pasture to die back substantially. (The death of pasture at Googong in January 2002, referred to above, was an exception.)

As evident in Figure 4.12, during this study only three data points were recorded representing relatively high growth. They were all recorded in autumn 2002, following 2-month rainfalls which were close to the long-term means for the sites. Temperature at the time was also conducive to growth. Missing from the data are the high values of ΔV expected from temperate sites, e.g. for spring growth, as modelled by Vere *et al*. (2001) (Figure 4.1).

4.3.6 Herbivore offtake

In Figure 4.10 the magnitude of herbivore offtake is apparent as the vertical displacement between the lines for grazed and ungrazed green herbage mass. Daily offtake was generally greater at higher herbage mass (Equation 4.4, Figure 4.15).

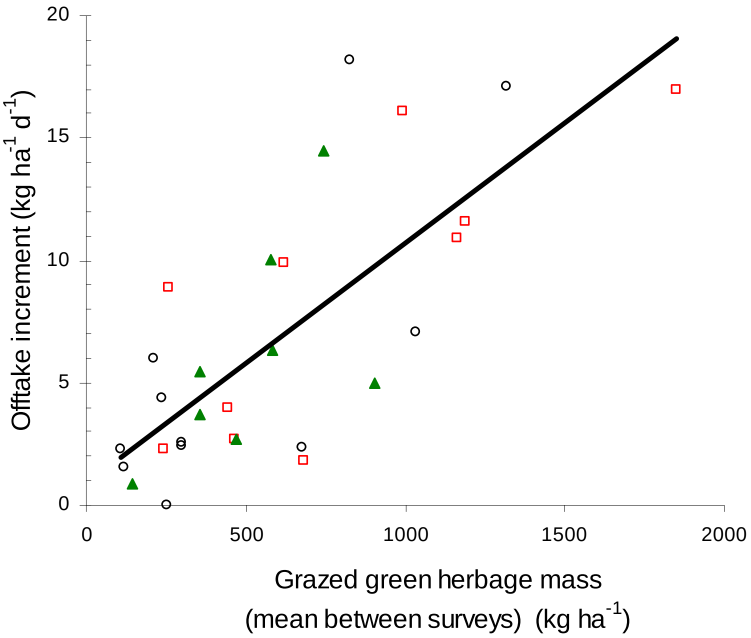


Figure 4.15: Daily herbivore offtake (the mean difference in green herbage mass between inside and outside the exclosure cages, divided by the number of days since the cage was repositioned, kg ha^{-1} d^{-1}) as a function of availability of green herbage (expressed as mean green herbage mass between surveys kg ha^{-1}). ○ Googong; □ Gudgenby; ▲ Tidbinbilla. Data pooled across sites. The fitted line is Equation 4.4.

The regression of offtake over herbage mass (pooled over sites) was highly significant (SE = 3.6; F =37.10; df =1, 28; $p<0.001$; $R^2 = 0.570$), i.e.

$$\text{Daily Offtake} = 0.0098\ \text{GV} + 0.8 \qquad \text{Eqn 4.4}$$

where Daily Offtake and GV (green herbage mass) are in kg ha^{-1} dry matter. The regressions for the individual sites were significant for Googong (F=12.6; df=1, 9; $p< 0.001$ R^2=0.584) and Gudgenby (F=15.9; df=1, 9; $p< 0.001$ R^2=0.633) but not for Tidbinbilla either before the bushfire (SE = 5.2; F =0.576; df = 1, 3; p = 0.503; $R^2 = 0.161$) or using all data points (SE = 3.78; F =3.20; df =1, 6; p = 0.124; $R^2 = 0.348$).

4.3.7 Groundcover

Percentage groundcover at Gudgenby changed relatively little during the study. The small decline (Figure 4.16) can be attributed to the drought, as there was no evidence of increased kangaroo density (Chapter 7). Groundcover at Tidbinbilla was closely aligned to that at Gudgenby until the end of 2002. A bushfire burned at high intensity across the Tidbinbilla site on 18 January 2003. After the fire, a high proportion of bare ground was observed when exclosure cages were replaced in February (e.g. Figure 4.17) but groundcover was not measured until 10 April, by which time it had increased to the level shown in Figure 4.16, due to a spurt of plant growth, probably in part from underground reserves, and reduced grazing pressure, due to a reduction in kangaroo density by the fire (Chapter 7).

There was a marked decline in groundcover at Googong in early 2003, as at Tidbinbilla, but Googong was not burnt. There was an intense storm in March 2003 (Section 3.5) which caused widespread surface erosion. During this study, measured mean groundcover was less than 70% only at the Googong site following the 2003 event.

Prior to the disturbance events in early 2003, there was relatively uniform groundcover within the Gudgenby and Tidbinbilla sites, indicated in Figure 4.18 by the smaller Standard Errors, compared to Googong. The range of variation between sampling strata was 23% at Googong (between the strata with maximum and minimum average groundcover) compared with 12 % at Gudgenby and 4% at Tidbinbilla. On all sites the steep, north-facing sampling stratum had least groundcover compared to the other sampling strata. Until the end of 2002 the average groundcover in the stratum with least groundcover at the site with lowest groundcover was 74%. Both sites affected by disturbance events, Tidbinbilla with low internal variation, and

Googong with higher internal variation, became less uniform after the disturbance (Table 4.11).

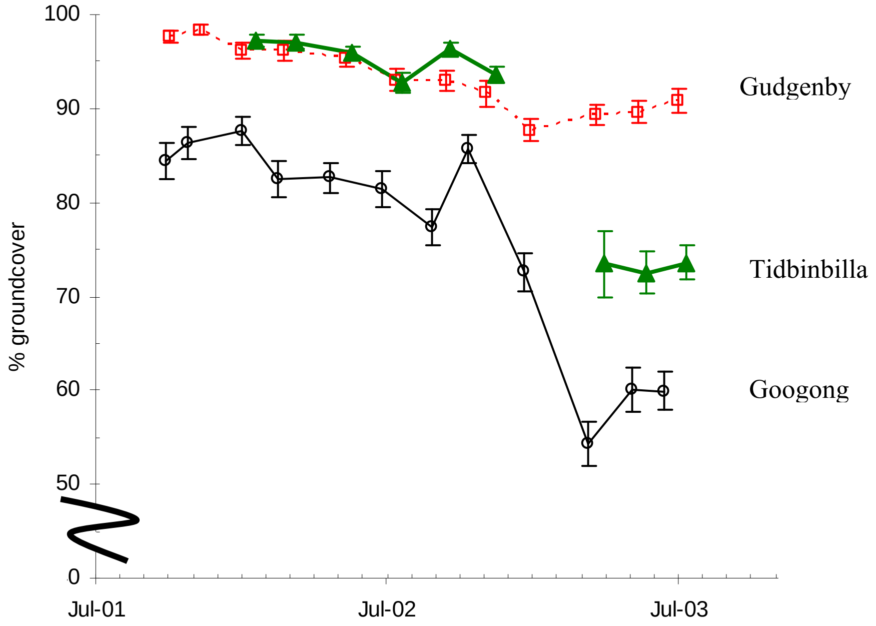


Figure 4.16: Mean groundcover (% ±SE) of grazed pasture at three study sites. —○— Googong; - - □- - Gudgenby; ▬▲▬ Tidbinbilla. During the gap in the Tidbinbilla series, ground cover was low following a bushfire then partially recovered to the measured level shown. See text for explanation.

Figure 4.17: As a result of a bushfire in January 2003, groundcover on the Tidbinbilla site was low when the exclosure cages were replaced in February. (In this illustration the remains of the burnt exclosure cage are being scraped up for removal.)

Table 4.11: Mean groundcover and variation of groundcover before and after episodic disturbance events in early 2003: Gudgenby, deepening drought but no episodic disturbance; Tidbinbilla, bushfire; Googong, storm (+ grazing pressure, see text). My Ref: Pasture Data Bms Calc 4 B.xls/ Sumry cells~G160.

	Gudgenby		Tidbinbilla		Googong	
	mean	CV	mean	CV	mean	CV
% cover to January 2003	94	14	96	10	82	33
% cover from March 2003	90	18	73	41	58	84

The effect on groundcover of short-term protection from grazing is obtainable by comparison between the groundcover estimates for the grazed pasture (above) with those from inside the exclosure cages. Measurement of cover inside the cages was commenced from May 2002. On occasions when there was little pasture growth, groundcover in the protected areas was the same as in the grazed pasture but on average it was 4% higher. The difference between the mean estimates of groundcover in protected and unprotected pasture from all surveys and sites was significant (paired t test; t = –5.35; df=22; p<0.001)

4.4 Discussion

4.4.1 The pasture response model

The model selection result is clear (Table 4.10), with only the most preferred model (Model 5) having ΔAICc less than 2.0 (Burnham and Anderson 2002). Comparison with Models 3 and 4 demonstrates that the removal of any weather variable from the preferred model results in a loss of explanatory power which more than offsets the statistical advantage gained by simplifying the model. Thus the preferred model is at once the most complex of the five simple models evaluated, and the most parsimonious explanation of the data. A negative, concave-up pattern of pasture growth (ΔV) on herbage mass (V) was also reported by Chaco (1993) and Chaco *et al.* (1999) in New Zealand when herbage mass was high.

Due to the drought, the herbage mass of my pastures did not return to the level it had been when my study commenced. Most of the time the pastures were in an eaten down condition. When well below its potential maximum level of herbage mass (K or carrying capacity) vegetation would be predicted to grow whenever there was sufficient moisture and warmth. When herbage mass was removed from the model, this is the relationship indicated by Model 2, (Figure 4.14).

Temperature was an important predictor of pasture growth as demonstrated by (a) the significant linear regressions of ΔGV on both T and R T over the preceding two months (Table 4.8); and (b) comparison of the results for pasture growth Models 3, 4 and 5 in Table 4.10. Models 3, 4 and 5 give increasing emphasis to temperature and produce successively lower ΔAICc scores. This contrasts with the report by Choquenot *et al.* (1998) that addition of temperature made no improvement to their model for pastures on the central tablelands. Only rainfall and herbage mass were necessary. However they used only R^2, not ΔAICc, to evaluate alternative models. The areas covered by the two studies are climatically similar and were combined by Vere *et al.* (2001) for the purpose of quantifying pasture production. When applied to my data, the model of Choquenot *et al.* (1998), and Robertson (1987a) (i.e. Model 3 in this study), accounted for 50% of the variation in the data. The weather-only model (Model 2) accounted for 55% of the variation, and the best model statistically (Model 5) accounted for 63%.

While the ΔAICc statistic distinguishes between alternative models, it tells us nothing about the quality of the preferred model. The simpler models of Robertson (1987a) and Choquenot *et al.* (1998) explained respectively 97.3% and 83% of the variation in each of those studies respectively. One interpretation of the results of this study could be that more complex modelling approaches are essential for the types of pastures measured in this study. However the rainfall experienced during this study was significantly below average on all sites (Table 4.3) and, during the two year study period, herbage mass declined significantly, reaching its lowest levels near the end of the study period (Table 4.4; Figure 4.8). These results were conspicuously different from the seasonal pattern of pasture growth stated for the central and southern tablelands by Vere *et al.* (2001). In particular, the normal pattern of most growth occurring in spring (Vere *et al.* 2001) did not happen during my study. The highest growth was recorded in autumn 2002 following heavy rainfall in February. If normal spring growth had been observed during the study, a different relationship between pasture growth and weather is likely to have emerged from the data. For modelling pasture growth, it may be advantageous to collect data over a longer period, including periods when the pasture is growing (herbage mass is increasing). This was done in the Kinchega study (Caughley *et al.* 1987), which included both entry to a drought and recovery from it. So, while resorting to more complex models is one possibility, another alternative is to re-evaluate the simple models after adding data collected in more typical pasture growth conditions.

4.4.2 Herbage mass

Consistent with expectation for temperate sites, the magnitude of grazed herbage mass in this study is greater than that encountered in the Kinchega kangaroo grazing study (Robertson 1987a, p 53). Even in the extreme circumstances after the bushfire at Tidbinbilla, during heavy grazing by cattle and kangaroos, and in a drought, the lowest pasture level recorded during this study was 80 kg ha^{-1} total herbage mass (63 kg ha^{-1} green herbage mass) compared to 9 kg ha^{-1} total herbage mass in the Kinchega study. Likewise, the maximum at Kinchega was approximately 1,100 (Robertson 1987a, his Figure 4.9), close to the median value in this project, whereas the maximum in this study was 2,802 kg ha^{-1} total herbage mass. The range of herbage mass encountered in this study is not proportionately greater, but compared to other grazing studies, is remarkably small across all sites and seasons, especially the range of green herbage mass, with an interquartile range of 453 kg ha^{-1}. At Kinchega there was more than 100-fold change (Robertson 1987a) but in my study the relative change was two-fold at Tidbinbilla (pre-bush fire), eight-fold at Gudgenby and 13-fold at Googong.

In contrast to the Kinchega results (Caughley 1987) grazing studies in temperate areas have found large and persistent effects of grazing on herbage mass. In a study of rabbit grazing, Croft *et al.* (2002) found that increasing densities of rabbits reduced pasture height, which was used to index herbage mass. The effect of herbivore density became greater as the three year project continued (Croft *et al.* 2002). Neave and Tanton (1989) examined exclosures that had been ungrazed for longer than six years by the time of their study on the Tidbinbilla site. They recorded that grazing by eastern grey kangaroos reduced the mean height of kangaroo grass (*Themeda australis*) from 13.8 – 23.5 cm in one hectare exclosures that were ungrazed or grazed only by rabbits, to 4.4 – 8.7 cm in exclosures that were accessible to kangaroos but not rabbits.

Low variation in green herbage mass between sites and seasons, as recorded in this study, is consistent with (a) the observed correlation between weather recorded on the three sites, (b) pastures which experience grazing which is constant and heavy but does not result in the death of the plants, (c) pastures which are restricted by the drought in their ability to grow strongly enough to outpace the functional response of the herbivores, and (d) kangaroo populations tending to operate at positions on the functional response that are below the saturation level (Chapter 5). The effect of (d) would be that the instantaneous consumption rate of the population would tend to automatically increase in response to small increases in pasture production, thereby partly offsetting the influence of favourable weather on the grazed herbage mass. During the study, small rainfalls were recorded on numerous occasions but only the rainfall of February 2002 resulted in pasture growth increments that are comparable with those considered typical by Vere *et al*. (2001).

The lower explanatory power of rainfall in relation to herbage mass in this study (45%) (Table 4.5) compared to that of Robertson (1987a) (71%) is to be expected. First, it is partly due to the seasonal nature of the temperate sites (greater influence of temperature). Second, kangaroo density is at least one order of magnitude higher on the temperate sites (Chapter 1) so there can be a greater effect of grazing pressure on herbage mass, reducing the potential influence of rainfall.

The effect of the bushfire at Tidbinbilla on herbage mass was short-lived because pasture growth was immediate. Within a few days of the fire long shoots were observed wherever the pasture was protected from grazing vertebrates. Simultaneously the grazing pressure was much reduced because the kangaroo density had been halved by the fire (Chapter 6, 7). A stronger recovery by the pasture was prevented by the grazing of cattle from a neighbouring property whose fences had been burnt. In the dry conditions, herbage mass again declined, reaching the lowest level (80 kg ha^{-1}) recorded in the study.

4.4.3 Rainfall

The relationship of pasture growth with rainfall was not the dome-shaped relationship discussed in the Methods. Especially at parameter values conducive to moderate or higher pasture growth, the relationship is close to linear. This is consistent with the models of Miller (1979), Robertson (1987a), and Choquenot *et al*. (1998).

4.4.4 Thermal index

There is a simple explanation for the superior performance in this study of temperature as a predictor of pasture growth, compared to the dome-shaped thermal index as used by e.g. Fitzpatrick and Nix (1970 and Moore *et al*. (1997), which appears to have a better theoretical basis. I sought relationships between pasture growth and bimonthly mean values of weather parameters. The use of the mean values, rather than modelling pasture growth on a daily time step, eliminated the more extreme values. Only the left side of a dome-shaped thermal index could apply. If pasture growth had been modelled on a daily time step, there would have been some days too hot for optimum plant growth, and the thermal index would be more likely to perform well.

4.4.5 Comparative yield method compared to disc meter method

A more detailed comparison of the two methods of estimating herbage mass is made in Chapter 5. As for the results in this chapter, there is a reassuring similarity between the estimates of herbage mass by the two different methods, across a wide range of conditions (Figure 4.5 and associated text). The greater precision of the herbage mass estimates obtained with the disc meter is an attractive feature, but it appears likely that the reservation about the disc meter expressed by t'Mannetje (2000) in regard to the effect of stemmy material, is not restricted to occasions when stiff, dead material is apparent in the pasture but applies also when the stems are merely soft green flowering stalks. This limitation could be overcome in various ways, e.g. by using additional series of reference plots and categorising each measurement in advance by which series it applied to, but the extra work required would offset the main advantage of the method, its ease of application. A simpler alternative, which may be acceptable for some kinds of studies, is to accept that the disc meter may sometimes overestimate.

4.4.6 Herbivore offtake

Sharrow and Motazedian (1983) showed that herbivore offtake, illustrated in Figure 4.15 and summarised in Equation 4.4, is overestimated by the widely used exclosure cage method, especially if the caged interval is long, which they define as more than three weeks. Similar findings are reported by Wagener *et al*. (1950) and Grelen (1967). Sharrow and Motazedian (1983) also found that two equations developed to correct for this are unsatisfactory. Sharrow and Motazedian (1983) noted that plots protected from defoliation grew faster than clipped plots, possibly because of proportionally greater leaf area. Faster growth on their protected plots resulted in overestimation of herbivore offtake ranging from 29% to 387%. The overestimation appears to be borne out in this study also (with 8-week intervals), as the offtake calculated from the functional response (Chapter 5) using realistic estimates for density and size of local eastern grey kangaroos (Chapters 6, 5), is lower than Equation 4.4 (Figure 4.18). In studies such as this one, using cages, there is also potential for a favourable microclimate created by the cage to exacerbate the problem.

The offtake estimates in this study are several times greater than those recorded by the same method in the Kinchega kangaroo project, which when converted to equivalent units ranged from approximately 0.1 to 2.75 kg ha^{-1}d^{-1} (Robertson 1987a). This can be attributed to the large difference in the density of kangaroos between the two areas (Chapter 1).

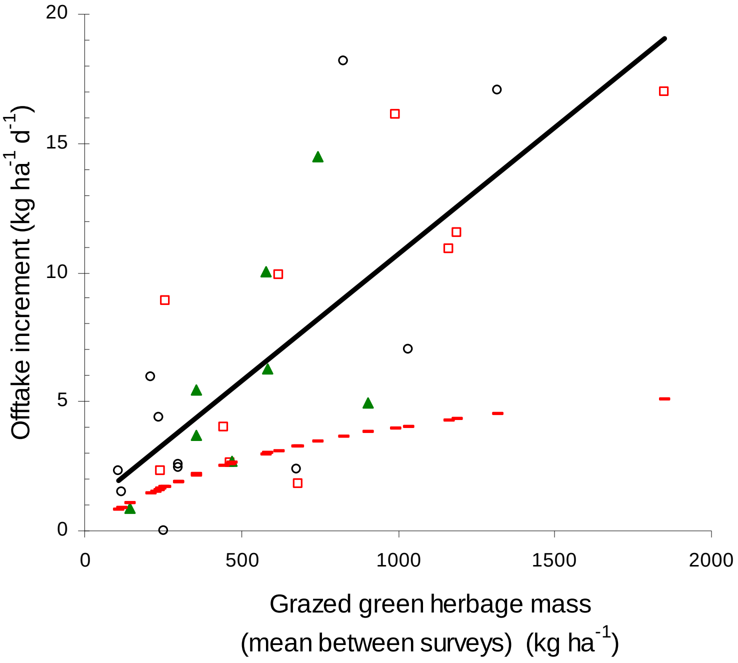


Figure 4.18: Herbivore offtake. ○ = Googong; □ = Gudgenby; ▲ = Tidbinbilla estimated from grazing exclosure cages; ▬▬ = Eqn 4.4; ■ ■ ■ (curve) = functional response estimated in Chapter 5, and calculated for 5 kangaroos ha^{-1}, each weighing 29kg live-weight.

4.4.7 Further research on the pasture response

As mentioned above, the lower explanatory power of the more complex pasture growth model resulting from this study, compared to those of Robertson (1987a) and Choquenot *et al.* (1998) may suggest that more complex models still are necessary to explain a higher proportion of the variation in growth of temperate pastures. That may be so, but before reaching that conclusion, it will be advisable to test the simpler models against data collected in periods of more normal weather, and during the recovery from a drought, as well as the entry to one. The correlation of bimonthly pasture growth between sites, and lack of correlation with the results of Vere *et al.* (2001) are compatible with the suggestions that pasture growth and dieback on the sites are linked by common regional weather patterns but that during this study, the weather fell outside the range considered typical by the agronomists who provided the estimates given by Vere *et al.* (2001). Numerous other research possibilities also exist, including the use of shorter time steps to model growth, and testing the explanatory power of other parameters such as evaporation. A variation of the necromass budget approach of Owen Smith (2002a, b) which models the death rate, as well as the growth rate, of the pasture, also suggests itself as a potential way forward which may be particularly applicable to temperate pastures, while maintaining a relatively simplified approach to the pasture component of the overall model.

In view of the results of this study, the logistic plus rain model of pasture growth (Robertson 1987a) warrants further evaluation, including against field measurement of grazed temperate pastures, given its widespread adoption to model herbivore populations (e.g. McLeod 1997; Choquenot 1998; Pech and Hood 1998; and Davis *et al.* 2003).

4.4.8 Ground cover

The lower ground cover at Googong compared to the other sites in the first year of the study probably reflects the greater steepness of Googong, and its different geology and soils (Chapter 3). Cover remained above the 70% target level set for the region by the local Murrumbidgee Catchment Management Board (2003), except following a bushfire at the Tidbinbilla site and following a storm at the Googong site. Although the 70% is widely quoted as a threshold level and supported by data such as that of Jefferies (1999) there are also many contrary data, e.g. those of Linse *et al.* (2001) and Giordanengo *et al.* (2003).

The exceptionally severe storm in March 2003 at Googong left obvious evidence of surface erosion, and scoured the litter from the pasture but it is of interest to managers to know how much of this unwanted effect to attribute to heavy grazing pressure. The 4% difference in groundcover between grazed plots and caged plots shows that even two months of relief from intense grazing increases groundcover but tells nothing about long-term effects of grazing. A different clue is suggested by the recovery of the pasture after the storm. If the groundcover returns to pre-storm levels under continued grazing pressure, more of the reduction in groundcover might be attributed to the storm and less to the grazing. The small increase in groundcover at Googong in May 2003, in spite of continued heavy grazing pressure, is consistent with the suggestion that much of the previous big decline was at least partially due to an extreme episodic event. Further evidence of the relative importance of the storm comes from point-step estimates of pasture groundcover at Googong subsequent to this project in 2004 and 2005 (M. Evans personal communication 2005). In both 2004 and 2005 mean groundcover was greater than 80%, and increased slightly from 2004 to 2005. However in spite of this evidence, any explanation that the storm was the main influence could be only a *post hoc* explanation, not based on experimental or even comparative evidence. An alternative explanation for low groundcover at Googong in 2004 is provided by Environment ACT (2004), namely that it was due to kangaroo grazing, with no mention of the storm.

The main emphasis in this chapter has been restricted to one trophic level – the vegetation. The next chapter, on the functional response, is the first which is mainly about the interaction between the eastern grey kangaroos and their food supply.

CHAPTER 5

THE FUNCTIONAL RESPONSE

To compare it to any European animal would be impossible
(Joseph Banks describing a kangaroo in 1788)

Kangaroo resting on a bare strip around the perimeter of a grazedown pen

CHAPTER CONTENTS

5 THE FUNCTIONAL RESPONSE

5.1 Introduction and literature review

This chapter has two components. The first, based on the literature, is an argument that the widespread classification of functional responses into three types is inadequate; there is both theoretical and empirical support for six types. The literature is also used to compare alternative methods for estimating functional responses that might be attempted with eastern grey kangaroos. The second component is an empirical estimate of the functional response of eastern grey kangaroos eating two different types of pasture, a freshly grown, high-quality, artificial pasture of *Phalaris aquatica*, and a naturally senescing kangaroo grass (*Themeda australis*) pasture. Both are relevant to kangaroo feeding behaviour on the study sites. Eastern grey kangaroos are grass specialists, with dicotyledenous plants comprising at most a few percent of their diet (Taylor 1983; Jarman and Phillips 1989; Woolnough and Johnson 2000). Large portions of the study sites are dominated by kangaroo grass associations and during my study the grass in these areas was kept short by heavy grazing pressure. On the study sites there are also favoured feeding patches of small size, where the grass tends to remain green during dry periods due to emerging groundwater. The grass on these patches comprises various native and exotic species and is generally similar in appearance to heavily grazed *Phalaris aquatica*.

The functional response of a consumer organism is the relationship between its rate of food intake and the availability of its food (Solomon 1949; Murdoch 1973; Noy-Meir 1975; Caughley 1981). Consumer organisms convert biomass between trophic levels at a rate limited by their functional response. The functional response is an important component of interactive models which relate the density of consumer organisms to the density and growth rate of food organisms, and vice versa (Caughley 1976a, 1987; May 1981; Caughley and Lawton 1981; Barlow 1987; McLeod 1997; Pech and Hood 1998; Owen-Smith 2002a, b; Davis *et al.* 2003). Such models may understandably be sensitive to the magnitude of the functional response, e.g. Owen-Smith (2002a). The concept of the functional response is essential to the understanding of foraging behaviour and the two-way relationship between a population of animals and its food supply (Noy-Meir 1975; Emlen 1984; Abrams 1990). A knowledge of the functional response of a population of herbivores can support a determination of whether the population is limited by its food, and enables assessment of whether or not there is competition for food between it and sympatric herbivores (Short 1985).

In spite of the importance of the functional response in ecology, measurements of functional responses in nature are quite rare (Abrams and Ginzburg 2000). Of 63 articles generated by a controversy in relation to functional response, Abrams and Ginzburg (2000) noted that only one included a measurement of a functional response. After highlighting the risks of indirect inference they stated the importance of measuring both functional and numerical responses in natural environments.

In contrast to the rarity of measured functional responses for wild vertebrates identified by Abrams and Ginzburg (2000), many food intake data have been published for domesticated sheep and cattle, sometimes in functional response form (e.g. Arnold and Dudzinski 1967a, b, and references given in Barlow 1987, his Fig. 1). However, most agronomic interest is in relatively high *per capita* levels of pasture abundance compared to the conditions experienced at crucial times by food-limited populations of wild herbivores. Considering that 90% of large terrestrial herbivores are thought to be food-limited (Sinclair 1996), the conditions in which food intake rates approach zero will often be at least as important as those in which intake rates are at agriculturally desirable levels.

Functional responses have been reported for a small number of herbivorous wildlife species (e.g. for wild ungulate species: Spalinger *et al.* 1988; Spalinger and Hobbs 1992; Shipley and Spalinger 1992; Gross *et al.* 1993; for red kangaroos and rabbits: Short 1985; for red kangaroos and western grey kangaroos: Short 1986; for snowshoe hares: Shipley and Spalinger 1992; for fox squirrels: Morgan *et al.* 1997; for moose: Lundberg and Danell 1990; and for feral pigs: Choquenot 1998). However, of these examples, only the functional responses of Short (1985, 1986), and Choquenot (1998) express intake in relation to a measure of food availability that can be related to real vegetation (see below). That may be because the work required is difficult. According to the review by Mayes and Dove (2000), determinations of intake and diet composition in free-ranging herbivores are difficult to undertake, and their errors are often large, mainly owing to the limitations of available measurement techniques. That is probably an understatement because 'free-ranging' here means unhoused, e.g. in paddocks. Wildlife species are typically more difficult to work with than domesticated ones.

The rate of food intake of herbivores is influenced by several other factors as well as food availability, including the structure and fibrousness of the forage (Cooper and Owen-Smith 1986; Forbes 1988; Wilman *et al.* 1996; Wilson and Kennedy 1996) and the height and density of the pasture (Arnold and Dudzinski 1967b; Black and Kenney 1984; Edwards *et al.* 1995; Gong *et al.* 1996c; Hassall *et al.* 2001) as well as the condition of the animals (Arnold and Dudzinski 1967a). Levels of plant defence chemicals may also be important (e.g. Short 1986; Lawler *et al.* 1998) or the ratio of defence chemicals to protein (e.g. Gauthier and Hughes 1995). Vegetation associations vary over both time and space in respect to their structure, fibrousness, spinescence, height, and concentrations of defence chemical and protein. It follows that a herbivore species does not have just one functional response, but many, although the contrary impression could be obtained from the literature, e.g. from Caughley and Sinclair (1994, p 73).

Although eastern grey kangaroos have a number of structural and functional similarities to some of the ungulate grazers of other continents, such as the anatomy of their feeding parts and digestive tract (Hume *et al.* 1989, their Fig. 29.2; McCulloch and McCulloch 2000, p 10), one interesting difference is a lower reliance on their front legs to support the weight of their body while feeding. Together with a manus capable of grasping plants, this creates the possibility of a hypothetical feeding efficiency compared to ungulates, namely a greater ability to separate desirable food items such as green grass from other material such as thatch. Other efficiencies relating to the structure and function of the digestive tract, and lower maintenance energy requirement of kangaroos compared to sheep and other eutherian herbivores have been previously reported (Hume 1974, 1982a, b, c; Hume *et al.* 1989, p 684 and Fig. 29.8; Nagy *et al.*1999).

5.1.1 Forms of functional response

Only three types of functional response are widely recognised whereas six main forms of functional response have been identified (Figure 5.1).

Type 1 to 3 functional responses

Holling (1959, 1965, 1966) classified functional responses as Type 1, 2 or 3, referring respectively to relationships that: (a) are ramp shaped, with food eaten rising linearly with increase in food available, then levelling off abruptly when the feeding apparatus of the consumer becomes saturated (Type 1); (b) increase at a decelerating rate, becoming asymptotic at high food availability (Type 2); and (c) are sigmoid in shape (Type 3). The common representation of Type 1 as linear and unsaturating (e.g. Ricklefs 1973, p 419; Smith 1974, pp 380 – 381; Hassell *et al.* 1976; Caughley and Sinclair 1994, pp 167 – 168; Sabelis 1992) has a logical appeal but is not true to Holling (1959, 1965, 1966) original presentation.

Noy-Meir (1978) recognised ramp, inverse exponential, Michaelis and sigmoid forms of theoretical functional responses. The ramp is equivalent to Holling’s Type 1 and the sigmoid to Holling’s Type 3. Both the Michaelis and the inverse exponential (Ivlev) functions fall within Holling’s definition of Type 2. They are mathematically distinct but Noy-Meir (1978) states that food intake data are not usually accurate enough to decide between them.

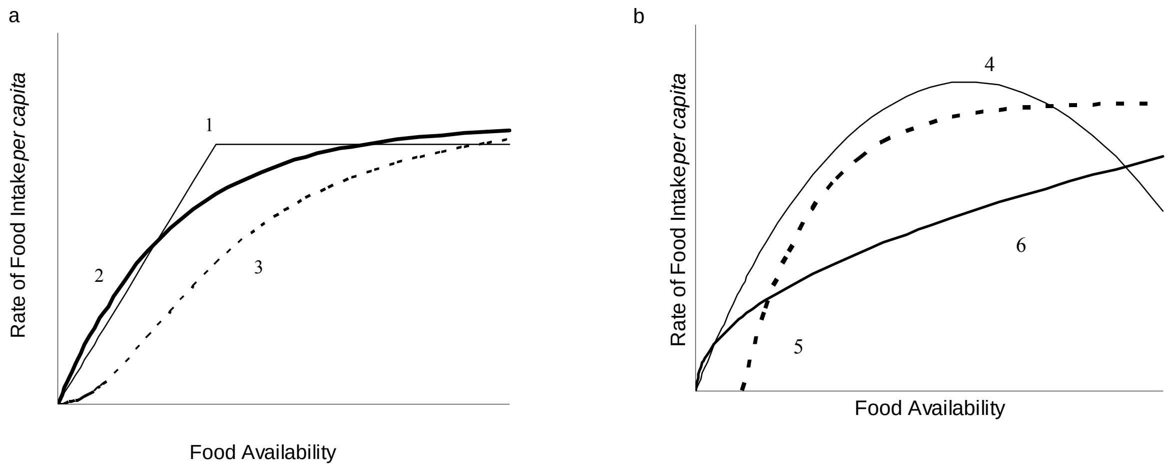


Figure 5.1: Theoretical forms of functional response: (a) —— Ramp (Type 1), ▬▬ Gradually saturating (Type 2), and – – Sigmoid (Type 3), after Holling (1965, 1966); (b) —— Dome shaped (Holling 1965) i.e. Type 4 (Caughley 1981), – – inaccessible prey or vegetation (Type 5, see text), and ▬ a 'square root' (Sabelis 1992), or power, functional response (Type 6, see text). My Ref: Kangaroos\Research\09 Functional Response \ Functional response types.xls

Functional responses of predators are described often in reference to only one of their available prey species (e.g. for arthropods: Hassell *et al.* 1976; Gismervik and Andersen 1997; for foxes: Pech *et al.*1992; for predators of rodents: Erlinge *et al.* 1983; and Sinclair *et al.* 1990). In this context, the concave-up portion of a Type 3 response can be interpreted as due to the predator switching to alternative prey when the subject species is in short supply although Hassell *et al.* (1977) reported predators having Type 3 functional responses to total prey and gave reasons why Type 3 responses may have tended to be overlooked. Herbivore functional responses are usually expressed in terms of total food availability so switching cannot apply. Reports of herbivores exhibiting Type 3 functional responses are rare but it is theoretically possible (Noy-Meir 1978; Caughley 1981). As with airborne hunters of pigs (Choquenot *et al.* 1999), a refuge mechanism may apply, e.g. if the remaining vestiges of edible vegetation were hard to find among inedible material. Also, the food could become physically less accessible, e.g. closer to the ground (Noy-Meir 1978) or better protected by spines or dead plant material. Among the rare examples, the functional response for sheep used in Barlow's (1987) grazing models for sheep and rabbits, is Type 3, based on eight published measurements of the relationship (references given in Barlow 1987, his Fig. 1).

The estimation of functional responses of predators (e.g. Holling 1966; Hassell *et al.* 1976; Gismervik and Andersen 1997) can arise from interest in prey as much as predators, and may be of considerable interest in regard to the conservation of the prey species (Sinclair *et al.*

1998). However, to use a herbivore functional response in a population model, the response to total food will be of more practical use. This affects the selection of methods for measuring herbivore functional responses.

Type 4 functional response

Holling (1965, his Fig. 6.6) referred to the possibility of dome shaped responses (a decline in intake at high food availability) and Hassell *et al.* (1976, 1977) occasionally recorded them. They were recognised as a distinct type by Emlen (1984) and termed the ‘Curve 4’ functional response by Caughley (1981) (Figure 5.1 b).

Type 5 functional response

Noy-Meir (1978) routinely included a term in functional response equations to refer to ungrazeable residual biomass. Short (1986) described the functional response of western grey kangaroos as one of inverse exponential (Ivlev) form with an ungrazeable residue of 180 kg ha^{-1}. In the same grazing trials the intake rate of red kangaroos reached zero at a pasture biomass 180kg ha^{-1} lower. Thus, Short (1986) defined the red kangaroo response as ‘Type 2’ and that of western grey kangaroos as ‘Type 2 with an ungrazeable residue’ (Figure 5.1 b). Inadequate recognition of this form could have the effect that models of functional response are unnecessarily rejected (Trexler *et al.* 1988) and that experimental procedures that would be unable to detect it are more likely to be adopted (see below). Some reported food intake data which have been fitted with a simple Type 2 curve (one forced through the origin) appear to be described better by this fifth type of functional response (e.g. the data for prairie dogs in Gross *et al.* 1993; and Fig. 3 of van Lenteren and Bakker 1976, cited as such by Trexler *et al.* 1988). Confusingly, this fifth form of functional response was termed a Type 3 functional response by Choquenot *et al.* (1999) in spite of their argument that they were not recording a sigmoidal response, but one in which the ‘predator intake rate’ (helicopter kill rate) reached zero while there was a positive prey density, corresponding to animals which could not be flushed from cover.

In discussing types of functional response for herbivores, more consideration should be given to the arbitrariness which is introduced by the limitations of methods for measuring pasture biomass. Researchers rarely measure true ‘biomass’, or even the total above-ground biomass, only what agronomists call ‘yield’ (that which is clipped for weighing), also known as ‘herbage mass’. The unclipped residue may be substantial, e.g. Macoon *et al.* (2003)

measured only the component of pasture more than 3 cm above ground level. It is unlikely that researchers always manage to clip the pasture exactly to the grazing limit for the subject grazing animal, so the researchers' 'zero' is not always the same as that of the subject herbivore, and different herbivores graze to different levels (e.g. Short 1986). It is thus unlikely that terrestrial herbivores can have a simple Type 2 functional response in reality. It follows that: (a) the measured herbage mass should be clipped at least as closely as the animal can graze, and (b) preferred forms for functional response equations should always include a term for ungrazeable residue, allowing the data to determine the magnitude of that term. Noy-Meir (1978), Short (1985, 1986) and Choquenot (1998) are among the few examples where this requirement has evidently been accounted for. The example of red and western grey kangaroos (above) shows that the ungrazeable residue may be biologically meaningful and is not necessarily just an artefact of an arbitrary measuring method. If such responses were to be labelled 'Type 5' it may serve to remind us of the importance of including a term for inaccessible residual herbage mass when fitting functional response equations. I use the 'Type 5' term hereafter.

Type 6 functional response

Sabelis (1992, p 243) proposed another distinct type of functional response, one intermediate between a linear unsaturating response (the sloping part of Type 1) and a saturating response such as Type 2. This is a functional response in which consumption initially increases more slowly than linearly (like Type 2) but never becomes asymptotic, such as a 'square root functional response' (Sabelis 1992). The pattern was also recognised as a distinct form by McCallum (2000, p 246). Sabelis (1992) provided several examples in which arthropod predation is of this form and hypothesised that it occurs if the predation rate is limited by gut fullness rather than handling time. Although Sibelus (1992) was writing about arthropod predation, the circumstances he described in which a saturating functional response (e.g. Type 2) would be replaced by a square root functional response, correspond well to herbivory, namely: prey easy to capture, handling time small, large individual prey size, and the 'predator' able to feed whenever its gut is not entirely full. Mite predation on eggs protected by webs was of Type 2, but without the webs it was a square root response (hereafter 'Type 6'). Although a high proportion of published herbivore functional responses are saturating Type 2 responses, it is also true that in nearly all of these cases the only equations fitted to the data were of Type 2 and I have not found any case in which data for a herbivore functional response was tested with a Type 6 equation. Thus the scarcity of Type 6 functional responses in the literature may be a poor guide to their real prevalence.

A power function is a more general form of Type 6 response than the square root and will be used hereafter. The Type 6 response is represented by Equation 5.1, in which the square root response corresponds to $b = 0.5$, as follows:

$$I = a\,V^{b} \qquad \text{(Eqn 5.1)}$$

where I is food intake, V is the herbage mass of vegetation or number of prey available and a and b are parameters to be estimated. It can be modified to allow for the inaccessible residue mentioned previously (Equation 5.2), thereby becoming Type 5 when $Vr = 0$ and Type 6 when $Vr > 0$.

$$I = a\,(V-Vr)^{b} \qquad \text{(Eqn 5.2)}$$

where Vr is inaccessible vegetation or prey occupying a refuge.

Alternative mathematical forms of Type 2 response

The Type 2 form of functional response has been reported most often, especially for herbivores (Lundberg 1988; Begon *et al.* 1996; McCallum 2000) and is important. Further elaboration is warranted to describe the three mathematical forms in which it has been represented. Holling’s (1959, 1965, 1966) Type 2 functional response was described by the so-called disc equation (named after an experiment involving human ’predation’ of paper discs):

$$I = aV / (1 + dV) \qquad \text{(Eqn 5.3)}$$

where I is food intake, V is the herbage mass of vegetation or number of prey available, and a and d are constants representing attack rate and handling time per prey item, respectively. Abrams (1990) stated the disc equation was the most commonly used model of a Type 2 functional response. To assist analysis of data of either Type 1, 2 or 3 form, Real (1977) generalised the disc equation to:

$$I = aV^{b} / (1 + dV^{b}) \qquad \text{(Eqn 5.4)}$$

which has the important advantage that the functional response is Type 2 when $b = 1$ and Type 3 when b is greater than 1. This ‘nested’ design helps overcome some of the statistical problems of non-linear model selection (McCallum 2000). As previously discussed, other nesting is also desirable to allow for ungrazeable residue, the combination producing a Type 2, 3 or 5 equation (Equation 5.5).

$$I = a(V\text{-}Vr)^b / [1+d(V\text{-}Vr)^b] \qquad \text{(Eqn 5.5)}$$

The same principle should be extended to the other mathematical forms of Type 2 responses, to provide Type 2, 3 or 5 nested designs. Type 2 responses can also be represented as Michaelis functions, equivalent to the Michaelis-Menton function of enzyme kinetics (Real 1977; Emlen 1984), derived theoretically from the assumption that the animal adjusts its average grazing effort to be linearly proportional to the difference between actual intake and satiated intake (Noy-Meir 1978). The Michaelis function is:

$$I = i_{max}[V / (V_f + V)] \qquad \text{(Eqn 5.6)}$$

where i_{max} is the maximum (satiated) food intake and V_f is the biomass at which a certain fraction, namely half, of the satiated food intake is consumed (Noy-Meir 1978; Owen-Smith 2002a). Michaelis functions have often been fitted to food intake data (e.g. for lemmings, ungulates, grizzly bears and other species: Gross *et al.* 1993; and for black-tailed deer: Spalinger *et al.* 1988).

The inverted exponential (Ivlev) alternative to the Michaelis equation has the form:

$$I = i_{max}[1 - e^{(-V/V_f)}] \qquad \text{(Eqn 5.7)}$$

The terms have the same meaning as for Equation 5.6 except that V_f is the biomass at which, not half, but $1 - e^{-1} \approx 0.63$, of the satiated food intake is consumed (Noy-Meir 1975; Short 1985). In similar fashion to the Michelis function, the Ivlev equation can be derived theoretically, according to Noy-Meir (1978), from the assumption that the animal adjusts its marginal (rather than average) grazing effort (marginal intake per unit of additional biomass) to be linearly proportional to the difference between actual intake and satiated intake. Curves of inverted exponential form have often been fitted to food intake data (e.g. for sheep, rabbits and red kangaroos: Short 1985; and for western grey kangaroos: Short 1986) and used in ecological models (e. g. Caughley 1982, 1987; Choquenot 1998). In reproducing Caughley's (1976a) interactive model, Owen-Smith (2002a) used a Michelis form for the functional response in preference to Caughley's Ivlev, stating that the hyperbolically saturating Michaelis-Menton function has become more widely adopted, because the controlling parameter is more easily interpreted.

Nested Type 2, 3 or 5 forms can also be written for the Michaelis and Ivlev functions:

$$I=i_{max}(V-Vr)^b / [(V_f-Vr)^b+(V-Vr)^b] \qquad \text{Eqn 5.8}$$

$$I=i_{max}\{1 - e^{[-(V-Vr)/(V_f-Vr)]\wedge b}\} \qquad \text{Eqn 5.9}$$

For the reasons given, these (or the equivalent version of the disc equation, Equation 5.5) should be fitted to functional response data in preference to the simpler original versions (Equation 5.3, Equation 5.6, Equation 5.7) allowing the data to determine in each case whether the parameters b and Vr (for sigmoidality and inaccessible food) are worth retaining.

Statistical limitations

Marshal and Boutin (1999) showed the practical difficulty of conducting an investigation of predation by wolves on moose which would have the statistical power to distinguish even a highly sigmoidal Type 3 response from Type 2. Although sufficient data will be easier to collect in some other studies, e.g. with some herbivores, the limited statistical power to distinguish between responses should be recognised. The use of statistics such as Δ AIC to select between models, rather than goodness of fit alone, is therefore important, as it will select the most parsimonious model with good fit to the data (Burnham and Anderson 2002, pp 5 – 77).

5.1.2 Empirical and mechanistic approaches compared for estimating functional responses

Published functional responses are mainly of Type 2, especially for herbivores (Lundberg 1988; Begon *et al.* 1996; McCallum 2000) with a lesser number of Type 3 functional responses for predators (e.g. Hassell *et al.* 1976, 1977; Pech *et al.* 1992). This might lead to the inference that the Type 2 and 3 functional responses of Holling (1959, 1965, 1966) had adequately described most of the relationship between intake and food availability. However, some functional response data fit alternative models better than these commonly fitted ones (e.g. examples cited above from van Lenteren and Bakker 1976; and Gross *et al.* 1993; see also Hassell *et al.* 1976; Sabelis 1992, p 240; and Spalinger and Hobbs 1992), and also, considerable variation is sometimes observed in functional response to vegetation availability (Ungar and Noy-Meir 1988; Spalinger and Hobbs 1992). According to Spalinger and Hobbs (1992) the biological meaning of the types of functional response models described in Section 5.1.1 is vague or has been abandoned. Sabelis (1992) observed that interpretation of functional response shapes can be ‘highly arbitrary’ and should be accompanied by quantitative models based on the underlying mechanisms.

In the attempt to elucidate the relationships between herbivore intake and vegetation, more complex mechanistic models have been developed (e.g. Ungar and Noy-Meir 1988) and there have been many investigations of the mechanics of feeding and digestion, including the ones mentioned under the heading ‘Behavioural approaches’ in Section 5.1.3. The mechanistic approach appears essential to develop a future understanding of functional responses. However at this stage the ‘functional responses’ resulting from investigations of the mechanism of feeding in highly contrived environments are of little use for inclusion in interactive models of real herbivore populations (Section 5.1.3), and therefore in this study I have taken the empirical approach to the estimation of herbivore intake rates.

5.1.3 Methods to measure functional responses

Techniques for estimating food intake in large herbivorous land mammals have been extensively reviewed (Langlands 1987; Dove and Mayes 1991; Mayes and Dove 2000). They fall into four groups: (a) measurements of herbage removed; (b) measurements of foraging behaviour; (c) measurement based on water turnover; and (d) measurement of faecal output and diet indigestibility, the latter also requiring a measurement of diet composition.

(a) Herbage removal methods

According to Mayes and Dove (2000), plant-based methods such as herbage removal are less often used than animal-based methods such as measurement of foraging behaviour, because the former are ‘reliable only over a very short time scale because of continuing plant growth, and thus are not applicable for continuously grazed areas’, and because separate estimates are not possible for individual animals. Moore (1996) reviewed methods of estimating pasture intake and commented that the herbage removal methods were ‘labour intensive’ and liable to produce ‘unacceptable’ estimates in low growth conditions or due to pasture variability, or excessive effects of trampling, or insect defoliation. Some of these reservations do not apply well to this project, e.g. the interactive model combines the individuals within the herbivore population so only a mean estimate *per capita* is needed, not individual estimates, and some other reservations can also be overcome. For example, this project also involved estimation of pasture growth (Chapter 4).

Macoon *et al.* (2003) trialled three of the methods of estimating herbivore intake that had been reviewed by Moore (1996) and favourably reviewed the herbage removal and animal production methods, compared to the pulsed-dose method. Short (1985, 1986) successfully used a herbage removal method (the grazedown – defined below) to estimate the functional responses of red kangaroos, western grey kangaroos, sheep and rabbits, and Choquenot (1994, 1998) used grazedowns to estimate a functional response for feral pigs.

(b) Behavioural methods

Behavioural methods estimate intake as the product of bite mass, bite rate and grazing time (Hodgson 1985; Forbes 1988). Bite mass varies considerably with plant species, plant part, and even time of day (Gibb *et al.* 1998). Animals usually compensate for declining bite mass by increasing their bite rate or feeding time (Allden and Whittaker 1970; Demment and Greenwood 1988; Edwards *et al.* 1995; Gong *et al.* 1996a, b).

There are strong reservations about behavioural approaches for estimating functional responses, at least in wild species of grazing mammals, mainly due to the methods that have to be adopted to overcome the difficulty of estimating bite mass. (In contrast, for browsing species, non-invasive measurement of bite mass appears feasible e.g. Vivas and Saether 1987; Shipley *et al.* 1998). Attempts to overcome the difficulty include the fitting of oesophageal fistulas to domestic livestock. Mayes and Dove (2000; pp 131, 115) express reservations about this method. Alternatively, 'feeding arenas' in zoos provide known amounts of food in the form of discrete sprouts protruding from holes in the floor, and many functional responses for wildlife species have been based on this method (e.g. Spalinger *et al.* 1988; Shipley and Spalinger 1992; Gross *et al.* 1993; Ginnett and Demment 1995). Because the measured food is a small fraction of the daily intake (e.g. less than 6 % Spalinger *et al.* 1988) and the animals are in a routine of returning to their zoo rations at the end of the brief measuring period, in effect these are estimates of only the upper right portion of the functional response. Therefore the data sometimes provide a poor fit to change in 'biomass'. Spalinger and Hobbs (1992) qualify models based on such measurements as predicting only intake rates on short time scales (minutes) in dense food patches. The review by Mayes and Dove (2000) omitted these methods from consideration.

(c) Methods based on water turnover

Food intake has been estimated from water turnover rates calculated from dilution in successive blood samples of a dose of water labelled with ^{3}H, ^{2}H, ^{18}O, or a combination (Nagy 1987; Nagy *et al*. 1987, 1990). This has mainly been done for animals in close confinement (e.g. metabolism cages) and can be extended to free ranging animals when the intake of drinking water is known, and the water content of the food can be accurately determined. An attempt was made to apply this approach during the kangaroo grazedown on *Phalaris aquatica*, using tritiated water, but it was not repeated in the *Themeda* grazedown. Wild-caught eastern grey kangaroos respond poorly to manual handling (necessary for a blood sample to be obtained), unless captured by anaesthetic dart (Jackson 2003). However the capture drug disrupts their water turnover. (I observed loss of saliva in the range from tens to hundreds of milliliters per animal, and unusually high water consumption). It is reasonable to take blood at the beginning and end of a grazing trial, and this enables an estimate of total food intake, but to calculate a functional response, a large number of estimates of intake are needed at varying levels of pasture availability. Also, dew and rain are potentially problematic for this method (Mayes and Dove 2000) as is any bias in the selection of pasture samples for water determination, compared to what the herbivores are really eating.

(d) Measurement of faecal output and diet indigestibility

Measures of faecal output and diet indigestibility have been attempted in numerous ways for domesticated stock (reviewed by Mayes and Dove 2000). In brief, a number of methods were ruled out for eastern grey kangaroos because the sacculated stomachs of kangaroos may not be suitable for implanted devices designed to reside in a rumen, nor are kangaroos well suited for the attachment of bags to collect faecal material.

More appropriately, faecal output could be estimated by the dilution in the faeces of an orally administered marker. A favoured method at present uses the ratio in faecal samples of dosed even-chain alkanes to the naturally occurring odd-chain alkanes (Mayes *et al.* 1986; Dove and Mayes 1991, 1996; Mayes and Dove 2000). The required approach and examples of attempts to apply it are outlined by Mayes and Dove (2000). Whereas diet composition has been successfully determined in free-ranging non-ruminants using *n*-alkanes, e.g. for kangaroos and hares (Woolnough and Johnson 2000; Hulbert *et al.* 2001), so far there are few measurement of intake from free-ranging non-ruminants including some equivocal results (Wilson *et al.* 1999; Mayes and Dove 2000). Dove and Mayes (2003) provide a more recent update indicating that the method is still in a developmental stage. For estimating the functional response of wild eastern grey kangaroos, the *n*-alkane method is likely to require a preliminary investment in trial and development which was not possible during this study.

Near-infrared reflectance spectroscopy (NIRS) has been used successfully to estimate intake. Wallis and Foley (2003) used NIRS of vegetation to successfully predict its rate of ingestion by captive possums, using a model of intake based on prior experiments, and Decruyenaere *et al.* (2003) found NIRS gave more accurate estimates of grass biomass fed to penned sheep than the *n*-alkane method. Decruyenaere *et al.* (2003) noted the dependence of the method on 'robust' calibrations as a 'major disadvantage'. For estimating the functional response of eastern grey kangaroos, the NIRS method also is likely to require a preliminary investment in trial and development which was not possible during this study.

5.1.4 The grazedown as method-of-choice for this study

None of the methods reviewed above (a to d) is entirely satisfactory, but the best choice was simple. The least promising (b) was unacceptable and the most promising methods (c and d) were insufficiently developed for application to eastern grey kangaroos. That left only method (a), herbage removal, in the form of a grazedown procedure.

A grazedown procedure, in which animals sourced from the wild are confined at high density on a representative area of vegetation (e.g. Short 1985, 1986, 1987; Choquenot 1994, 1998) is a way to estimate food intake in relatively realistic conditions because the only food available to the animals is the measured vegetation and this remains the case, typically for a period of weeks, until the area is eaten out. As a means of estimating the functional response of wild grazing animals, the grazedown method has the further advantage that the intake data can be expressed in relation to direct measures of food availability (such as herbage mass, sward height, leaf length, percent cover etc) which may be directly applicable in the natural environment. The daily reduction in herbage mass represents the animals' food intake, with corrections for growth or dieback of the vegetation and for trampling, if necessary. Removal of vegetation by other organisms such as insects is disregarded due to the short time of the trial and the magnitude of the decrement in herbage mass due to feeding by the subject animals. The functional response curve is the rate of food intake, preferably expressed in terms of metabolic bodyweight, plotted as a function of vegetation availability, e.g. as herbage mass per hectare.

The grazedown also has the potential to identify correctly each of the main theoretical forms of functional response if they apply to that species, unlike for example, a feeding experiment using favoured plant species. For example the functional response of western grey kangaroos in chenopod shrublands was Type 5 (i.e. Type 2 with an inaccessible residue) (Short 1986) whereas a feeding experiment using favoured plant species would be unable to separate this from a Type 2 functional response.

Few grazedown experiments have been reported for wildlife species. Short (1985, 1986) used grazedown experiments to report the only known estimates of the functional response of any marsupial species, for red kangaroos and western grey kangaroos, at Kinchega National Park in the sheep rangelands of western NSW. Functional responses of sheep and rabbits in the same environment were also estimated with grazedown procedures (Short 1985). Choquenot (1998) used a grazedown to estimate a functional response for feral pigs.

5.2 Methods

5.2.1 Experimental yards and pastures

Pre-existing permanent kangaroo yards at the CSIRO Division of Sustainable Ecosystems in Canberra were used for a grazedown on artificial *Phalaris aquatica* pasture. For a later grazedown on natural kangaroo grass (*Themeda australis*), portable security fencing was installed within the Tidbinbilla study site (Figure 5.2 and Chapter 3). The following description is of the purpose-built yards on the natural pasture, noting any important differences to the *Phalaris* grazedown.

Design of the kangaroo yards was adapted from Short (1985, 1986). There were three grazedown pens, each 20 m by 20 m, connected via gateways to a ‘refuge pen’ of the same size (for the *Phalaris* grazedown there were two smaller grazedown pens). To reduce the likelihood that interactions between the two kangaroos in each pen (three in the *Phalaris* grazedown) might interfere with feeding behaviour, at 400 m^2 each grazedown pen was larger than the 250 m^2 minimum enclosure size recommended for long-term management of two eastern grey kangaroos (Jackson 2003).

An improvement compared to Short’s (1985, 1986) design was the creation of a 2 m wide bare perimeter in each pen. The bare perimeter was intended to reduce the risk of kangaroos colliding with the fences if they were startled while feeding. Part of this strip was often shaded by the hessian on the fences. Additional shade was provided by ‘shadecloth’ fabric stretched across three corners of each pen. Most of the kangaroos’ resting, social interaction and movement took place on the bare strip, especially in the corners, thus reducing trampling of the pasture, and simplifying the pasture assessment. In preparation for the *Phalaris* grazedown, the bare areas, including the refuge pen, were repeatedly sprayed with herbicide, cut and raked; during the later grazedown on native pasture, they were made ‘bare’ by covering them with old carpet. The artificial pasture was a *Phalaris* monoculture that had been sown many years previously. In the weeks prior to the procedure, it had been mown hard, raked and watered in an attempt to maintain a high proportion of green leaf and to bring the herbage mass to around 2,000 kg ha^{-1}. Fences were made from transportable steel frames supporting chainlink netting and were 2.1 m high. Fences were covered with hessian to increase their visibility to the kangaroos, and thereby reduce the risk of injuries.

Outdoor pens of the size indicated are desirable to enable more natural behaviours and minimise interference between animals feeding. However the growing conditions, and hence pasture density, are not under the control of the researcher. One grazedown attempt was prevented when a bushfire removed the pasture. The following year good growth conditions resulted in too much *Themeda* pasture for two kangaroos to consume in a reasonable time. Rather than reducing the *per capita* food content of the pen by mowing, which would create a less natural pasture, or by increasing the number of animals, which would result in unnatural behaviour, instead an additional portion of each pen was made ‘bare’ by carpeting it. The carpeted area was placed centrally to disperse the food supply over the available area and minimise the chance of interference between animals. This ‘food dispersal’ appears to be a useful design improvement to make the feeding conditions more realistic by reducing crowding of the animals on the pasture. Other researchers conducting grazedowns should consider incorporating it into their plans from the beginning. Two buckets each containing 2.0 litres of fresh water were replaced in each pen each day.

Figure 5.2: (a) The temporary kangaroo yards in kangaroo grass (*Themeda*) pasture in summer at Tidbinbilla. (The landscape shows signs of a bushfire one year previously); (b) View inside one pen showing arrangement of central, carpeted 'bare' area, exclosure cages, and eaten down pasture. Kangaroo dung has been continually moved from the pasture onto the carpet. Hessian previously attached to all fences has been removed from the internal fences between pens but remains on the outer side of the external fence.

The natural *Themeda* pasture was similar to that found on open north-facing slopes throughout the study sites at Googong, Gudgenby and Tidbinbilla, but had been protected from grazing animals during the previous spring, so the starting biomass was greater than generally observed on these sites during the period of this study. It was heavily dominated by kangaroo grass, *Themeda australis*. Other relatively abundant species were *Lomandra filiformis, Eragrostis brownii*, *Elymus scabrus*, *Panicum effusum*, *Astroloma humifusum, Anthoxanthum odoratum, Tricoryne elatior*, and a native *Euchiton* species. A total of 57 species was identified in the yards. Because the *Themeda* grazedown was conducted in mid-summer, most of the native forbs evident in spring had disappeared. Most grasses had seeded and many had dried out. *Themeda australis,* a summer growing C4 species, was an exception, and remained green throughout the period. Dry flower stalks of *Themeda australis* were prominent. The total herbage densities in the three pens at the start of the *Themeda* grazedown were 2,288, 2,313, and 3,039 kg ha^{-1} (dry matter).

5.2.2 Management of the experimental animals

The behaviour of the study animals is an important consideration. Due to their experience, wild-caught animals may feed differently than captive bred stock e.g. Distel *et al.* (1996) showed that the food intake of sheep which had grazed on low quality pasture when they were young was 15% higher than sheep which had not grazed on low quality pasture. Therefore in spite of the nervous temperament of eastern grey kangaroos (Jackson 2003), the study animals were ones that had been captured from wild populations four years previously and kept in a large enclosure at the CSIRO Division of Sustainable Ecosystems, Gungahlin. Females exclusively were used to reduce the potential for escapes over the 2.1 m fences. None were lactating, having been separated from males since capture.

The six kangaroos were captured from the CSIRO enclosure using a Pneudart® rifle (Pneudart®, Williamsport PA, USA) or a Telinject Vario gas pistol (Telinject® Agua Dulce CA, USA). A 1 mL dart containing 250 mg of the sedative drugs tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®, Virbac, Sydney) was fired into the hindquarters. Sedation was achieved within 5 minutes. Two animals which began to recover prematurely were injected by hand with an additional 1 mL of the same drug during the 45 minute journey to the grazedown yards. In view of the findings of Shepherd (1981) that handling and darting methods have the potential to cause capture myopathy in red kangaroos, care was taken to minimise the impact force of the darts, based on prior testing of the equipment, and to minimise stressful procedures prior to and following the darting, following advice given variously by Tribe and Spielman (1996), Nielsen (1999), Kreeger *et al.* (2002) and English (2004).

One older and more dominant kangaroo and one younger kangaroo were moved into each grazedown pen after eleven days in a larger adjoining pen to acclimatise to the pasture and local conditions (longer acclimatisation period in the *Phalaris* grazedown, and three kangaroos per pen). Acclimatisation was assisted by the administration of 1 mg kg^{-1} of Zuclopenthixol deconoate (Chlopixol Depot® Lundbeck, Denmark), a long acting tranquilliser which reduces stress reactions of kangaroos (such as flight response), without affecting feeding behaviour (Blyde 1999; D. Blyde, Veterinarian at Western Plains Zoo, personal communication, 2002). During the acclimatisation period, efforts were made to accustom the kangaroos to the daily routine that would apply during the grazedown period.

While the pasture was being assessed in each pen, the gate into the refuge pen was left open so the two kangaroos could move there to avoid the researcher. On some days pasture assessment was discontinued to reduce the risk of stressed animals overheating or colliding with fences, resulting in gaps in the data recorded. However by the tenth day of the grazedown all of the kangaroos were readily making use of the refuge area, and on some occasions, calmly returning into the grazedown pens while pasture assessment was still underway, and thereafter showed few signs of anxiety (Figure 5.3)

Figure 5.3: The eastern grey kangaroos (lying in far corner in a) had habituated to the *Themeda* grazedown procedure after the first 10 days and a prior 11-day acclimatisation period. (b) Eventually one individual became unusually bold.

The kangaroos were weighed before and after the study. On being moved to the acclimatisation pen, the kangaroos had a mean live weight of 39 kg, and a combined weight in the three grazedown pens of 70.5, 81.0 and 82.1 kg respectively. The mean weight loss of kangaroos during the procedure was 19.5 % (min. 11 %, max. 32 %). The combined kangaroo live weights in each pen were averaged over the grazedown period for use in calculations of food intake, i.e. 66.2, 72.1 and 72.5 kg. Weight loss in the grazedown on *Phalaris* was negligible. In that case the decline in herbage mass had been more precipitous, and to a lower total herbage mass, so it was clear when to terminate the procedure. Procedures were approved in advance by the University of Canberra Animal Ethics Experimentation Committee (Reference CEAE 03/13).

5.2.3 Estimating per capita food intake

Estimating herbage mass

In each grazedown pen the herbage mass was measured non-destructively on three days out of four. This ‘daily’ estimate for each pen was the mean of 20 estimates made in a 0.25 m^2 circular quadrat placed at random within equal rectangular areas covering the available pasture. In common with other researchers, for example those using the BOTANAL method (Tothill *et al.* 1992; Hargreaves and Kerr 1992; McDonald *et al.* 1996) I also used these quadrats for the other pasture measurements (see below). All values were entered directly to a pocket computer, again as for BOTANAL.

To non-destructively estimate herbage mass, I used the same two methods as for pasture assessment on the study sites (Chapter 4) and conducted the following tests to select between them. I used the comparative yield method (Haydock and Shaw 1975; Friedel and Bastin 1988; Waite 1994; Cayley and Bird 1996; t'Mannetje and Jones 2000) as done during grazedowns reported by Short (1985; 1986) and Choquenot (1998). Secondly, a disc meter was also used (Bransby 1977; Earle and McGowan 1979; Michell 1982; Cayley and Bird 1996; Li *et al.* 1998; t'Mannetje and Jones 2000). A comparison of three methods of estimating pasture intake, reported by Macoon *et al.* (2003), favourably reviewed the 'biomass removal' method, using such a disc meter to estimate herbage mass. Li *et al.* (1998) stated that disc meters outperform 'visual estimates' (in which category they presumably place the comparative yield method) especially on grazed pasture. Disc meters are also referred to in the literature as 'rising plate', 'falling plate', 'weighted disc', 'drop disc' and 'pasture' meters (t'Mannetje 2000). They are considered convenient and useful on shorter types of pastures although less accurate on stemmy material (t'Mannetje 2000).

To calibrate both methods of measuring herbage mass so as to give results in terms of pasture weight per area, seven reference plots were initially established just outside the experimental pens and a further seven plots were set up within the pens during the grazedown period to incorporate the changed appearance and texture of the eaten-down pasture. All fourteen reference plots were protected with exclosure cages until they were cut for drying and weighing. A photograph of each plot was available as a memory aide between visits to the plots, which occurred several times per day. The regression of the dried weights of the reference plots against the comparative yield ranks initially assigned to them (on a 5 point scale) was linear through the origin with a slope multiplier of 555 kg ha^{-1} (SE = 23; F = 131.77; df = 1, 12; $p<0.001$; $R^2 = 0.910$). In a test of the application of the comparative yield method, similar to the 'Type 3' calibration procedure of Haydock and Shaw (1975) an additional 20 plots were ranked, clipped, dried and weighed. The regression of actual (cut) herbage mass against estimated herbage mass was significant (SE = 0.047; F = 64.348; df = 1, 18; $p<0.001$; $R^2 = 0.772$):

$$AY = 1.232\ CYE \qquad \text{Eqn 5.10}$$

where AY = actual herbage mass in kg ha^{-1} and CYE = comparative yield estimate in kg ha^{-1}.

The slope of this line (1.232; ± 0.047 SE) is significantly different from 1 (t value = 4.976; df=19; $p < 0.005$) therefore the herbage mass estimates were adjusted accordingly.

The disc meter method has the apparent advantage over the comparative yield method of objectivity. However, in my tests, the disc meter was outperformed on both precision and accuracy by the comparative yield method. Disc meter readings taken in the reference plots were less tightly related to the true herbage mass than were the comparative yield estimates (SE = 29; F = 19.705; df = 1, 9; p = 0.002; R^2 = 0. 686). Also the regression of disc meter readings against herbage mass was linear but not through the origin:

$$HM = 127.3\ DMR + 621 \qquad \text{Eqn 5.11}$$

where HM = herbage mass in kg ha^{-1} and DMR = disc meter reading. The intercept (621 ± 236 SE) was significantly different from 0 (t = 2.6; df = 10; p = 0.027).

A disadvantage of this equation (considering that meter readings are always greater than zero) is that it indicates difficulty measuring pastures less than 621 kg ha^{-1}. Alternatively, the regression can be forced through the origin (slope multiplier 187 kg ha^{-1}) but it then becomes markedly less precise (R^2 = 0. 44). A very similar result to Equation 5.11 was obtained for the disc meter from the 20 plots clipped as a retrospective test of both methods (SE = 354; F=57.121; df = 1, 18; $p < 0.001$; R^2 = 0.704).

$$HM = 136.73\ DMR + 621.71 \qquad \text{Eqn 5.12}$$

At low herbage mass, disc meter readings could be influenced by topographic variation in the substrate, as well as by the herbage mass. To examine this potential source of error, disc meter measurements were taken in plots after they had been clipped (Mean = 1.070; SE= 0.241) (Figure 5.4). Subtracting this amount from every reading would reduce the lowest measurable herbage mass to 475 kg ha^{-1}, but that is still a problematical limitation in the context of this investigation, and in any case it does not make the precision (R^2 = 0.70) better than for the comparative yield method (R^2 = 0.77, based on the test plots which were ranked before clipping). Therefore the comparative yield results have been used in preference to the disc meter results.

Figure 5.4**:** A clipped plot in grazed pasture. Additional disc meter readings were taken after clipping (as well as before) to consider the effect of terrain on the disk meter.

Estimating the proportion of living pasture

The food of herbivores grazing temperate pastures closely approximates the amount of green (living) material in the pasture, so it is of little use to know the total dry matter herbage mass alone (Cowan and O'Grady 1976; t'Mannetje and Ebersohn 1980; t'Mannetje 2000). To facilitate valid comparison between seasons and sites, in agricultural practice it is usual to disregard the dead material and report only the green component. Therefore in this study the proportion of living material was estimated, based on the method of Waite and Kerr (1996). Quadrats were selected to span the range of greenness in the pasture, given a greenness ranking, and photographed as a reference standard. Several photographs of each plot were printed with a range of colour intensities. The one most closely representing the appearance of the actual sample was selected on site before the sample was cut, hand sorted into living and dead material, dried and weighed. To deal with changed pasture appearance resulting from grazing, additional greenness reference samples were photographed and cut in the three pens during the grazedown. At higher greenness, my visual estimates consistently overestimated the proportion of living material, compared to measurement of hand-sorted samples, as shown by Equation 5.13 ($F = 152$; df =2, 14; $p < 0.001$; $R^2 = 0.884$). The greenness estimates were adjusted accordingly:

$$AG = 0.997\ Vegp^{0.810} \qquad \text{Eqn 5.13}$$

where AG = actual proportion of green pasture in kg ha^{-1} and Vegp = visual estimate of greenness percentage.

Pasture growth estimates in the Phalaris grazedown

In the *Phalaris* grazedown, a separate ungrazed area was used to estimate growth as done by Short (1985, 1986) and Choquenot (1998). Herbage mass was estimated on eight occasions in the separate area. Two growth estimation procedures were adopted, A and B, for estimating growth in the grazedown pens.

A) Empirical: It was assumed that pasture growth is logistic (Caughley 1976a; Caughley and Lawton 1981; Thornley and Johnson 1990). That is, the plot of exponential growth rate on herbage mass is linear. Growth increment (dV/dT / V) was modelled as:

$$(dV/dT) / V = r_m - (r_m/K)\ V_t \qquad \text{Eqn 5.14}$$

where V = herbage mass, T = time, r_m = the maximum rate of growth (that is, the Y intercept of the plot of growth rate over herbage mass), and K = maximum herbage mass, (carrying capacity) the X intercept of the same plot. The regression was estimated by least squares analysis.

B) Mechanistic: The simulation program GrassGro Ver 2.0.3b (Moore *et al.* 1997) was used with locally measured weather and soil information, to estimate pasture growth. Clark *et al.* (2000) evaluated favourably the ability of GrassGro to predict pasture, grazing and animal production parameters compared to measurements taken at widely separated sites in south-eastern Australia. The model was used first to closely reproduce the measured decline in herbage mass by substituting for the kangaroos a density of 120 merino wethers ha^{-1}. Then the simulation was run without the sheep to provide pasture growth estimates. As the model had overestimated the growth measured in the ungrazed pen by 32% its estimates for growth in the grazed pens were reduced accordingly.

Herbage mass in the ungrazed area continued to increase throughout the period. The pasture grew more rapidly for the first sixteen days (mean 46 kg ha^{-1}) then more slowly (mean 24 kg ha^{-1}).

The two methods (A and B) of estimating pasture growth in the grazedown pens produced similar and plausible results. With either method, growth contributed substantially to the calculation of food intake at intermediate herbage mass (200 to 900 kg ha^{-1}) but made little difference at low herbage mass. Method A produced a higher estimate than method B at low herbage mass but this was reversed above 550 kg ha^{-1}. The choice between A and B made little difference to the shape of the functional response. The average growth estimate of the two methods was used in calculating the result presented.

The equations used for method B (GrassGro program) are reported by Moore *et al.* (1997). The equation used for method A to model the daily growth increment (dV) was:

$$dV = -2.03 + 0.2157\,V - 0.00021\,V^2 \qquad \text{(Eqn 5.15)}$$

where V = herbage mass in kg ha^{-1} ($R^2 = 0.97$; $n = 7$; $p < 0.001$). Standard errors and p levels for each term are given in Table 5.1.

Table 5.1: Standard errors and p levels for terms of the polynomial regression used in growth estimation method A for the *Phalaris* grazedown.

Value	– 2.03	0.2157	0.00021
Std. Error	0.42	0.0024	< 0.00001
p level	< 0.001	< 0.001	< 0.001

Pasture growth estimates in the Themeda grazedown

Daily measurements of herbage mass reflected the combined effect of pasture growth and kangaroo grazing:

$$V_i = V_{i-1} - I + G \qquad \text{Eqn 5.16}$$

where V_i = Herbage mass on day i; I= Intake; and G = growth, so rearranging, for calculation of food intake by kangaroos,

$$I = V_{i-1} - V_i + G \qquad \text{Eqn 5.17}$$

To estimate pasture growth in the *Themeda* grazedown, 21 exclosure cages, 0.3 m^2 in area, were placed in the three kangaroo pens (Figure 5.2b). Herbage mass was estimated at the 21 locations before and after caging. The cages were moved to new locations and the procedure repeated so as to provide independent pasture growth estimates for each of seven time intervals. The cages were plastic and posed a low risk of injuring any kangaroos that collided with them. The 21 plots were less than the minimum 32 recommended for such purposes by Waddington and Cooke (1971) because there was a concern about the possibility of either entangling the kangaroos in the mesh cages or interfering with their feeding behaviour. Prior experience suggested 21 would be sufficient if pasture growth increments were large enough to strongly influence the estimate of food intake per kangaroo.

In principle, measurement of pasture growth within the grazing pens was an improvement on the procedure adopted by Short (1986, 1987), by Choquenot (1998), and in the *Phalaris* grazedown, in which growth was estimated in a separate ungrazed area. That is because pasture grows as a function of its biomass (Caughley 1976a; Caughley and Lawton 1981; Crawley 1983; Thornley and Johnson 1990) with no growth occurring when herbage mass is at its maximum. As a grazedown progresses, the grazed areas (herbage mass decreasing to a low level) and separate ungrazed areas (herbage mass high) become markedly dissimilar, and therefore it may be inaccurate to estimate growth in one by measurement in the other. Also, grazing itself may affect growth rate, (the grazing optimisation hypothesis, Crawley 1983, pp 42 – 44; Fox *et al.* 1998), and any such effect would be overlooked if growth of grazed pasture was estimated in an ungrazed area.

The *Themeda* grazedown took place during February and March 2004, months that were record-breaking for high temperature, high solar radiation, high wind and low rainfall (Bureau of Meteorology 2004a, b, c) and it would be reasonable to expect little or no pasture growth to have occurred, other than the production of small shoots in response to heavy grazing, from energy and nutrient stored in the roots. In fact, three of the seven growth estimates were significantly greater than zero (Table 5.2, Figure 5.5).

Table 5.2: Estimates of *Themeda* pasture growth (significant values only).

Growth interval (days)	6 to 11	12 to 17	32 to 41
Growth estimate (pens combined) (kg ha^{-1} d^{-1})	131	29	13

To obtain daily estimates of G in Equation 5.17, when growth has been measured at multi-day intervals, it is necessary to have some model for daily pasture growth from which to interpolate. In this case, with only three significant values, there is not a significant linear relationship between either growth or $\log_e$ (growth), and either of the simple predictors, time or herbage mass (Table 5.3). However, of these four relationships, the one which is best statistically (highest R^2), is also the one that makes most biological sense, the natural logarithm of pasture growth rate generally being linear on herbage mass (references cited above), i.e. Equation 5.18 (Table 5.3, Figure 5.5).

Table 5.3: Parameters, with SE, R^2 and p values, of four linear equations predicting growth as a function of time (T) or herbage mass (HM). None is significant; the best is that in the third row, between $\log_e$ growth and herbage mass. G = Growth (kg ha^{-1} d^{-1}); HM =Herbage mass (kg ha^{-1}) ; T = Time (days).

Function	Slope	Intercept	R^2	SE	p (slope)
G = f (HM)	0.094	–73.156	0.712	48.549	0.36
G = f (T)	–3.140	121.489	0.593	57.771	0.44
$\log_e$ G = f (HM)	0.002	0.895	0.892	0.55	0.21
$\log_e$ G = f (T)	–0.067	4.970	0.802	0.743	0.29

$$G = 2.447 \exp (0.002\ HM) \qquad \text{Eqn 5.18}$$

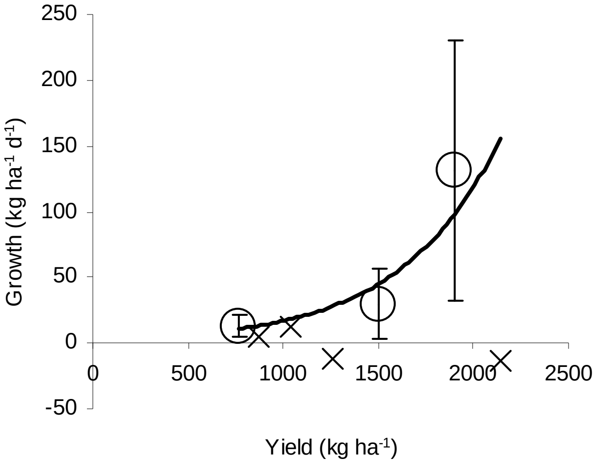


Figure 5.5: Pasture growth estimates plotted as a function of herbage mass; o = growth estimates significantly different from zero; error bars show 95% confidence interval. X = non-significant values. The curve (Equation 5.18), estimated from the three significant values by linear regression of $\log_e$ (growth), is the best of four non-significant relationships (Table 5.3):

Converting the decline in herbage mass to food intake

Conceptually the simplest way to obtain estimates of intake is incrementally (referred to hereafter as the ‘Incremental Model’) i.e. to apply Equation 5.17 to the daily data from each pen, and fit a functional response curve(s) to the resulting points. However the successive daily estimates of herbage mass are not a smooth decline; increases are sometimes recorded due to measurement error. The resulting negative values of food intake are invalid. Although these data may be effectively lost, the incremental method has an advantage of making few assumptions about the underlying relationship before it is modelled. The scatter of data around the fitted relationship would be greater using this approach. An alternative approach is usually adopted (e.g. Short 1985, 1986; Choquenot 1998), namely to smooth the decline of herbage mass until the daily decrements of herbage mass are positive. The purpose is to convert the trend of herbage mass to a mathematically tractable form that is as faithful as possible to the raw data, rather than to elucidate an underlying biological relationship. However the shape of the functional response may be influenced by how this is done. The effects of three alternative smoothing methods are reported below.

The most parsimonious of the smoothing methods used here is (a) a moving average. Moving averages were also used by Short (1985, 1986) and Choquenot (1998). In addition, I tested (b) a linear regression of logged herbage mass (‘exponential model’), and (c) a ‘double exponential’ or ‘proportional hazard’ model (Equation 5.19, Manly 1992, p 259), because the result of (b) for two of the *Themeda* pens retained some curvature, so that the double exponential provided a more even distribution of residuals and a better fit (higher R^2 values; see Table 5.4).

$$\text{Herbage mass} = \exp(a \exp(b\ t)) \qquad \text{Eqn 5.19}$$

Table 5.4: R^2 values for exponential and double exponential models fitted to the green herbage mass recorded in each pen during the *Themeda* grazedown. The R^2 value for Pen 2 and Pen 3 is slightly greater for the double exponential model because the plot of $\log_e$ (herbage mass) is slightly curved.

Model	R^2 Pen 1	R^2 Pen 2	R^2 Pen 3
Exponential model	0.80	0.93	0.91
Double exponential model	0.79	0.96	0.92

In all four cases the daily decrements of green herbage mass in each pen (kg ha^{-1}) (or total herbage mass where stated) were converted to food intake values (grams per metabolic kilogram per day) by multiplying by the area of pasture and dividing by the combined metabolic weight of the two kangaroos eating it. Metabolic weight (usually taken to be $\text{bodyweight}^{0.75}$ for mammals) is preferred over live-weight as the basis on which to express food intake (e.g. Short 1985, 1986; Nagy 1987; Caughley and Sinclair 1994). Numerous studies have found metabolic demands scale with the metabolic weight rather than the live-weight (e.g. review by Nagy *et al.* 1999) so the use of this unit facilitates comparison between species, and calculation of feeding rates for different sized individuals within a population (however see Discussion). The impression that live-weight is a simpler measurement is wrong, and merely a consequence of its exponent (1.0) disappearing when viewed from a perspective that is more familiar with live-weight but the alternative perspective would be equally valid, that live-weight is metabolic weight raised to the power of 1.33 (i.e. 1 / 0.75).

There is an opinion that the exponent used to convert liveweight to metabolic weight should be 0.59 for marsupials, rather than 0.75 (Nagy *et al.* 1999), as discussed below together with an explanation of the practical consequences of using an inappropriate value. In recognition of the widespread use of 0.75 as the exponent used to convert liveweight to metabolic weight, I have conformed to that convention but intake values calculated on the basis of 'marsupial metabolic weight' are also presented under Discussion.

To assist comparison between pens of the decline in herbage mass over time (Figure 5.7) and to simplify data analysis, all three *Themeda* pens were commenced from a similar starting value by disregarding the first two estimates of herbage mass from one pen with higher green herbage mass, treating the third day as the starting day.

Is 0.75 the correct exponent for marsupials?

While the choice of 0.75 as the exponent (Short 1985, 1986), is appropriate for study of eutherian mammals, it may not necessarily be applicable to kangaroos. A review by Nagy *et al.* (1999) found that metabolic demands in eutherian mammals scaled with the 0.772 power, not significantly different from the common theoretical value of 0.75, but they also found the metabolic demand of marsupials scales with the 0.590 (95% confidence interval 0.545 – 0.635) power of live-weight, significantly different from that of terrestrial eutherian mammals. Unfortunately the proposal by Nagy *et al.* (1999) that 0.590 is the allometric scaling exponent for marsupial metabolic demand, rather than 0.75, is based mainly on data for small marsupials with only one data point for large (kangaroo-sized) marsupials and contradictory results are not explained, including Green's (1989) finding that metabolic demands for macropodoids scales with the 0.74 power of body mass. Green (1997) commented that more estimates are needed of field metabolic rates in large marsupials, a call that it is easy to agree with. The importance of resolving the issue can be illustrated by example. Short's (1985) estimates of satiated intake for rabbits, sheep and kangaroos are almost the same when expressed in the units he used, namely g $\text{kg}^{-0.75}$ d^{-1}, but if the satiated intake values for red kangaroo and western grey kangaroos are rescaled using 0.59 as the exponent, they increase to 178% of the published value, much higher on a metabolic basis than the intake rate of sheep in the same conditions. A second example assumes the 0.59 exponent was the correct scaling factor for a hypothetical kangaroo-sized species, but this fact was not known to investigators who measured the food intake of a sample of test animals. When they expressed their results in functional response form, a calculation of the intake of animals twice the weight of the test animals would overestimate by 33% if it were carried out in terms of live-weight (exponent of 1.0) and by 12% if it were carried out in terms of the 0.75 exponent.

Selection of an incorrect exponent would introduce no error if the test animals were of the same weight as the ones to which the intake rates were to be applied. In this study the weights of kangaroos used in the grazedowns are similar to expected mean weights of wild kangaroo populations. The mean live weight of the kangaroos in the *Themeda* grazedown was 35 kg and in the *Phalaris* grazedown 25 kg. The mean live weight of eastern grey kangaroos in high density populations can be estimated from the weights of a sample of 332 kangaroos shot at Tidbinbilla in June 1997 (Graeme Coulson, personal communication, 2003) to be 29 kg. (That is an adjustment of the actual mean liveweight of the shot sample, 26.4 kg, to allow for seasonal effects, as explained in Discussion. Kangaroos in shot populations, such as on grazing properties, are likely to be smaller due to selective harvesting, also explained in Discussion).

Selecting functional response models

Many reported functional responses give details of assessment in regard to only one of the theoretical forms (Gross *et al.* 1993; Ginnett and Demment 1995). In this study, at least one equation representing each of the six types of functional responses was fitted to the food intake values by non-linear least squares regression in Statistica 6 (Statsoft 2004). Selection between models is based on the Akaike Information Criterion corrected for small samples (AICc) (McCallum 2000; Burnham and Anderson 2002). The most convenient form of this statistic is the difference between the AICc for each model and the best model, or ΔAIC_c. The preferred models resulting from each data set (two grazedowns, and three degrees of data smoothing) are those with minimum ΔAICc. Models with ΔAIC_c less than two are considered by Burnham and Anderson (2002) to have substantial support from the data.

Table 5.5: Theoretical functional response equations obtained or modified from the literature. The term ‘r’ to provide for any inaccessible residue of food, has been added to the original equation as a matter of course, only its omission being noted, i.e. a Type 5 functional response is nested within the original equation. The prefix ‘Sigmo‘ indicates the addition of an exponent ‘b’ which should evaluate to 1 for no sigmoidality and >2 for high sigmoidality, i.e. in these cases a Type 3 functional response has been nested within the equation. I = intake rate; V = food density (e.g. vegetation); i_{max} = maximum intake rate; V_f = a value of V at which a certain fraction of i_{max} occurs (0.5 for ‘Michaelis’, 0.63 for ‘Ivlev’); s_{max} = maximum slope of the functional response; Break = breakpoint; a and d = other parameters.

Row No	Type	Name of equation and [Number of parameters]	Equation	Reference
1	0	Linear [2]	$I=s_{max}V + a$	
2	1	Ramp [4]	$I=s_{max}(V-r)$ when $(V-r) < \text{Break}$ and $I=i_{max}$ when $(V-r) \geq \text{Break}$	
3	2 or 5	Disc [3]	$I=a(V-r)/[1+d(V-r)]$	Holling (1965)
4	2 or 5	Michaelis [3]	$I= i_{max}(V-r)/[(V_f-r)+(V-r)]$	Noy-Meir (1978)
5	2 or 5	Ivlev [3]	$I= i_{max}\{1 - e^{[-(V-r)/(V_f-r)]}\}$	Noy-Meir (1978)
6	2, 3 or 5	Sigmo-Disc [4]	$I=a(V-r)^b/[1+d(V-r)^b]$	Real (1977)
7	2, 3 or 5	Sigmo-Michelis [4]	$I=i_{max}(V-r)^b/[(V_f-r)^b+(V-r)^b]$	From Noy-Meir (1978) using concept of Real (1977)
8	2, 3 or 5	Sigmo-Ivlev [4]	$I=i_{max}\{1 - e^{[-(V-r)/(V_f-r)]\text{^}b}\}$	From Noy-Meir (1978) using concept of Real (1977)
9	4	Domed [3]	$I=a(V-r) - d(V-r)^2$	Concept from Holling (1965) and Caughley (1981)
10	6	Square root [2]	$I= a \sqrt{}(V-r)$	Concept from Sibelis (1992)
11	6	Power [3]	$I= a (V-r)^b$	Generalised from the square root function

5.3 Results

5.3.1 The decline in herbage mass

On *Phalaris* the three kangaroos in each pen reduced the pasture from 1138 and 1156 kg ha^{-1} (dry weight of green material) to 64 and 11 kg ha^{-1} in 24 days (Figure 5.6). By the last day the residue was mainly thatch and litter, with green leaves poking through.

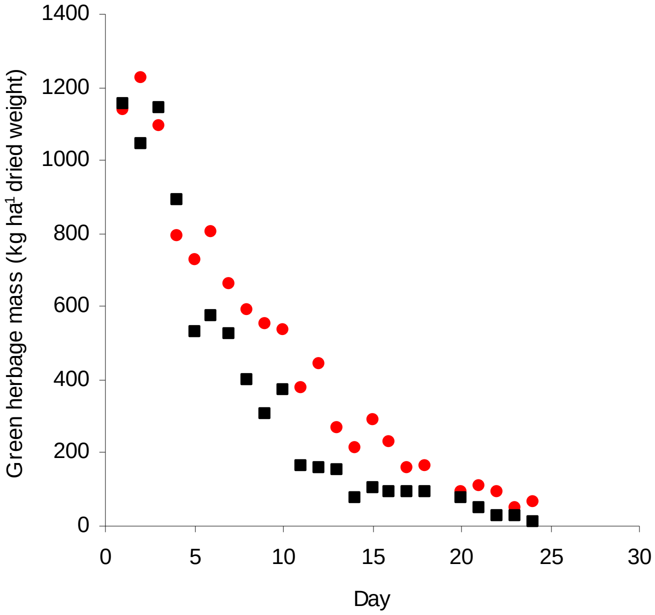


Figure 5.6: The decline in green herbage mass of *Phalaris* pastures in two pens containing kangaroos. Circles = Pen 1; squares = Pen 2.

The change in *Phalaris* herbage mass was smoothed with a (3-point) moving average, but was also well represented by an exponential model. Herbage mass declined at a rate proportional to the herbage mass remaining, or in other words the $\log_e$ of herbage mass declined in a linear fashion, as follows, with the more rapid decline being that in pen 2 (Equation 5.20 SE = 0.18; F = 615.66; df = 1, 21; $p < 0.001$; $R^2 = 0.96$. Equation 5.21 SE = 0.28; F = 453.96; df = 1, 21; $p < 0.001$; $R^2 = 0.95$.):

(Pen 1) $\text{Log}_e\, V = 7.40 - 0.1333\, t$ Eqn 5.20

(Pen 2) $\text{Log}_e\, V = 7.39 - 0.1807\, t$ Eqn 5.21

Standard errors and p levels for each term of both equations are given in Table 5.6.

Table 5.6: Standard errors and p levels for terms of the straight line functions describing the decline in $\log_e$ green herbage mass over time in two *Phalaris* pastures grazed by eastern grey kangaroos.

Parameter	Pen	Value	SE	p level
a	Pen 1	7.40	0.75	< 0.001
	Pen 2	7.39	0.12	< 0.001
b	Pen 1	–0.1333	0.0088	< 0.001
	Pen 2	- 0.1807	< 0.001	< 0.001

The *Themeda* pastures started at similar total herbage mass as the *Phalaris* (a mean of 2326 kg ha^{-1} total dry weight of *Themeda* compared to 2370 kg ha^{-1} of *Phalaris*) but the starting density of green material was lower, with 666, 609, and 704 kg ha^{-1} (dry weight of green material) in the three pens compared to a mean of 1147 kg ha^{-1} for *Phalaris*. On *Themeda*, the green herbage mass declined relatively rapidly for 20 days to an average of 66 kg ha^{-1} and thereafter appeared asymptotic (Figure 5.7), ending at only 8 and 9 kg ha^{-1} in the two pens which were run longest and reached the lowest herbage mass. Total herbage mass continued to decline steeply for longer than green herbage mass (40 days) before it too became asymptotic at about 600 kg ha^{-1}. The ungrazed residue comprised mainly dead parts of the favoured species, *Themeda australis.*

The initial (20 day) slope of the decline in *Themeda* herbage mass was steeper for total herbage mass than for green herbage mass (Table 5.7). This implies that dead material was being eaten, or lost from the pasture in other ways, such as by decomposition or the action of the wind. Total herbage mass continued to decline steeply for longer than green herbage mass before it too became asymptotic at about day 40 (Figure 5.7), further evidence that dead material, as well as green, was being removed. Total herbage mass became asymptotic at 600 – 700 kg ha^{-1}.

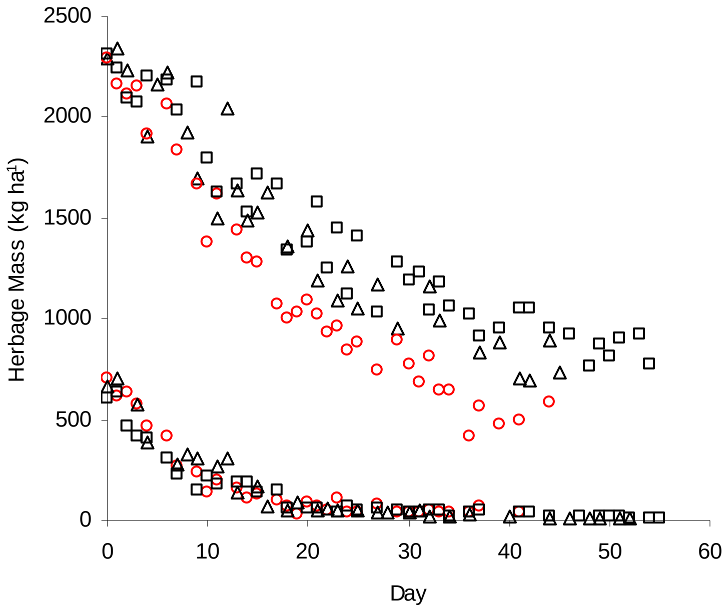


Figure 5.7: Total herbage mass (upper groups of points), and green herbage mass (lower groups) in 3 pens containing *Themeda* pasture being eaten by eastern grey kangaroos. (o = Pen 1; □ = Pen 2; Δ = Pen 3).

Table 5.7**:** Regression terms for the decline in herbage mass of *Themeda* pasture over the first 20 days in three pens.

Parameter	Pen	Slope term	SE	t	df	p value	R^2
	Pen 1	–66.1	3.7	–17.7	16	< 0.001	0.954
Total herbage	Pen 2	–46.4	5.2	–9.0	15	< 0.001	0.852
	Pen 3	–49.0	6.6	30.6	15	< 0.001	0.795
	Pen 1	–35.8	3.2	–11.2	14	< 0.001	0.906
Green herbage	Pen 2	–27.1	3.4	–8.1	14	< 0.001	0.834
	Pen 3	–32.8	3.5	–9.5	12	< 0.001	0.891

5.3.2 Moving average

A 4–point moving average was used to smooth the decline in green herbage mass of *Themeda* (Figure 5.8). (A 3-point moving average was used for the less variable data for *Phalaris*.)

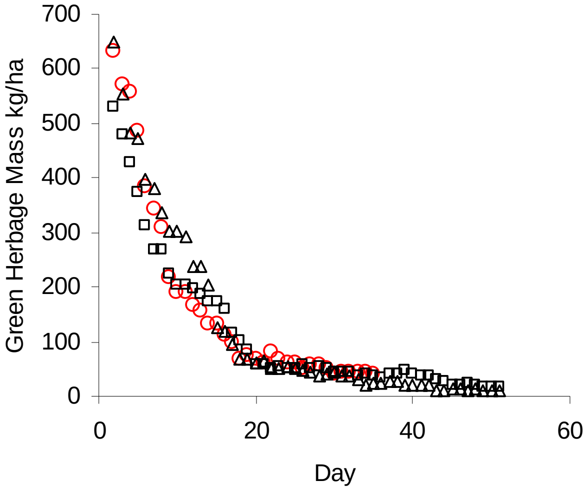


Figure 5.8: Trends in daily estimates of green herbage mass in three pens containing kangaroo grass (*Themeda australis*) being eaten by eastern grey kangaroos. Values are 4-point moving averages (o = Pen 1; □ = Pen 2; Δ = Pen 3).

5.3.3 Double exponential

Trends in the herbage mass estimates for each pen containing *Themeda* were obtained using the double exponential model (Equation 5.19) and non-linear least squares regression. The results are given in Equation 5.22 to Equation 5.24 and Table 5.8 (R^2 = 0.970, 0.972, and 0.958 respectively). Figure 5.9 illustrates the three models. Compared to the more ‘noisy’ moving average, the double exponential appears to have resulted in three smoother and more similar relationships,

$$V = \exp(6.620 \exp(-0.0205\ t)) \qquad \text{Eqn 5.22}$$

$$V = \exp(6.442 \exp(-0.0193\ t)) \qquad \text{Eqn 5.23}$$

$$V = \exp(6.596 \exp(-0.0187\ t)) \qquad \text{Eqn 5.24}$$

where V = green herbage mass in kg ha^{-1} and t = time in days.

Table 5.8: Parameter and errors values for Equation 5.22 to Equation 5.24 for trends in green herbage mass in *Themeda* pastures grazed by kangaroos.

Parameter	Pen	Value	SE	t	df	p value
a	Pen 1	6.620	0.031	213.5	30	<0.001
	Pen 2	6.442	0.029	223.0	37	<0.001
	Pen 3	6.596	0.036	182.6	30	<0.001
b	Pen 1	–0.0205	0.0010	–20.1	30	<0.001
	Pen 2	–0.0193	0.0009	–20.5	37	<0.001
	Pen 3	–0.0187	0.0011	–17. 0	30	<0.001

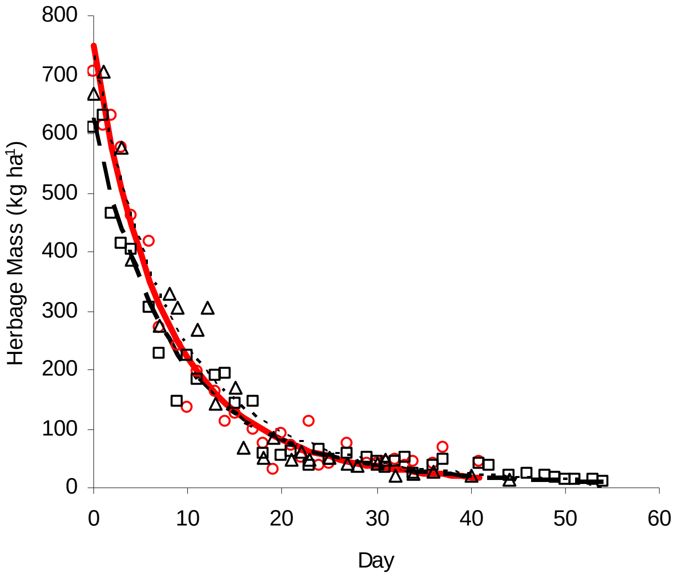


Figure 5.9**:** Daily estimates (symbols) and double exponential models (lines) of green herbage mass in three pens containing kangaroo grass (*Themeda australis*) being eaten by eastern grey kangaroos (o = Pen1; □ = Pen 2; Δ = Pen3).

The effect of the different methods of smoothing the data from the *Phalaris* grazedown is illustrated in Figure 5.10 which also includes the functional responses which provide the most parsimonious explanation of the pattern (see below).

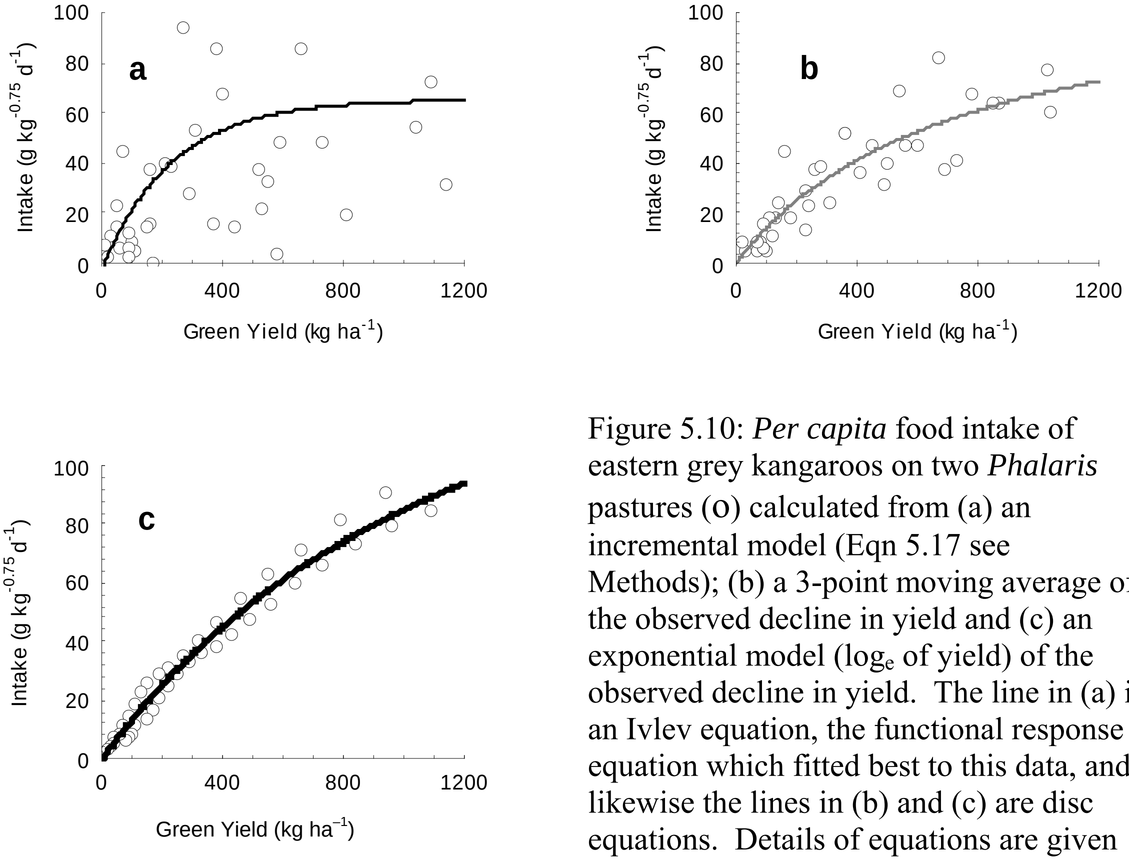


Figure 5.10: *Per capita* food intake of eastern grey kangaroos on two *Phalaris* pastures (o) calculated from (a) an incremental model (Eqn 5.17 see Methods); (b) a 3-point moving average of the observed decline in yield and (c) an exponential model (log$_e$ of yield) of the observed decline in yield. The line in (a) is an Ivlev equation, the functional response equation which fitted best to this data, and likewise the lines in (b) and (c) are disc equations. Details of equations are given in Table 5.10.

On *Themeda* the estimate of the kangaroo's intake from the incremental model (Equation 5.17 see Methods) produces the expected scatter of points (Figure 5.11). The use of a 4-day moving average to smooth the decline in herbage mass in each pen, reduced the scatter of points on the plot of intake against herbage mass, as expected (Figure 5.12).

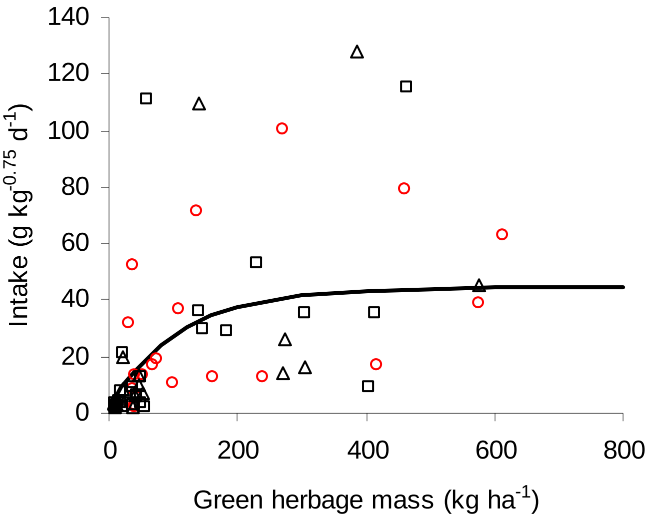


Figure 5.11: *Per capita* food intake of kangaroos on *Themeda* pastures (o = Pen1; □ = Pen 2; Δ = Pen3) calculated by the incremental model (Equation 5.17). Adjustment for pasture growth was by Equation 5.18. The solid line is the theoretical functional response which fitted best to these data, an inverse exponential (Ivlev) equation. (See Results and Table 5.11 Row 5a.) Disc and Michaelis equations fitted almost as well, and the curves are visually indistinguishable at this scale. The estimate of the inaccessible residue of vegetation was 4 kg ha^{-1} for the Ivlev and 8 kg ha^{-1} for the disc and Michaelis curves however the residual amounts were not significantly different from zero.

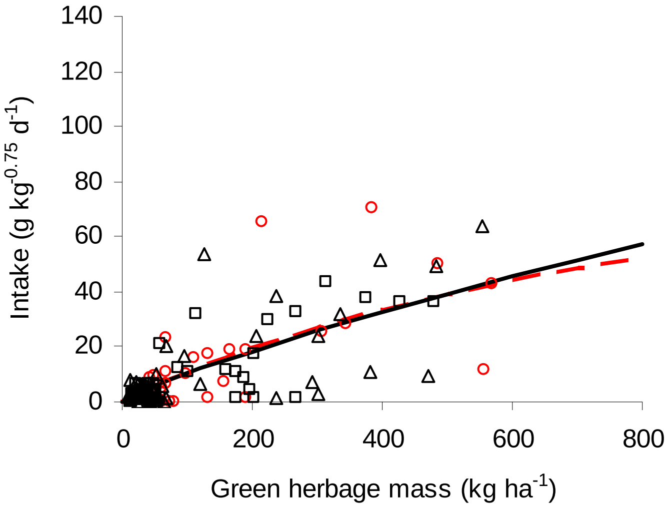


Figure 5.12: *Per capita* food intake of kangaroos on *Themeda* pastures (o = Pen 1; □ = Pen 2; Δ = Pen 3) calculated from a 4-point moving average of the observed decline in herbage mass. Adjustment for pasture growth was by Equation 5.18. The two lines are a disc equation (dashed) and a power equation (continuous), both lacking a term for inaccessible residue of vegetation, these being the functional response equations which fitted best to this data (in spite of their mathematical dissimilarity). Details of models are in Table 5.11 rows 3b and 10c.

When the double exponential model was used to smooth the decline in herbage mass, the resulting plot of intake data from the three *Themeda* pens (Figure 5.13) was refined to a line of points for each pen.

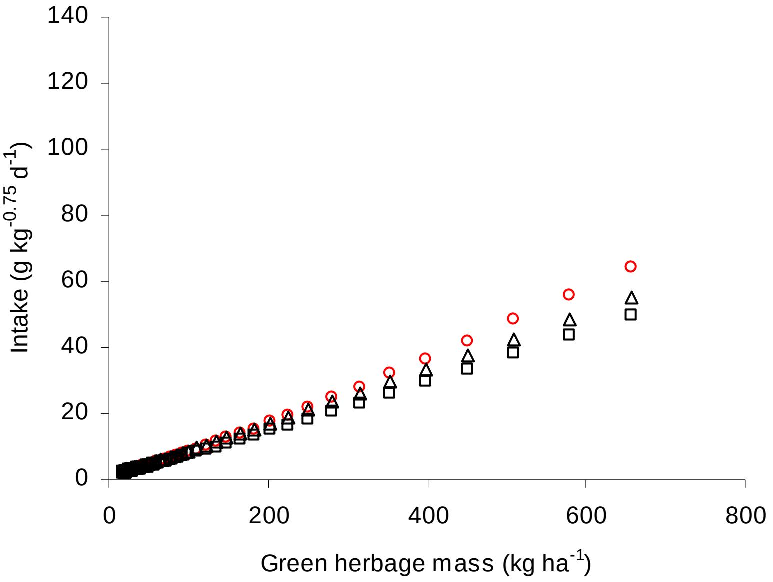
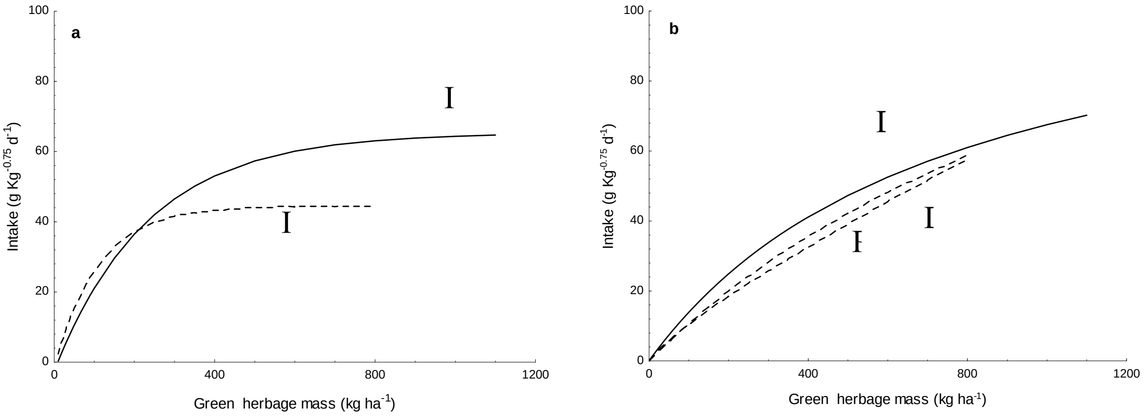


Figure 5.13: *Per capita* food intake of eastern grey kangaroos on kangaroo grass (*Themeda australis)* pastures (o = Pen 1; □ = Pen 2; Δ = Pen 3) calculated using a double exponential model to smooth the observed decline in herbage mass. Adjustment for pasture growth was by Equation 5.18.

The simpler but less accurate exponential smoothing model, [taking $\log_e$ (green herbage mass)] produces a broadly similar pattern of intake to that of the double exponential model, but in this case the kangaroos' intake starts lower, and intersects the Y axis before reaching zero. It was not used in the estimation of food intake rates.

5.3.4 Fitted per capita functional responses

The estimation of parameters from the *Phalaris* and *Themeda* data for some of the more complex equations including the nested Type 2, 3 or 5, proved problematical for the statistical software used, or if resolved, none of the parameters were significant. Removal of one of the added terms (r or b) sometimes enabled the function to be resolved satisfactorily. Results are presented in Table 5.10 for *Phalaris* and Table 5.11 for *Themeda* and the preferred equations are plotted in Figure 5.15.



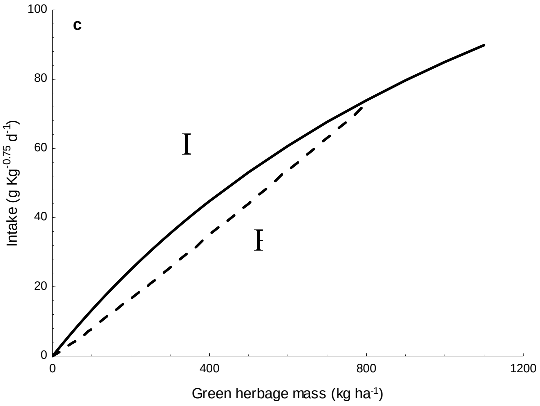


Figure 5.15: Functional responses of eastern grey kangaroos grazing artificial *Phalaris* pasture (continuous lines and range 0 – 1100 kg ha^{-1} green herbage mass) compared with natural *Themeda* pasture (dashed lines and range 0 – 800 kg ha^{-1} green herbage mass). The three charts are based on data resulting from three degrees of smoothing (a) unsmoothed, i.e. incremental model; (b) moving average; (c) exponential model (*Phalaris*) or double exponential model (*Themeda*). Chart (b) has two lines for the *Themeda* pasture because two functional responses had equal best ΔAICc scores. I= Ivlev function; D= disc function; P= power function. Details for fitted equations are in Table 5.10 for *Phalaris* and Table 5.11 for *Themeda*.

The *per capita* rate of food intake on both *Phalaris* and *Themeda* is seen in Figure 5.15 to decelerate gradually with increasing yield, but to become obviously asymptotic only using the data from the incremental model. The statistical outcome is definite. The Δ AIC$_c$ values from the *Phalaris* grazedown indicate a simple disc equation, lacking a term for an ungrazed residue, to be preferable to other types of functional response, whether a moving average is used to smooth the change in yield, or an exponential model, but for the data from the incremental model, an inverse exponential (Ivlev) equation (which generates a very similar shaped response as the disc or Michaelis equation) is preferred, including a term for inaccessible residue. As disc, Ivlev and Michaelis equations are almost interchangeable, it is unremarkable that, turning to the moving average data, the Δ AIC$_c$ value indicate weak support also for a disc equation with a term for ungrazeable residue.

On *Themeda*, the scattered plot of data generated by the incremental model of decline (Figure 5.15 a) resulted in a more limited ability to select between functional response models. Type 2 or 5 equations (Table 5.11 Rows 3a, 4a, and 5a) resulted in similar Δ AIC$_c$ values which were superior to all other equations, and similar R^2 values. Sharper distinctions between models resulted from the use of a moving average or double exponential model to smooth the decline in herbage mass. For data smoothed by a moving average, either the disc equation or the power equation was preferred (based on Δ AIC$_c$ score) providing the residue term was omitted. The power equation was preferred for the data from the double exponential smoothing model.

Table 5.10: ΔAICc values, R^2 values and parameter values for theoretical functional responses fitted to data from eastern grey kangaroos grazing ***Phalaris*** pasture: Row numbers correspond to Table 5.5. Bold lines enclose equations with ΔAICc = 0 and these are represented in Figure 5.15. For each of the pasture types, three sets of data, resulting from different degrees of smoothing (see text) were used to evaluate each equation. The ΔAICc values and R^2 values for individual equations should be compared only within columns. ##=Fitting not attempted (inappropriate); && = Unable to calculate or result nonsensical.

Row No.	Name of equation and formula	Data = Incremental model		Data = Moving average		Data=Exponential model	
		ΔAICc (R^2)	Parameter value (SE) p value	ΔAICc (R^2)	Parameter value (SE) p value	ΔAICc (R^2)	Parameter value (SE) p value
1	Linear I= s_{max} V + a	11.3 (0.178)	s_{max} =0.050 (0.017) p=0.005 a=20.7 (8.8) p=0.02	8.6 (0.747)	s_{max} =0.0662 (0.0064) p<0.001 a=9.4 (3.0) p=0.003	23.2 (0.953)	s_{max} =0.0854 (0.0031) p<0.001 r=6.3 (1.4) p=0.085
2	Ramp I=s_{max} V when V< Break and I= I_{max} when V≥ Break		Evaluates to linear fit	##	s_{max} =0.112 (0.027) p<0.001 r = –14 (45) p=0.76 i_{max} = –0.072 (0.030) p=0.02 Break =360 (109) p=0.002	## (0.970)	s_{max} =0.1051 (0.0078) p<0.001 r= –24 (19) p<0.001 i_{max} = –0.048 (0.012) p<0.001 Break =526 (76) p<0.001
3a	Disc I=a(V-r)/[1+d(V-r)]	3.8 (0.252)	a=0.39 (0.029) p=0.939 r=13 (54) p=0.123 d=0.0044 (0.0049) p=0.014	1.2 (0.788)	a=0.169 (0.071) p=0.022 r=10 (43) p=0.816 d=0.0015 (0.0012) p=0.208	2.9 (0.973)	a=0.146 (0.14) p<0.001 r=5 (13) p<0.001 d=0.00071 (0.00018) p<0.001
3b	Disc without r I=aV/(1+dV)	5.2 (0.251)	a=0.32 (0.17) p=0.664 d=0.0038 (0.0030) p=0.01	**0.0** (0.787)	a=0.158 (0.029) p<0.001 d=0.00134 (0.00055) p=0.011	**0.0** (0.973)	a=0.1419 (0.0076) p<0.001 d=0.00067 (0.00011) p<0.001

Row No.	Name of equation and formula	Data = Incremental model		Data = Moving average		Data=Exponential model	
		ΔAICc (R^2)	Parameter value (SE) p value	ΔAICc (R^2)	Parameter value (SE) p value	ΔAICc (R^2)	Parameter value (SE) p value
8	Sigmo-Ivlev $I=I_{max}\{1-e^{[-(V-r)/(V_f-r)]^b}\}$	**0.0** (0.258)	I_{max}=65.3 (14) $p<0.001$ r=9 (65) p=0.887 b=722 (>10^7) p=1 V_f =168546 (>10^7) p=1	&&	&&	&&	&&
9b	Domed without r $I=aV-dV^2$	6 (0.279)	a= 0.187(0.032) $p<0.001$ d=0.000124 (0.000036) $p<0.001$	3.3 (0.782)	a=0.128 (0.012) $p<0.001$ d=0.000063 (0.000015) $p<0.001$	1.9 (0.973)	a=0.1310 (0.0046) $p<0.001$ d=0.000047 (0.000006) $p<0.001$
10	Square root $I=a\sqrt{(V-r)}$	9 (0.223)	a=2.28 (0.32) $p<0.001$ r=6.3 (49) p=0.899	6.50 (761)	a=2.091 (0.097) $p<0.001$ r=20.5 (1.8) $p<0.001$	&&	&&
11b	Power without r $I=aV^b$	8.9 (0.226)	a=3.3 (3.5) p=0.339 b=0.44 (0.16) p=0.011	4.1 (0.777)	a=0.74 (0.62) p=0.240 b=0.66 (0.13) $p<0.001$	8.3 (0.968)	a=0.41 (0.11) p $p<0.001$ b=0.777 (0.41) $p<0.001$

Model selection results for the following equations are not included above in Table 5.10 because they could not be evaluated for the moving average nor double exponential data sets and are not well supported using the incremental data set (ΔAICc >2). The bracketed numbers correspond to the row numbers in Table 5.5. (4) Michaelis, (5) Ivlev, (6) Sigmo-Disc, (7) Sigmo-Michelis, (8) Sigmo-Ivlev, (9a) Domed, (11a) Power.

Table 5.11: ΔAICc values, R^2 values and parameter values for theoretical functional responses fitted to data from eastern grey kangaroos grazing ***Themeda*** pasture. Row numbers correspond to Table 5.5. Bold lines enclose equations with ΔAICc = 0 and these are represented in Figure 5.15. For each of the pasture types, three sets of data resulting from different degrees of smoothing (see text) were used to evaluate each equation. The ΔAICc and R^2 values should be compared only within columns. ##=Fitting not attempted (inappropriate); && = Unable to calculate or result nonsensical.

Row No.	Name of equation and formula	Data = Incremental model		Data = Moving average		Data=Exponential model	
		ΔAICc (R^2)	Parameter value (SE) p value	ΔAICc (R^2)	Parameter value (SE) p value	ΔAICc (R^2)	Parameter value (SE) p value
1	Linear $I= s_{max} V + a$	13.4 (0.192)	s_{max} =0.070 (0.015) p<0.001 a=12.3 (3.2) p<0.001	0.9 (0.502)	s_{max} =0.0779 (0.0072) p<0.001 a=1.9 (1.4) p=0.18	29.2 (0.990)	s_{max} =0.08713 (0.00074) p<0.001 a = –0.12 (0.15) p=0.446
2	Ramp $I=s_{max} V$ when V< Break and $I= I_{max}$ when V≥ Break		Resolves to linear fit		Resolves to linear fit		Resolves to linear fit
3a	Disc $I=a(V-r)/[1+d(V-r)]$	0.3 (0.271)	a=0.55 (0.52) p=0.288 r=8 (19) p=0.684 d=0.010 (0.013) p=0.440	2.1 (0.477)	a=0.107 (0.044) p=0.018 r = –5 (25) p=0.84 d = 0.0008 (0.0012) p = 0.53	##	##
3b	Disc without r $I=aV/(1+dV)$	3.7 (0.269)	a=0.45 (0.16) p=0.006 d=0.0080 (0.0044) p=0.074	**0.0** (0.506)	a=0.114 (0.022) p<0.001 d=0.00093 (0.00070) p=0.184	##	##
5a	Ivlev $I= i_{max}\{1 - e^{[-(V-r)/(V_f-r)]}\}$	**0.0** (0.273)	i_{max} =44.4 (6.6) p<0.001 r=4 (16) p= 0.806 V_f=112 (45) p=0.014	&&	&&	##	##
11b	Power without residue $I=a V^b$	7.0 (0.243)	a=2.8 (1.4) p=0.047 b=0.453 (0.089) p<0.001	**0.0** (0.506)	a=0.24 (0.15) p=0.112 b=0.82 (0.11) p<0.001	**0.0** (0.992)	a=0.0588 (0.0055) p<0.001 b=1.065 (0.015) p<0.001

Model selection results for the following equations are not included above in Table 5.11 because they could not be evaluated for the moving average nor double exponential data sets and are not well supported using the incremental data set (ΔAICc >2). The bracketed numbers correspond to the row numbers in Table 5.5. (4a) Michaelis, (4b) Michaelis without r, (5b) Ivlev without r, (6) Sigmo-Disc, (7) Sigmo-Michelis, (8) Sigmo-Ivlev, (9) Domed, (10a) Square root, (10b) Square root without r, (11a) Power.

5.4 Discussion

The widely used ‘Type 1, 2, 3’ classification of functional responses introduced by Holling (1959, 1965, 1966), and extended by Caughley (1981) to include Type 4 functional responses, has been further extended in this chapter, to refer to Type 5 and 6, for ‘inaccessible residue’, and ‘power’ functional responses, respectively. The common recognition of but three forms of functional response is inadequate, in view of the publication of both the theoretical basis, and supporting data, for domed, inaccessible residue, and power forms as well (Holling 1966; Noy-Meir 1975; Hassell *et al.* 1976, 1977; Short 1986; Sabelis 1992).

The previous paragraph refers to mainly theoretical considerations. However this chapter has also answered the calls by Abrams and Ginzburg (2000) for measurement of functional responses in conditions as close to natural as possible. Many of the published functional responses for large wild herbivores have been measured in unrealistic conditions, such as during brief bouts in feeding arenas (e.g. Spalinger *et al.* 1988; Shipley and Spalinger 1992; Gross *et al.* 1993; Ginnett and Demment 1995). The results given in this chapter join the few exceptions, including the results of Short (1985, 1986, 1987) and Choquenot (1998).

Most estimates of herbivore functional responses have fitted only one of the six forms of functional response to the data, or rarely two. For example Short (1986) recognised Types 2 and 5. In some cases the data appears more likely to fit forms that were not tested, e.g. the plot of Short’s (1985) data for red kangaroos and Short’s (1986) data for western grey kangaroos appear to be of an unsaturating pattern (i.e. Type 6). However Short (1985, 1986) reported only the fitting of a (saturating) inverse exponential curve (Type 2 or 5) and no statistic was reported to indicate how well it fitted. A similar equation also fitted the intake data from this study, but a Type 6 functional response provided a better fit to the *Themeda* data.

5.4.1 Estimation of the ‘best’ functional response model

The similar R^2 values for several of the functions (Tables 5.10, 5.11), especially for the *Phalaris* grazedown, emphasise the limitations of this statistic alone (e.g. McCallum 2000) for selecting between alternative non-linear models. ΔAICc provided greater ability to discriminate between alternatives as it selected the most parsimonious model with good fit to the data (Burnham and Anderson 2002, pp 5 – 77).

Marshal and Boutin (1999) showed the practical difficulty of conducting an investigation which would have the statistical power to distinguish even very different types of functional response. In this investigation the apparent variation from day to day in the estimates of intake of *Themeda* pasture would suggest the need for similar caution. It is fortunate that the estimates made in the *Phalaris* pasture were less variable.

Sabelis (1992) commented that interpretation of functional response shapes can be 'highly arbitrary' and should be accompanied by quantitative models based on the underlying mechanisms. This study has been empirical rather than mechanistic, yet some of the models tested are based on mechanistic considerations e.g. having terms for 'attack rate' and 'handling time' of prey.

Seven functional responses preferred on statistical grounds alone resulted from the six data sets from the two grazedowns (Figure 5.15, Table 5.10, Table 5.11). In making the final selection between alternatives (some due to different ways of smoothing the raw data) it is best to consider biological as well as statistical criteria.

Phalaris and *Themeda* pastures are obviously different, including in their value as food for herbivores (Ayres *et al*. 2000), otherwise graziers would not expend the considerable effort to replace one with the other, yet the functional responses to them of eastern grey kangaroos are similar for the moving average data and exponential model data (Figure 5.15), with the higher intake rates in both cases observed on the *Phalaris*. The incremental model also generates broadly similar responses for both pasture types but in that case there is a greater separation of maximum intake rates between the artificial *Phalaris* pasture and the lower quality natural pasture.

Compared to the data from the incremental models and the exponential (or double exponential) models, the moving average datasets seem to be a reasonable compromise between 'noisy' data and 'overfitting' (Figure 5.10 to Figure 5.13). Moving averages have been used previously for the same purpose (Short 1985, 1986; Choquenot 1998). Three functional responses fit the two sets of moving average data equally well. A disc equation and a power equation fit equally well to the *Themeda* data, and a disc equation provided the best fit to the *Phalaris* data. Terms for inaccessible residue, and for sigmoidality were not supported (Table 5.10, Table 5.11).

The statistical estimation of disc equations for both pasture types is fortuitous as it simplifies comparison. It is also possible to ascertain that the corresponding parameters for the two different pastures are not significantly different (Table 5.12).

Table 5.12: Parameter values (95% confidence intervals) for disc equations fitted to *per capita* intake data for eastern grey kangaroos grazing *Phalaris* and *Themeda* pastures.

Parameter	*Phalaris*		*Themeda*	
a	0.158	(0.100 – 0.226)	0.114	(0.070 – 0.158)
d	0.00134	(0.00024 – 0.0024)	0.00093	(0.00047 – 0.00233)

Thus, the preferred equation, using the average of these parameters is:

$$I = 0.136\ V / (1 + 0.001135\ V) \qquad \text{Eqn 5.25}$$

where I is intake rate (g kg$^{-0.75}$ d^{-1}) and V is green pasture herbage mass (kg DM ha^{-1}).

This (Type 2) form of functional response with no inaccessible residue is the form reported most often, especially for herbivores (Lundberg 1988; Begon *et al.* 1996; McCallum 2000). Its mathematical representation by a disc equation is the one originally used by Holling (1959, 1965, 1966) and the one most commonly fitted, and differs from the use exclusively of Ivlev equations for functional responses of kangaroos and other herbivores in Australia by Short (1985, 1986, 1987), Caughley (1987), Choquenot (1998), and Choquenot *et al*. (1998).

The disc equation provides a saturating form of functional response, but as evident from Figure 5.15, Equation 5.25 is not saturating in the range of herbage mass presented to the kangaroos in this study (0 to 1100 kg ha^{-1} green herbage mass on *Phalaris* and 0 to 800 kg ha^{-1} on *Themeda*). This is apparent in another way also; with a (Type 6) power function among the strong contenders for the preferred functional response on *Themeda*, it is clear that the functional response is not saturating. However this is at best only weak support for the theoretical predictions of Sabelis (1992) mentioned in the introduction which can be interpreted as suggesting the possibility of unsaturating herbivore functional responses. Notably, the less variable data from the *Phalaris* pasture did not support a Type 6 equation.

The preferred approach of evaluating nested mathematical forms of functional response equations (McCallum 2000, Section 5.2.3) was handicapped by the limitations of statistical routines available and small data sets. Some of the more complex equations with four parameters including terms for both inaccessible residue and sigmoidality, could not be evaluated for any of the data sets.

There is no support for an inaccessible residue of green herbage mass (Type 5 functional response) because the term for the residue is not significantly different from zero. Likewise with the exponent for sigmoidality (Type 3 functional response) which either could not be evaluated or was not significantly different from 1 (no sigmoidality). Thus the functional response of eastern grey kangaroos as presented here (Equation 5.25, Figure 5.15) is more similar to the functional response for red kangaroos in the sheep rangelands (Short 1985; 1986) than to that for western grey kangaroos (Short 1986). Whereas western grey kangaroos stopped eating when the pasture declined to 180 kg ha^{-1} (Short 1986) eastern grey kangaroos (this study) and red kangaroos (Short 1985, 1986) reduced the green herbage mass to virtually nothing and continued to feed at low herbage mass, including by digging up roots. On the other hand, Short's functional responses are to total herbage mass, whereas this study used green herbage mass for the abscissa. When considered in relation to total herbage mass, the eastern grey kangaroos left a substantial ungrazeable residue, especially in the *Themeda* grazedown, ranging between pens 500 – 700 kg ha^{-1}.

That ungrazeable residue really is a resource that is inaccessible to the kangaroos. At the end of the *Themeda* procedure the kangaroos were nearly starving. All six kangaroos had visibly lost condition, not just the old ones, and the average weight loss was 19.5%. They had eaten all that they could of the green parts of species normally eaten by kangaroos and they had also consumed the accessible parts of certain species rarely eaten by wild kangaroos such as *Kunzea phylicoides* (a tea tree containing pungent oil) and *Astroloma humifusum* (a low heath with spiky leaves); they had dug up grass tussocks to eat roots and they had even eaten sections of the hessian lining the fences (which was then removed). In other words, it is certain that the residue remained only because the kangaroos were incapable of consuming it. Comparable circumstances occur naturally, and persist for longer (Caughley *et al*. 1985; Robertson 1986; McCullough and McCullough 2000) and when they do the kangaroo population is likely to collapse, such as the 70% decline in kangaroo density recorded by Robertson (1986). The result from this grazedown suggests that in temperate pastures the kangaroo population will begin to collapse before it denudes the pasture any further than what took place in this procedure. In the real world (outside a short-lived grazedown procedure) until pasture growth resumes, further reduction of the pasture residue is likely, but from decay, surface water flow, wind, and other grazing animals, rather than from grazing by kangaroos.

The greater similarity between the functional response of eastern grey kangaroos and that of red kangaroos and the contrast to that of western grey kangaroos may appear paradoxical if considered mainly in terms of taxonomic relatedness of kangaroos. But it merely demonstrates that the pasture is an important contributor to the functional response relationship. On *Phalaris*, the eastern grey kangaroos were able to maintain a food intake at low herbage mass as were the red kangaroos in Short's (1986) study but it is considered likely that the western grey kangaroos would do the same on a *Phalaris* pasture. The combined results reflect the adaptation of eastern grey kangaroos to temperate grasslands and the adaptation of red kangaroos to the vegetation and environment of the sheep rangelands where Short's (1986) study was based. Likewise, the variation in the size of the ungrazeable residue between the western grey kangaroos in the chenopod shrublands and the eastern grey kangaroos in kangaroo grass, is likely to reflect differences in the vegetation, as much or more than differences between kangaroo species.

The *per capita* functional response of eastern grey kangaroos estimated in this chapter has the potential to be a key component of interactive models for eastern grey kangaroos in temperate grasslands, equivalent to the functional responses in the models of Caughley (1976a, 1987), Barlow (1987); McLeod (1997); Choquenot (1998), Choquenot *et al*. (1998) and Owen-Smith (2002a, b). Used in that way, the functional response, combined with kangaroo density, determines how much herbage is removed by the kangaroo population per unit time, and therefore, in combination with pasture growth, the functional response affects how much herbage is available to determine the kangaroos' population growth rate.

In temperate grazing systems, with less-erratic rainfall than arid lands, a food-limited population of herbivores is often able to maintain the vegetation in an even, eaten-down condition, sometimes termed a 'marsupial lawn' (Newsome 1975; Pharo and Kirkpatrick 1994). These are likely to comprise a higher proportion of green leaf and a lower component of stems and dead material than the pastures in the grazedowns. By comparison, the grazedown pastures had been suddenly reduced by extreme stocking, and had not had time to 'accommodate' to a relatively constant level of harvesting. They still retained a high proportion of long dead stems. For this reason, I assume that intake rates at low herbage mass in the wild will be higher than ones recorded here.

5.4.2 Maximum intake rate

Maximum *per capita* intake rates for kangaroo species range from 44.4 to 87 g $kg^{-0.75}$ d^{-1} (Table 5.9). The three values for maximum intake in Table 5.9 between 62 and 66 g $kg^{-0.75}$ d^{-1} are consistent with the idea that they approximate the satiated intake for two kangaroo species feeding in vegetation types to which each species is reasonably well suited, chenopod shrubland for red kangaroos and long green grass (*Phalaris*) for eastern grey kangaroos. The higher value for western grey kangaroos (87 g $kg^{-0.75}$ d^{-1}) perhaps reflects the estimation uncertainty mentioned in that case by Short (1986). The lower value for eastern grey kangaroos on *Themeda* (kangaroo grass) may then appear anomalous, but at least some of this difference is understandable, for two reasons. The *Phalaris* provided superior feeding conditions to the *Themeda*, with a high proportion of green leaf, so maximum intake rates would be expected to be lower on *Themeda*. Secondly, the mean water content of the *Themeda* pasture was 28% which is below the level at which intake is reduced (Green 1997) whereas the *Phalaris* pasture was 83% water, which is conducive to a high intake rate.

Table 5.9: Maximum *per capita* intake rates estimated in kangaroo grazing studies using the metabolic scaling exponents of 0.75 and 0.59 in an Ivlev equation.

Name of kangaroo grazing study	Maximum Intake, using exponent 0.75	Maximum Intake, using exponent 0.59
This study, eastern grey kangaroos on *Phalaris*	65.3 (SE = 14)	109.1
This study, eastern grey kangaroos on *Themeda*	44.4 (SE = 6.6)	78.5
Short (1985), red kangaroos in chenopod shrublands	62.3	104.7
Short (1986), red kangaroos in chenopod shrublands	66	115.1
Short (1986), western grey kangaroos in chenopod shrublands	87	151.5

5.4.3 Kangaroo grazing compared to sheep

The concept of 'total grazing pressure' (Freudenberger 1995) has had widespread use, not only in the sheep rangelands, but also in temperate areas (ACT Kangaroo Advisory Committee 1996, 1997). The application of the concept of total grazing pressure requires the consumption of all vertebrate herbivores to be taken into account, not just domesticated ones, in a process intended to reduce unsustainable management practice. It therefore requires a means for converting the consumption by herbivores such as rabbits, horses, cattle, feral goats and kangaroos to common units. These are ‘dry sheep equivalents’ (DSE), meaning the annual consumption of a non-lactating sheep. The ‘grazing pressure’ expressed in DSE, for the population of each grazing species, becomes the basis for strategic and economic decisions (Freudenberger 1995; Grigg 2002), such as whether to harvest species such as feral goats and kangaroos, to control either species as a pest, or to apply the effort to something else.

Based on calculations of kangaroo energetics, Grigg (2002) argues that the conventionally accepted factor for estimating the contribution of kangaroos to total grazing pressure is an overestimate at 0.70 DSE, and that the true value may be as low as 0.15 for harvested kangaroo populations and 0.25 for unharvested ones (the difference between the two being due to the lower mean live-weight of kangaroos in harvested populations). He discusses Short’s (1985, 1986) contrasting results for satiated intake which by Grigg’s (2002) calculations suggest the DSE values would be 0.37 to 0.62 depending whether the populations were harvested and whether the size of kangaroos more closely matches that recorded in Queensland (Pople, unpublished data cited in Grigg 2002) or South Australia (Cairns, unpublished data cited in Grigg 2002).

After calculating a range of DSE values for kangaroos by various indirect methods (all values being less than 0.7) Grigg (2002) concludes ‘having a good estimate of an appropriate value for the DSE is important before any meaningful conclusions can be drawn about how much benefit can be expected from the reduction of kangaroo numbers.’ This study has provided an opportunity to calculate such an estimate.

The kangaroo functional response from this study can be compared with the functional response for sheep reported by Barlow (1987) for temperate pastures of New Zealand (but based on a range of studies, including ones from temperate Australia) and also with the one for sheep in the chenopod shrublands of arid Australia reported by Short (1985) in order to resolve the wide variation in these estimates of kangaroo grazing pressure (from 0.15 to 0.7 DSE).

There is a convention that all sheep weigh 45kg (live-weight) for purposes of estimating DSE (Grigg 2002) but the weight of kangaroos varies more widely than that of sheep, both within and between populations, so a variable, or a range of values, is more appropriate. The lowest mean live-weight of kangaroos used by Grigg (2002), based on Pople (unpublished), is 16 kg (for a harvested Queensland population) and the highest, based on Cairns (unpublished), is 32 kg (for an unharvested South Australian population).

The mean live-weight of an unharvested eastern grey kangaroo population on one of the study sites in June 1997 was 26.4 kg based on 332 randomly selected kangaroos (data from Graeme Coulson, personal communication). That would be an underestimate of mean live-weight over the full year because the sample was taken in June, before the usual period of late-winter mortality of many sub-adults and some old animals (Chapter 6). The sub-adults and very old animals can be excluded from Coulson's sample, by restricting the sample to those animals whose age was estimated from molar progression (Chapter 6) to be between 2.0 and 13.9 years. The remaining animals had a mean live-weight of 31.3 kg. That would be an overestimate because it totally excludes these age classes, and for the whole year, but the two values together define a range within which the true value must lie. Based on these June 1997 estimates, I estimate the full-year mean live-weight for the unharvested populations on the study sites to be 29 kg, (near the mid point between 26.4 kg and 31.9 kg) and for harvested populations in the local region, 17 kg, based on the scaling relationship in Griggs (2002) values [calculated by Pople (unpublished data) for harvested and unharvested populations in Queensland and South Australia].

Grigg (2002) calculates DSE values of kangaroos from Short's (1985, 1986) results for satiated intake of sheep, red kangaroos and western grey kangaroos, i.e. for harvested populations 0.37 (Queensland) and 0.42 (South Australia), and for unharvested populations 0.54 (Queensland) and 0.62 (South Australia).

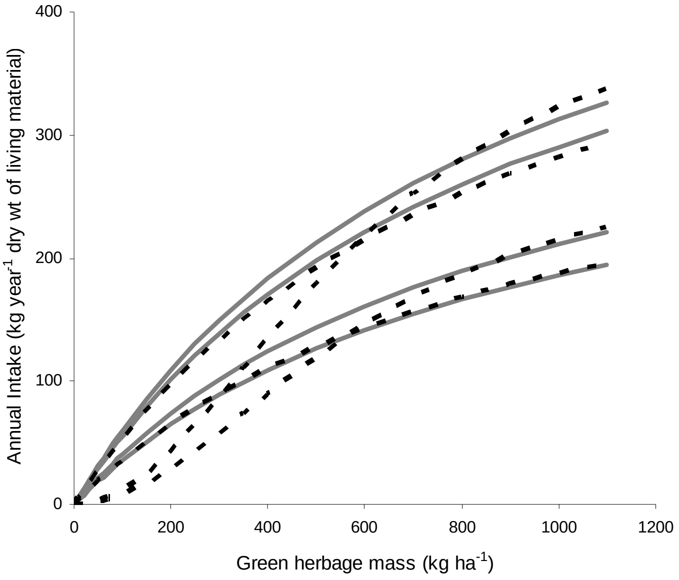


Figure 5.16: Continuous lines = functional responses for eastern grey kangaroos of 16, 19, 29 and 32 kg live-weight. The two lower lines represent mean live-weights typical of harvested populations and the upper two are representative of unharvested populations (see text). Dashed lines = functional responses for fractions of sheep: Upper pair of lines 0.6 sheep, lower pair 0.4 sheep. Within each pair the sigmoid functional response is that reported by Barlow (1987) for sheep in temperate grasslands and the other is Short's (1985) functional response for sheep in chenopod shrublands in the Australian arid zone.

Figure 5.16, based on the conventional 'mammalian metabolic weight' (live-weight$^{0.75}$), shows that no single DSE value can represent the true comparison of sheep and kangaroo consumption rates well. The sigmoid functional response for sheep in temperate grassland (Barlow 1987), shows sheep eating at a lower rate than eastern grey kangaroos when the pasture is at low herbage mass and at a higher rate than kangaroos when herbage mass is high. However, values of 0.4 DSE for harvested eastern grey kangaroo populations and 0.6 DSE for unharvested ones provide a better visual match to the sheep functional responses than DSE values 0.1 higher or lower. More exactly, for a pasture of 600 kg ha^{-1} green herbage mass, the intake of an eastern grey kangaroo population with a mean live-weight of 16 kg [Grigg's (2002) harvested population, and close to my estimate for local harvested populations] is the equivalent of 0.43 DSE using Short's (1985) functional response for sheep in the arid zone and 0.39 DSE using Barlow's (1987) functional response for sheep in temperate grassland. Thus the DSE value for a harvested eastern grey kangaroo population in temperate grassland compared to sheep in temperate grassland (i.e. 0.39) falls between the two values calculated by Grigg (2002) from Short's (1985, 1986) results for similar harvested kangaroo species in chenopod shrublands, i.e. 0.37 (for Queensland) and 0.42 (for South Australia).

It is the same with the results for unharvested populations of kangaroos. For a pasture of 600 kg ha^{-1} green herbage mass, the intake of an eastern grey kangaroo population with a mean live-weight of 29 kg (i.e. the Tidbinbilla site) is the equivalent of 0.66 DSE using Short's (1985) functional response for sheep in the arid zone and 0.61 DSE using Barlow's (1987) functional response for sheep in temperate grassland. Thus the value for unharvested eastern grey kangaroos in temperate grassland compared to sheep in temperate grassland (i.e. 0.61) falls between the two values calculated by Grigg 2002 from Short's (1985, 1986) results for similar species in chenopod shrublands, i.e. 0.54 (for Queensland) and 0.62 (for South Australia).

The contribution of kangaroos to total grazing pressure is of most interest on grazing properties, where kangaroo populations are often harvested, or shot as pests, therefore of these values, 0.4 DSE is the statistic of more general interest. An exception may occur in temperate grasslands when herbage mass is below 400 kg ha^{-1} green herbage mass.

Thus, Grigg's (2002) contention that the 0.7 DSE rating is an overestimate is supported, and so are his calculations based on the satiated intake values estimated by Short (1985,1986). Grigg (2002) then extends his analysis further to argue for DSE values much lower than the ones he calculated from Short's (1986, 1986) data, by reference to the different resting and field metabolic rates applying to marsupials and eutherians, and he justifies the discrepancy between these lower values and those calculated from Short's (1985,1986) results with reference to the artificial conditions of a grazedown, contending that (a) food was plentiful and the kangaroos may have been taking an opportunity to increase body condition and (b) that perhaps in a small pen the kangaroos were constrained to a pentapedal gait, their most inefficient form of locomotion. However Grigg's (2002) analysis in regard to metabolic rates is circumvented by the grazedown procedure; the intake estimates already incorporate the effects of any metabolic factors applying to the species. However as mentioned above, the choice of the metabolic scaling exponent in which to express the result can have an important effect. The live-weight of the kangaroos is known for all of the kangaroo grazedown studies so the functional responses can easily be reworked using 'marsupial metabolic weight' (live-$weight^{0.59}$). If the contention of Nagy *et al*. (1999) about the need for a 0.59 'marsupial' metabolic scaling exponent is accepted, (not withstanding the reservations expressed in section 5.2.3) the metabolic weight of the kangaroos in the grazedowns is reduced but the biomass of vegetation they consumed is the same; this means they consumed faster on a metabolic basis. The effect is that the DSE value for harvested populations becomes 0.55 and for unharvested populations, 0.77.

As for Grigg's (2002) arguments about the artificial conditions of a grazedown, in this study the kangaroos lost body condition, so his argument (a) is not applicable. Grigg's (2002) argument (b) is unlikely, in that (1) the primary mode of movement of the kangaroos observed in this grazedown, other than when feeding, was not pentapedal, but their typical hopping mode, and (2) that wild kangaroos would undoubtedly travel much further every day. Any issue with efficiency seems more likely to be in the opposite direction, meaning the kangaroos in the grazedowns were more efficient than wild ones, because their food, water, shade and refuge from predators were co-located.

Thus this study provides no support for the lowest values proposed by Grigg (2002) for the grazing pressure of kangaroos (0.15 – 0.25 DSE), but if the mammalian metabolic scaling exponent (0.75) is accepted for kangaroos, there is support from this study and those of Short (1985, 1986) for values of 0.4 DSE for harvested populations and 0.6 DSE for unharvested ones, rather than the conventionally accepted 0.7 DSE.

The previous chapter was about the vegetation and this one has examined the feeding by kangaroos on the vegetation. The next three chapters are mainly about the kangaroos, starting with a chapter which evaluates the assumption implicit in the interactive model that the herbivore population is food limited.

CHAPTER 6

DEMOGRAPHIC PROCESSES AND POPULATION LIMITATION

The Indians sometimes kill the kangaroo; but their greatest destroyer is the wild dog, who feeds on them. I once found in the woods the greatest part of a kangaroo, just killed by the dogs, which afforded to three of us a most welcome repast. Marks of its turns and struggles on the ground were very visible. – Watkin Tench - 1788

Nine dingoes were individually recognizable at Gudgenby.

CHAPTER CONTENTS

6 DEMOGRAPHIC PROCESSES AND POPULATION LIMITATION

6.1 Introduction and literature review

A central assumption of Caughley's (1976a) interactive model is that herbivore population growth rate is determined by food supply. This chapter tests that assumption for the study sites using evidence from dead or killed kangaroos. It is clearly a safe assumption for the arid and semi-arid regions, where much of the research on kangaroo population dynamics has been based (Chapter 1). Little has been published on kangaroo population dynamics from outside that region (Chapter 1) but there are data supporting the *a priori* expectation of Arnold *et al.* (1991) that in more temperate areas, factors other than food would limit kangaroo population growth, as follows.

Predation is the alternative factor for which there are the most data and hypotheses. Robertshaw and Harden (1986) showed dingo (*Canis lupus*) predation to be limiting the density of a large forest-dwelling macropod, the swamp wallaby (*Wallabia bicolor*) and Robertshaw and Harden (1989) hypothesized that some populations of eastern grey kangaroos had been eliminated by dingo predation. Arnold *et al*. (1991) hypothesized that fox predation of juvenile kangaroos, as well as starvation, explained high and variable mortality of western grey kangaroos, although no predated carcasses were found. Thompson (1992) found dingo predation reduced kangaroo populations to such low levels, the predation even appeared to work to the detriment of the dingo population. Finally, Banks *et al*. (2000) demonstrated experimentally that fox predation limited recruitment in temperate eastern grey kangaroo populations. Whereas the kangaroo populations in arid and semi-arid regions are subject to death by starvation on an obvious and sometimes massive scale (Caughley 1962; Poole 1973; Robertson 1986, 1987a; Shepherd 1987), starvation is less apparent for kangaroo populations in temperate areas. The literature is equivocal. On one hand, food stress, or variants such as flooding, was identified as a necessary requirement for population crashes apparently caused by disease (Speare *et al*. 1989); starvation was considered to be a significant cause of mortality in temperate kangaroo populations by Dawson (1995, p. 55, pp 58 – 59) probably based partly on the observations of Jaremovik (1984); and the ACT Kangaroo Advisory Committee (1997) recommended culling to avert starvation, and reported the numbers of starved kangaroo carcasses found in searches at Tidbinbilla. On the other hand, starvation was not mentioned in discussion of the cause of episodes of heavy winter mortality by Quin (1989); starvation was only described as a possible mechanism by Arnold *et al*. (1991); and in an intensive study on four sites near Gudgenby, Banks *et al*. (2000) found no carcasses of sub-adult kangaroos killed by either predators or starvation.

As explained in Chapter 3, foxes were poisoned on all of the study sites to reduce the influence of fox predation, but the dingo population at the Gudgenby site was apparently unaffected. It was argued in Chapter 1 that predation is unlikely to be a significant influence at Googong (no dingoes, little poaching) or Tidbinbilla (few dingoes, no poaching). Evidence of dingoes at the Gudgenby site (14 km^2) was reported in Chapter 1, including 44 individual sightings and identification of at least nine individual dingoes by variations in their appearance.

In this chapter I present evidence comparing the condition of the living and dead kangaroos that indicates whether the study populations were food limited, or predator limited, or both.

Also, the age classes at which mortality is greatest are identified, and its seasonal timing. Further, the evidence available regarding adult survival and fecundity is also presented here. In their review of herbivore population dynamics, Gaillard *et al*. (2000) reported they found virtually no useful information on demographic rates for kangaroos. Long-term field studies of marked animals are the most desirable source of that information (Gaillard *et al*. 2000) but the estimates given here will be valuable, at least until such long-term studies have been completed.

6.1.1 Discerning the limiting mechanisms

I use the terms 'regulation' and 'limitation' following Sinclair (1989), Boutin (1992) and Krebs (2002).

Population regulation: the processes by which a population returns toward an equilibrium density after it is perturbed. A regulating process must have a density dependent effect, i.e. one that increases, in proportional terms, with increasing density. Regulation is synonymous with Caughley's (1987) 'centripetality'.

Population limitation: the processes that, in combination, set the equilibrium density, including both density dependent and density independent factors.

Population dynamics: the analysis of the causes for change in population density, including both regulation and limitation.

Three controversies in ecology (a) between the density-dependent school and its opponents (Krebs 2002), (b) over the perceived conflict between regulation and limitation of populations (Sinclair 1989; Turchin 1999), and (c) over the cause of cycles in the abundance of boreal mammals (Hik 1995; Turchin and Hanski 1997) have generated bodies of literature that may create the impression that it is difficult to say with confidence what processes limit the abundance of any population of wild vertebrate animals. Some conflicts persist too long. It is possible now to see 'answers' or at least explanations, in each of these cases and a growing number of examples of field-based research teasing out an explanation of processes determining population dynamics, e.g. Krebs *et al*. (2001). Much of the debate over (a) and (b) has been resolved in review papers (Sinclair 1989; Van Ballenberghe and Ballard 1994; Krebs 1995; Sinclair 1996; Murray 1999; Turchin 1999; Krebs 2002; Sinclair and Krebs 2003), by definitions of terminology (e.g. Sinclair and Pech 1996; Krebs 2002) and by definitions of requirements for research design (Krebs 2002). Similarly, in regard to (c), Krebs *et al*. (1995) pointed out that in all cyclic populations many factors change in correlation with population density, so causes can be recognised only by experimental manipulations. Relatively few attempts to explain the cycles have been experimental, with the notable exception of a large body of work elucidating the causes of cycles in voles and other small mammals by Erkki Korpimaki and his co-workers (Korpimaki and Norrdahl 1998; Klemola *et al*. 2000; Korpimaki *et al*. 2004).

In fact there are many published examples where limiting mechanisms have been experimentally demonstrated or reasonably inferred. Examples of studies reporting evidence for food limitation include ones for wildebeest (Mduma *et al*. 1999), for wild pigs (Choquenot and Ruscoe 2003), for barn owls (Taylor 1994; Hone and Sibly 2003), and for large African grazing mammals (Sinclair *et al*. 2003). Examples of predation limited populations include kangaroos and emus (Caughley *et al*. 1980; Pople *et al*. 2000; but see Newsome *et al*. 2001 for a contrary view), rabbits (Pech *et al*. 1992; Banks *et al*. 1998), a range of small and medium-sized native Australian mammals (Sinclair *et al*. 1998), three species of small mammals (Risbey *et al*. 2000), and small African grazing mammals (Sinclair *et al*. 2003). Demonstrating that populations may be limited by an interaction of food and predation is more demanding than demonstrating these factors individually, but that too has been done successfully, e.g. for snowshoe hares (Krebs *et al*. 1995; Hodges *et al*. 1999).

To demonstrate that a process is regulating, the definitional requirement (Sinclair 1989; Krebs 2002) is that the slope of the percentage loss/gain on density must be positive for a loss process such as mortality, and negative for a process that increases density. In this study the density of the eastern grey kangaroo populations remained high (Chapter 7, 8) so the required test could not be carried out. The critical experiments outlined by Boutin (1992) to discriminate between hypotheses about limitation and regulation of moose illustrate the problem well, because all four of his alternative hypotheses for limitation or regulation generate the same result when the prey is at high density (his Table 3) and can only be separated when the density of the prey species is reduced, or varies naturally. Such variation or reduction was not part of this study. Although it has been claimed repeatedly that demonstrating that a process is limiting is trivial (Sinclair 1989; Van Ballenberghe and Ballard 1994; Sinclair and Pech 1996; Krebs 2002), to determine the most important limiting process(es) has always been, and continues to be, a significant result, e.g. Grange *et al*. (2004) have sought to determine what limits a keystone species, the Serengeti zebra (*Equus burchelli*). The zebra population has remained stable since 1960 when rinderpest disease was eliminated while two sympatric keystone ungulates have increased, wildebeest (*Connochaetes* *taurinus*) and buffalo (*Syncercus caffer*). Knowing the main factors limiting a population is potentially important for wildlife conservation and management.

Limitation can be studied by experimentally manipulating the food supply, predation level, or both, e.g. Banks *et al*. (2000) manipulated predation. Another approach, or one combined with the manipulation, has been to identify the cause of death of a sample of animals fitted with mortality transmitters. Those options were not possible within resources available for this study. Instead, the sites were unmanipulated and the data observational. In the same circumstances, Sinclair and Arcese (1995) were able to use only the percentage of fat in femur marrow (FMF) to evaluate alternative hypotheses about limiting mechanisms for a free ranging population of wildebeest, as per Table 6.1.

The similar use of FMF reported in this chapter is based on the hypothesis that predation risk influences foraging behaviour. An individual animal faces a hypothetical dilemma, to minimise the risk of predation, e.g. by remaining in the centre of the herd, yet to maintain adequate body reserves in the face of competition for food, e.g. by foraging at the edge of the herd where competition is lower (Hik 1995; Sinclair and Arcese 1995). Eastern grey kangaroos on the study sites respond to this dilemma. Colagross and Cockburn (1993) showed that eastern grey kangaroos at the Tidbinbilla site spent more time in vigilance behaviour when at the edge of a group than when on its interior, and attributed this behaviour to differences in perceived risk of predation. The spatial aspect of the optimisation dilemma has been recognised in the literature, such as use of risky habitats or safer ones (e.g. Werner *et al*. 1983; Hik 1995; Banks *et al*. 1999; Banks 2001). Kangaroos in the region of the study sites exhibit spatial responses to predation risk. Banks (2001) showed that kangaroos in valleys near the Gudgenby site foraged further from cover after fox density had been reduced, than kangaroos in valleys with higher fox density. Banks (1997, 2001) also showed females with young-at-foot forage alone or in smaller groups to a greater extent where predation risk is lower. Thus, foraging alone or in small groups seems likely to be a mechanism to mitigate costs of group foraging, and the use of this mechanism to be limited by the perceived risk of predation. In summary, eastern grey kangaroos in the region of the study sites do respond to the optimisation dilemma of reducing predation risk while increasing foraging opportunity. The measurement of FMF is one way to discern whether the kangaroos' response to the dilemma is the population limiting mechanism.

Table 6.1: Relative proportion of fat in femur marrow (FMF) of living, predator killed and starved animals under three limitation hypotheses, based on Sinclair and Arcese (1995).

Hypothesis	FMF of living animals	FMF of predator kills	FMF of non-predation ('starved') deaths
Predation	High	High	Not applicable or Low
Predator sensitive food	High	Intermediate	Low
Surplus / Food	High	Low	Low

To evaluate limiting mechanisms using evidence from carcasses, three hypotheses need to be considered. First, the predator limitation hypothesis proposes that predators hold the population well below starvation levels (Boutin 1992; Van Ballenberghe and Ballard 1994). Following Sinclair and Arcese (1995), bone marrow fat, the last fat reserve to be depleted in a starving mammal, should be high in both the predator kills and the live samples (Table 6.1). Second, the predator-sensitive food hypothesis (Abrams 1991; Hik 1995; Sinclair and Arcese 1995; Krebs *et al*. 1996) proposes that predation and food limit the population in combination. As food becomes less available, animals take greater risks, or in other ways become more vulnerable, and some are predated. While food is limiting (starvation is occurring) predators are removing prey that would otherwise have survived a further continuation of competition and food depletion. Predator kills should have marrow fat levels lower on average than live animals but higher than starvation (non-predation) deaths (Table 6.1). Third, in the surplus hypothesis, or 'doomed surplus' (Errington 1946) food is limiting and the losses to predators (if any) comprise individuals that would have dispersed, or died from starvation, disease or other causes, if predators had not intervened. The surplus hypothesis would result in mean marrow fat levels that were low in both starved and predator-killed animals but high in live animals (Sinclair and Arcese 1995). (The three hypotheses cannot be distinguished merely by estimating the ratio between the numbers of predated and non-predated carcasses because of large differences in their relative detectability.)

6.1.2 Body condition in kangaroos

Caughley and Sinclair (1994) provide a succinct and comprehensive introduction to the literature on indexes of condition, drawing on a more detailed overview by Hanks (1981). Although the kidney fat index (KFI) (Riney 1955) has been the most widely used to estimate body condition (Anderson *et al*. 1972), especially in North American deer species, more than one such index is needed to span the possible range of body conditions encountered across the range of animals in a population, and through varied seasonal conditions. As the condition of a group of animals declines, first the variation in their KFI may indicate their relative condition, but when their KFI values have declined to near zero, differences in their FMF will be more informative. In particular, the KFI declines to zero too soon to identify starving animals (Caughley and Sinclair 1994). Suttie (1983) reported an exception to this relationship in a population of red deer (*Cervus elaphas*), where marrow fat and kidney fat were depleted in parallel below a KFI of 40%.

Few examinations of body condition of any kangaroo species have been published, contrary to the situation with large mammals on other continents, such as a range of ungulates in Africa (Hanks 1981), and mule deer, white-tailed deer, caribou and moose in north America. Weight over length types of index have had limited use on live kangaroos (Arnold *et al.* 1991; Moss and Croft 1999; Nave *et al.* 2002) but Shepherd's (1987) KFI data for red kangaroos and western grey kangaroos at Kinchega appear to be the only published measures of fat in kangaroos. Giles (1980) recorded FMF in feral pigs in Australia but I have found no published data on bone marrow fat in any marsupial species, nor any other fat levels of kangaroos, except Shepherd's (1987) KFI results for red kangaroos and western grey kangaroos in the semi-arid rangelands.

6.2 Methods

The living population of kangaroos on the sites could not be deliberately sampled (by shooting) for logistic and political reasons. Instead, data were gleaned from kangaroos that had been killed in sudden accidents, such as a storm at Googong in March 2003 and a bushfire at Tidbinbilla in January 2003 (Chapter 3), but my main recourse was to examine kangaroos killed by motor vehicle accidents on the roads between the sites. From all eastern grey kangaroo carcasses I sought both a kidney fat index and femur marrow fat index, as well as the age and sex of each animal and its cause of death.

Five sets of data from dead kangaroos were available (Table 6.2). First, there was the data collected from kangaroo carcasses found during visits to pasture assessment locations (Chapter 4). The second sample was also carcasses found during pasture work, of eastern grey kangaroos killed by the bushfire on the Tidbinbilla site in January 2003 (Chapter 3). Thirdly, 42 animals killed on roads between the study sites were examined for comparison with the animals that had died on the study sites. These were augmented by three carcasses of kangaroos killed by a storm at Googong. Fourthly, Graeme Coulson provided data from 333 adult eastern grey kangaroos which had been shot non-selectively on the Tidbinbilla site in

1997, and their 161 dependent young, and fifthly, Lyn Nelson allowed me to use kidney fat data she had collected from 119 of those adults.

Table 6.2: Sources of data used in this chapter on the age, condition and breeding of eastern grey kangaroos.

Source of dead kangaroos	Population represented	Number	Age data	Condition - Kidney Fat Index?	Condition - Marrow Fat Index?	Breeding information?
1. Carcasses found on sites	Kangaroos dying (various causes)	234	Yes	Yes - few	Yes	No
2. Bush fire kills found on Tidbinbilla site	Living population sampled at birth pulse	84	Yes	No	No	No
3. Road and storm kills	Living population	42+3	Yes	Yes - few	Yes	Yes
4. Sample shot 1997	Living population	333	Yes	No	No	Yes
5. Sample shot 1997 - kidney fat sub-sample	Living population	119	Yes	Yes	No	No

Kangaroos killed by car, bullet, bushfire or storm are samples of the living population. Only the first row of Table 6.1 represents the dead population. None of these data sets is comprehensive, for example, percentage of fat in bone marrow was obtained only from the roadkills and the first set of found carcasses, but their sex was often recorded as ‘unknown’ due to removal of the pouch and gonads by scavengers. Another limitation is the potential for confounding effects due to the use of samples from different sites and years. A preferable approach would be to take shot samples, as well as carcasses, from the study sites. That was not possible during this study.

6.2.1 Kangaroo body condition assessment

Kidney fat index

Providing the kidneys had not been removed by predators or scavengers, a visual estimate of kidney fat index was recorded on a 5 point scale using a set of reference photographs of kidney fat of eastern grey kangaroos taken at Tidbinbilla in 1976 by Mike Braysher (personal communication). In 1997, Lyn Nelson had used these photos to visually rate 170 kidney fat deposits before removing the fat and kidneys to measure the kidney fat index conventionally (e.g. Shepherd 1987). Using Nelson’s data (Lyn Nelson NSW NPWS personal communication), a significant relationship was found (SE = 1.986; F = 2544; df = 1, 169; p<

0.001, $R^2 = 0.938$) between the square root transformation of percentage kidney fat index and the visual rating, so that, when back transformed:

$$\text{Kidney Fat Percent} = 9.200\ \text{Visual Rating}^2 \qquad \text{Eqn 6.1.}$$

The finding that the KFI differs bilaterally in some herbivore species (Anderson *et al*. 1972; Torbit *et al*. 1988) was checked for eastern grey kangaroos. In previously published studies KFI has been assessed on either the left side (e.g. Shepherd 1987) or the right side (e.g. Caughley 1962, according to Shepherd 1987). Nelson's data include 52 animals from which both kidneys were removed. The weights of the left and right kidneys are significantly different (paired t test, mean difference = 0.5 g, $t=2.16$, $p < 0.05$, $df = 51$) and so are the weights of the fat (paired t test, mean difference = 1.4 g, $t=2.54$, $p < 0.05$, $df = 51$) but these weight differences are small and cancel each other, so the kidney fat indexes are not significantly different (paired t test, mean difference = 2.1, $t=1.27$, $p > 0.2$, $df = 51$). The absence of a strong bilateral asymmetry of KFI in eastern grey kangaroos means KFI results may be more easily compared between studies. From the carcasses in this study I took the visual rating of kidney fat index as the average of both sides, but either side was used alone if the other side was damaged or discoloured, which was often the case.

Percentage fat in bone marrow

When bone marrow fat is metabolised, it is replaced with water, so either a low level of fat in the marrow or a high water content is indicative of starvation (Nieland 1970; Hanks 1981). Following the procedure described by Caughley and Sinclair (1994), the marrow was removed from the middle third of one femur. Marrow samples that smelt rotten or showed any sign of shrinkage away from the inner surface of the bone were rejected. The drying method of estimating fat content of the bone marrow was used (Nieland 1970; Hanks 1981; Caughley and Sinclair 1994). The drying method is an appropriate compromise between speed, precision and safety. It is faster and cheaper than fat extraction with a Soxhlet apparatus, safer than the method used by Verme and Holland (1973) of dissolving the fat in chloroform, and has been shown to be precise and accurate for a range of ungulate species, unlike the widely used but imprecise visual estimation based on colour and consistency (Verme and Holland 1973; Hanks 1981; O'Gara and Harris 1988).

A correction was developed by Brooks *et al*. (1977) to allow for non-fat, non-water residues in ungulate species , namely:

Percent marrow fat = (100 Dry Weight / Wet Weight) - 7 Eqn 6.2

The relationship between fat content and dry weight percent represented by Equation 6.2 was thought likely to reflect the properties of most mammalian marrow, not just ungulates, but to confirm that it applied to eastern grey kangaroos, the fat in a subset of the marrow samples was also assayed using a Soxhlet apparatus for comparison with the estimate obtained by the drying method. Ian Wallis of the School of Botany and Zoology at the Australian National University, carried out the work.

Figure 6.1: Carcasses vary widely in detectability and persistence. (a) Peter Hann, pictured, has seen this carcass of a starved 21-month-old sub-adult but most disappear unseen; (b) Carcass of a sub-adult apparently eaten by a wedge-tailed eagle and a fox; (c) Of various measurements and samples taken from dead kangaroos, some of the most useful evidence came from femur marrow samples (being taken with saw).

The regression of percentage dry weight (PDW) against fat percentage measured in the Soxhlet apparatus (SOX) had an X intercept of 10% rather than 7% (Equation 6.3 PDW = 1.06 SOX - 10, $R^2 = 0.97$) and the difference was significant (t-test, t = 2.52, df = 31, p = 0.017). In other words I adjusted the % dried weight estimates by 10% rather than the 7% used by Hanks (1981) and others. Although some more recent work has used Equation 6.2 without the 7% adjustment for the non-fat, non-water content (Husseman *et al*. 2003), in my results that would introduce a large bias at the lowest fat levels recorded and I therefore followed the practice as originally described by Nieland (1970) and recommended by Hanks (1981), Caughley and Sinclair (1994) and others. The higher intercept value for kangaroos than ungulates indicates either that the femur marrow of eastern grey kangaroos contains slightly lower proportions of fat and water than samples from the average ungulate, or that the samples from this study (from carcasses) had partly dried out before I weighed them, or both. The eight African ungulate species contributing to the 7% average include one with an intercept term as high as 10% (Brooks *et al.* 1977). Which of the alternatives was correct (dried samples or kangaroos different to the average ungulate) could readily be resolved by measuring fresh samples from shot kangaroos but it would be unnecessary for this study. Rather, the tight regression (high R^2 value) demonstrates that the drying method works in a marsupial species and produces estimates of fat content of femur marrow from carcasses of eastern grey kangaroos that are amply good enough for the comparative use given here to discern causes of mortality (e.g. comparison between road kills and starved animals).

$$\text{Percent marrow fat} = (100\ \text{Dry Weight} / \text{Wet Weight}) - 10 \qquad \text{Eqn 6.3}$$

Percentage of femur marrow fat from eastern grey kangaroos was examined in relation to age because results from young animals of some species appear to be unreliable (Hanks *et al.* 1976) or have been considered unsuitable for combination with measurements from adults (Torbit *et al.* 1988). These difficulties may be partly due to the relationship demonstrated by Adams (2003) who showed caribou FMF increased rapidly in the first 20 days of life. However kangaroos of equivalent age were not sampled for FMF in this study.

To distinguish between the three limitation hypotheses (Table 6.1) fewer marrow samples were available in this study than to Sinclair and Arcese (1995), i.e. in this study 59 from carcasses and 36 from living eastern grey kangaroos, but the sampling rate in this study was more intense due to the shorter time period. Sinclair and Arcese (1995) had 226 records of FMF from wildebeest carcasses found during the ‘stationary phase’ of the Serengeti wildebeest population, 1977 – 1991, which is the stage most comparable to this study. Sinclair and Arcese (1995) also had 158 FMF records from living wildebeest, taken during two years of the ‘increase phase’.

6.2.2 Identification of cause of death

Carcasses of kangaroos that had been killed and eaten by dingoes were often indistinguishable from the carcasses of kangaroos that had been scavenged by dingoes. Sinclair and Arcese (1995) used signs on the ground to distinguish predation from scavenging but such evidence is not always present where dingoes have killed kangaroos so the eaten carcasses were all recorded as ‘unknown’. Fortunately, dingoes commonly indulge in surplus killing of kangaroos (Dawson 1995, p. 57).

Until they had been skinned, the surplus killed kangaroos were indistinguishable from ones that had died by starvation. At the beginning of the study, illustrations of sheep (*Ovis aries*) killed by dingoes (Fleming *et al*. 2001) were a helpful diagnostic aid (making allowance for the much stronger skin of kangaroos which the dingoes seem incapable of penetrating while the kangaroo is still mobile). After skinning, the cause of death was obvious if the kangaroo had been killed by dingoes. The main sign of dingo attack on large male kangaroos was that the rump was severely bruised (Figure 6.2 c, d). The neck was also damaged. Small surplus-killed kangaroos lacked damage to the rump but the neck was damaged or the chest had been crushed, resulting in massive bleeding when ribs penetrated the lungs and heart (Figure 6.2 a, b). The term ‘surplus’ here means only that the carcass had not been eaten by the time I found it, and retained the soft tissues essential for me to diagnose it as having been killed, rather than scavenged. In reality, dingoes return to carcasses days or even weeks after earlier visits, so it is uncertain whether any predator killed carcass was truly a surplus, unless it was monitored until it decayed.

Carcasses of kangaroos killed, as distinct from scavenged, by wedge-tailed eagles (*Aquila audax*) (WTE) were apparently rare, but difficult to identify because the areas on the head that would retain some of the diagnostic marks are often the first to be damaged by the eagles when they start to feed. Four carcasses were noted as ‘possible WTE kill’. The number of eagles on the study sites is small, and they mainly scavenge rather than kill kangaroos (Chapter 3), so any error in identification of eagle kills is likely to be insignificant.

Both wedge-tailed eagles and dingoes continued to hunt kangaroos when carcasses were readily available, but both also scavenged carcasses of kangaroos that had died from starvation, and dingoes returned to scavenge carcasses they had previously killed and left uneaten. The rump muscle was usually missing from a carcass eaten by dingoes and large bones had often been chewed. Wedge-tailed eagles often commenced work on a carcass at the uppermost ear, then removed the flesh from the head. Alternatively, they started by opening the abdomen and consuming internal organs. The apparent inability of the dingoes to break the skin of the kangaroos until after they were on the ground, meant that intact carcasses had to be skinned to determine cause of death. Kangaroo carcasses were identified as ‘starved’ if they lacked evidence of predation or diseases such as large cancerous growths, or severe ‘lumpy jaw’ which causes loss of teeth, eventual fracture of the lower jaw, and death (Arundel *et al*. 1977). The placement of quotation marks around ‘starved’ is a reminder that its diagnosis is really the lack of evidence for other causes.

Figure 6.2: Carcasses of eastern grey kangaroos killed but not eaten by dingoes (see Section 6.2.2 for method of determining cause of death). Patches have been roughly skinned to look for evidence of dingo attacks; (a) sub-adult with crushed chest but no bites to rump; (b) internal view of same kangaroo showing broken and dislocated ribs (this carcass lacked external signs of damage); (c) severely damaged muscle on carcass of large male kangaroo which also had no visible external damage (d) carcass of large adult male kangaroo showing ante-mortem damage to rump muscles (uneaten), neck, and upper back. It may have been an eagle that removed the internal organs and the intercostal muscle, leaving the ribs almost intact.

6.2.3 Age determination

The age at death was estimated from molar progression using Kirkpatrick's (1964) regression for eastern grey kangaroos based on the forward movement of molars, and their successive replacement at the back of the molar arcade. A simple clear plastic (acrylic, 'perspex') template was used to record the index in tenths of the last molar (Figure 6.3). The reference-line on the skull from which the molar index is measured, is the line joining the anterior edges of the orbits viewed from below, i.e. looking at the roof of the mouth with the soft tissue removed. To provide visual access to the orbits it is common practice to de-flesh the skulls by burial or boiling (e.g. Wilson 1975; Norbury *et al.* 1988; Coulson 1989b; Augusteyn *et al.* 2004) which is a time-consuming process. I used the method of Pearse (1981), a simple dissection to provide a perpendicular view of the upper molars and expose the orbits to view (Figure 6.4). The dissection does not require any cross-matching of samples, is faster than the traditional de-fleshing, and does not introduce an additional source of measurement error, unlike the method of estimating age from the molar index, and molar index from the protein content of the eye lens (Augusteyn *et al.* 2004).

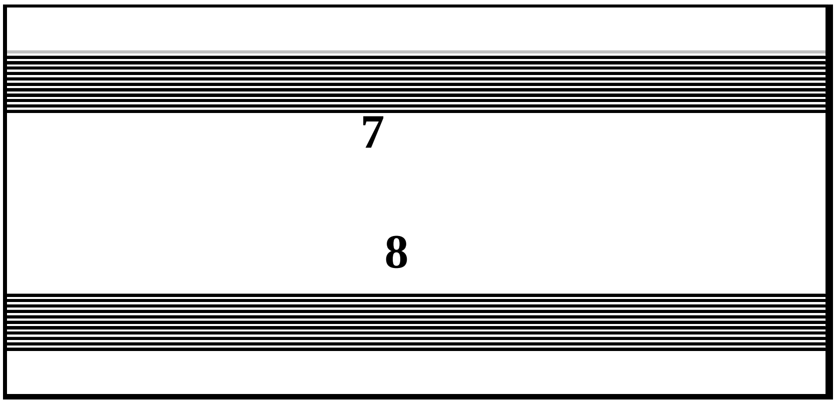


Figure 6.3 Design of one part of a four-part acrylic template to measure the molar index to the nearest tenth of a molar. On the four parts, sets of parallel lines have been scratched with a sharp blade to divide into tenths, each millimetre interval from 7 mm to 14 mm. (No molars were found less than 6.5 mm or more than 14.5 mm long.) To make it easier to quickly locate the appropriate set of index lines in the field, the engraved number indicates the length of molar (mm) to which that set of lines is applicable.

If the head had been damaged in a way that prevented ageing from the molar index, animals up to approximately 3 years (the majority) could be aged from the lengths of their heads, legs, and feet using the regressions published by Poole *et al.* (1982). The value 5.79315 given by Poole *et al.* (1982) for their term b4 in the regression for male leg length was replaced with 5.783 following advice (Graeme Coulson personal communication) that this correction was necessary to generate the same results as those given in tabular form by Poole *et al.* (1982).

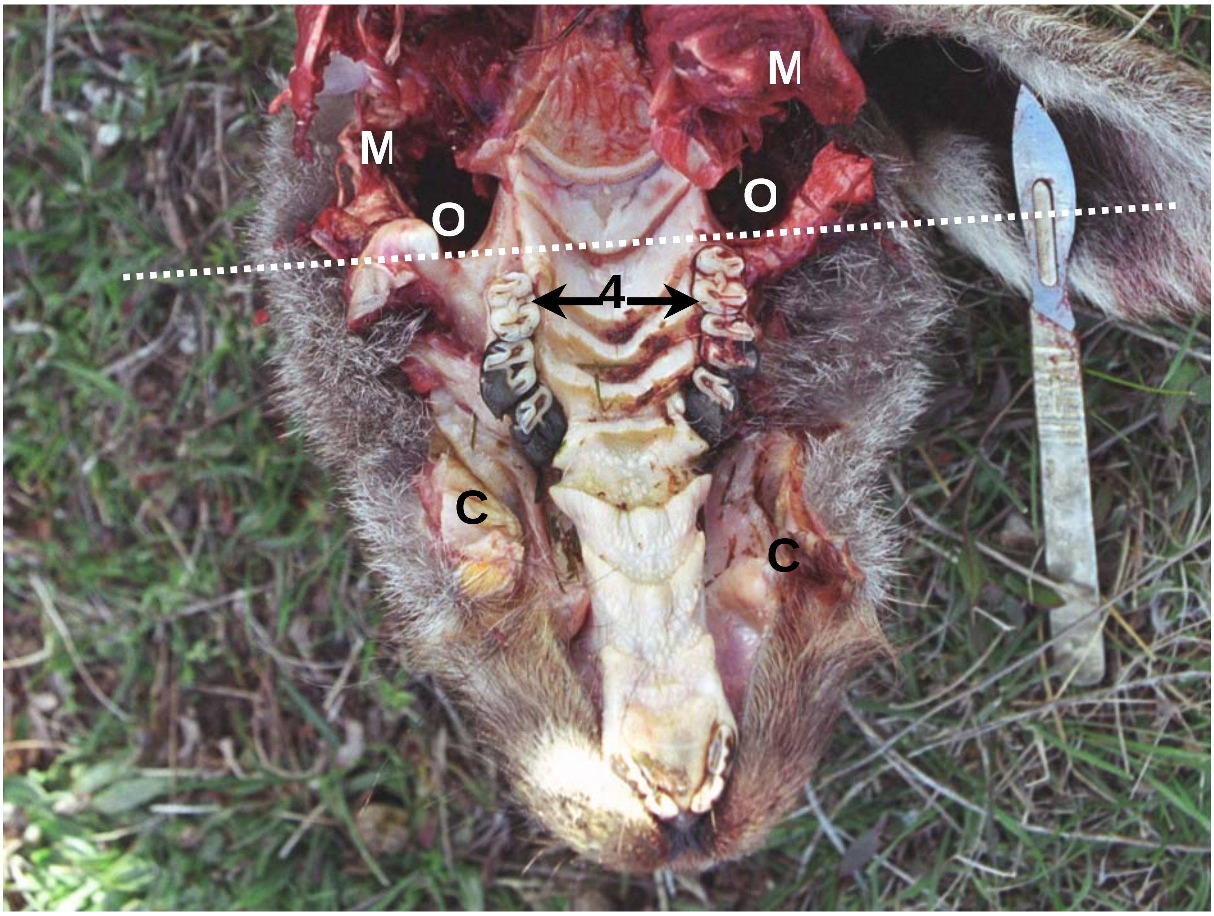


Figure 6.4: The molar index can be read in the field to save time. This is an attached head on a kangaroo carcass in palatal view which has been quickly dissected where found, ready to read the molar index as per Kirkpatrick (1964). The cheeks (C) and jaw muscles (M) have been roughly cut, enabling the lower jaw to be torn away, leaving the ridged palate, fourth molars (4), and orbits (O) clearly visible. A thin layer of tissue has been scraped away to expose the bone forming the anterior rims of the orbits, which are to be aligned as marked with the baseline of a perspex template (Figure 6.3) from which the molar index is measured.

The definition of 'juvenile' used by Gaillard *et al*. (1998) for ungulates was adopted here, i.e. animals less than one year old, with 'sub-adult' kangaroos defined as those one to two years old. These definitions are not entirely satisfactory, but in female eastern grey kangaroos there is no ideal definition of the boundary between sub-adult and adult. Eastern grey kangaroos permanently vacate their mother's pouch at 10.5 months of age (Poole 1975). During their second year, they gradually transfer their feeding from milk to vegetation, and some of the females start breeding. Some females continue to suckle occasionally even after commencing to suckle their own young (Poole 1975).

6.2.4 Mortality rate (q_x)

Method 6 of Caughley (1977a p. 92) was applied to the age distribution of carcasses killed by the bushfire on 18_{th} January 2003 at Tidbinbilla, to generate a life table and hence the age specific mortality rate per 1000 females (q_x). The main requirement, explained by Caughley (1966), is that the population has a stationary age distribution (a special case of a stable age distribution). The population growth rate *r* must be zero, the season of births must be restricted, and the sample must be taken at the birth pulse, for reasons given by Caughley (1966).

The bushfire was well timed for the purpose, close to the mean date of birth (7 January ± 3 SE) as estimated from Graeme Coulson's 1997 shot sample, and more importantly, to its median (30 December) because the birth pattern has the usual skew toward the earlier part of the breeding season (Figure 6.11). The necessary assumption of constant density is supported (Chapter 7). The sample size (87) exceeds the minimum requirement of 50 given by Caughley (1966) for ages taken from dead animals. Graeme Coulson's larger sample, shot in June 1997, is unsuitable for the purpose because it was taken mid way between birth pulses (Caughley 1966). Caughley (1966) explains why q_x is robust to the likelihood (mentioned earlier) that the first age class is under-represented. There is also the question of sampling bias. Caughley (1966) tested the bias of his age distribution for Himalayan thar (*Hemitragus jemlahicus*) by using χ^2 tests between sub-samples. His data were sub-divided according to whether the thar had been aware of the shooter or not, and whether they were shot at long or short range. In similar fashion, a χ^2 test was used in this study to test for differences between the age distributions of the fire-killed sample and the sample shot non-selectively in 1997. Lack of difference would support the use of the fire-killed sample to estimate q_x because it would imply the bias of the fire-killed sample is not significantly different to that of a sample shot in the attempt to eliminate bias. The age distribution was corrected for the missing first age class following Caughley (1977a), likewise the smoothing procedure explained by Caughley (1966) was used. A quadratic term in the regression equation was significant, but not a cubic term.

6.2.5 *Survival of marked kangaroos*

Viggers and Hearn (2005) marked eastern grey kangaroos with radio-transmitters and ear tags at the Googong and Tidbinbilla sites, and another site, in a separate investigation which overlapped with my study. After their radio tracking had been completed I continued to monitor the survival of the ear-tagged animals for an additional year, making two years in total, until it became impractical to continue at Tidbinbilla due to the death of all but two of the marked animals in a bushfire, and difficult at Googong due to loss of ear tags from the males. Between the two sites there were 18 radio-collared or ear-tagged eastern grey kangaroos. All of the females had previously produced young (Viggers and Hearn 2005). None of the males were juveniles or sub-adults. At Tidbinbilla one male moved off the site during the one year radio tracking study (Viggers and Hearn 2005) and in the year after the radio tracking study, an ear-tagged male living in a less accessible part of the site proved too time consuming to monitor. These two kangaroos were excluded from the study leaving 11 females and 5 males (= 16).

At Gudgenby, one female and four males photographed at the commencement of my study had some unique and permanent disfiguration, increasing the sample size to 21, and extending it to the third site. Additional distinctive animals were observed later in the study but they had not been recorded at the beginning of the two year period and therefore are not included in the results. Except for the disfigured animals, the recognition of individual kangaroos as described by Jarman *et al.* (1989) was impractical in this project as thousands, not tens, of kangaroos were present on each site.

6.2.6 Proportion of females breeding

In southern Australia, eastern grey kangaroos are seasonal breeders (Pearse 1981; Poole 1983; Quin 1989; Figure 6.11). In late September, many female eastern grey kangaroos have bulging pouches, which are clearly visible from any direction, due to the presence of large pouch young about to make their final emergence. Before dark during late September 2002 I approached feeding groups of eastern grey kangaroos to within 100 m, and using binoculars, assigned every animal in the group to a sex, age and breeding class. I classified every animal in each group, to reduce the potential for bias. Females with pouch young are readily identifiable but the proportion of nulliparous females might be underestimated if they were listed as ‘unknown’ or confused with sub-adults and young males. Shepherd (1987 p. 148) suggests that western grey kangaroos cannot be reliably sexed in field conditions if they are less than 40 kg, based partly on the results of Johnson and Bayliss (1981) who had attempted to do so. That size includes all females. There are only slight differences in appearance between western grey kangaroos and eastern grey kangaroos (Kirsch and Poole 1972; Caughley *et al.* 1984; McCullough and McCullough 2000). In contrast to other workers, I found I could not reliably sex every member of a group of eastern grey kangaroos, especially in late summer, however in late September the task was much easier.

The proportion of adult females raising young to the stage of permanent pouch emergence enables an upper limit to be placed on the rate of in-pouch mortality, and can be combined with an estimate of the proportion of females in the population, to calculate the annual mortality which must take place to maintain constant density. My observations of feeding groups of kangaroos were intended only to estimate the proportion of females with large pouch young and do not provide an unbiased estimate of the proportion of females in the population. That is because at this time of year, some of the large male eastern grey kangaroos are still segregated in localised areas of good pasture growth such as creek flats (Jaremovik and Croft 1991; personal observation) similarly to red kangaroos (Johnson and Bayliss 1981), and my sampling was not intended to account for such segregation. Instead Graeme Coulson's data from the non-selective shot sample carried out at Tidbinbilla in 1997 provides an estimate of the proportion of females. Coulson's data also enable an independent estimate to be made of the proportion of females that were breeding that can be used for comparison with my estimates. Thirdly, Coulson's data enable an estimate to be made of the fecundity rate with age.

Eberhardt (1985) provided equations and examples for fitting fecundity rate curves. Using Coulson's data from the shot sample, equations of the recommended form were fit by non-linear least squares regression in Statistica 5.3 (Statsoft 1995) to the proportion of females breeding as a function of age. Following conventional practice with demographic data, ages were annual, based on the anniversary of birth, so an animal 1.8 years old would be assigned to the 1 year old age class.

6.2.7 Demographic sensitivity analysis

The equations of Lande (1988) were used to calculate the demographic sensitivity of eastern grey kangaroos on the study sites. The estimates of the required demographic parameters to be used as inputs to the equations were obtained from the sampling described above, and are stated with the results of the sensitivity analysis. Under Discussion they are compared to estimates of elasticity and sensitivity of other populations. Elasticity measures relative sensitivity (Gaillard *et al*. 2000), the change in λ for a given proportional change in a demographic rate, whereas sensitivity is the change in λ for a unit change in a demographic rate (Lande 1988).

6.3 Results

The information from many carcasses is incomplete because only a proportion of carcasses were both fresh and intact. Age at death was the statistic most resistant to the effects of scavengers and decay (14% loss); kidney fat index the least (84% loss), followed by femur marrow fat index (52% loss).

6.3.1 Condition indexes of dead kangaroos

Kidney fat index

Intact kidneys remained in only 24 of the ‘starved’ kangaroos (ones not apparently killed by predators and lacking noticeable signs of disease or other cause of death). None of these had any kidney fat (mean KFI = 0%). Of 10 predator kills with intact kidneys, 2 had some kidney fat, 37%, and 21%, and eight had none, like the one illustrated in Figure 6.2b, giving a mean KFI of 5.8% ± 4.02 SE. Of 25 road killed kangaroos with intact kidneys, eight had some kidney fat, with a mean KFI of 7.2% ± 2.55 SE and a maximum of 37%. These are all low values, even that for the road kills, compared to Lyn Nelson’s shot sample from Tidbinbilla in 1997 which had a mean KFI of 53.6% ± 6.3 SE (n = 119) and ranged from 0 to 230%. The differences in KFI were significant between ‘starved’ kangaroos and those killed by dingoes or cars (ANOVA; F=3.497; df= 2, 56; p= 0.037); but the KFIs of road kills and dingo kills were not significantly different from each other (ANOVA; F=0.090; df= 1, 33; p= 0.766).

Femur marrow fat

Marrow fat results from carcasses of male and female kangaroos were similar and have been combined, including those of unknown sex. The percentage of fat in femur marrow was not significantly different between males and females, for carcasses resulting from roadkills, dingo predation or ‘starvation’ (ANOVA; F = 0.385; df= 1, 62; p= 0.537) (Figure 6.5). There were too few marrow samples from kangaroos killed by the other causes to test them. The three marrow samples from kangaroos killed by a storm were all from females and the three from kangaroos killed by disease were all from males.

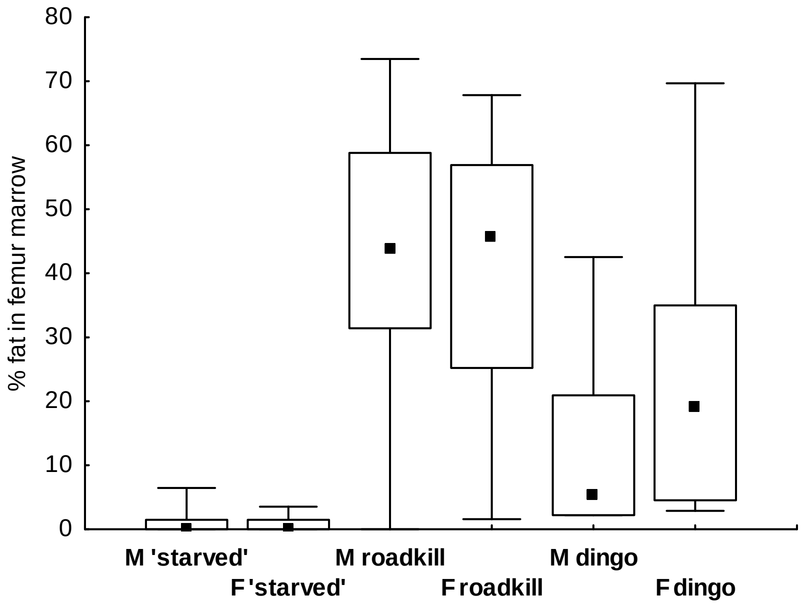


Figure 6.5: Comparison of marrow fat level between male (M) and female (F) eastern grey kangaroos. Illustrated for three causes of death, starvation, roadkill, and dingo predation (sites combined). Dot = Median; Box = Quartile Range; Whisker = Range.

For simplicity the ‘starved’ samples were pooled among sites for comparison with other causes of death. Although there was a significant difference between the FMF of the ‘starved’ kangaroos at Gudgenby and the 3 at Tidbinbilla (t-test; t= –2.491, df= 23, p=0.020), the FMF of ‘starved’ kangaroos at Googong was not significantly different from that at the other two sites (Gudgenby t-test; t= –0.550, df= 26, p= 0.587; Tidbinbilla t-test; t= –2.267, df=7, p=0.058).

Roadkilled kangaroos spanned a wide range of femur marrow fat index (FMF) values. Motor cars killed both starving subadults with low FMF, subadults in relatively good condition with high FMF, and a few kangaroos of all ages in good condition (Figure 6.6). That result is in contrast to the ‘starved’ sample, all of which had low FMF, irrespective of age. The FMFs of the three kangaroos killed by the storm in March 2003 at Googong are as high as the road kills. Kangaroos killed by dingoes fall into three groups - starving sub-adults, older animals (at least ten years old) in fair to poor condition, and kangaroos of prime breeding age (three to nine years old) in good condition. The prime kangaroos are not strongly represented in any sample.

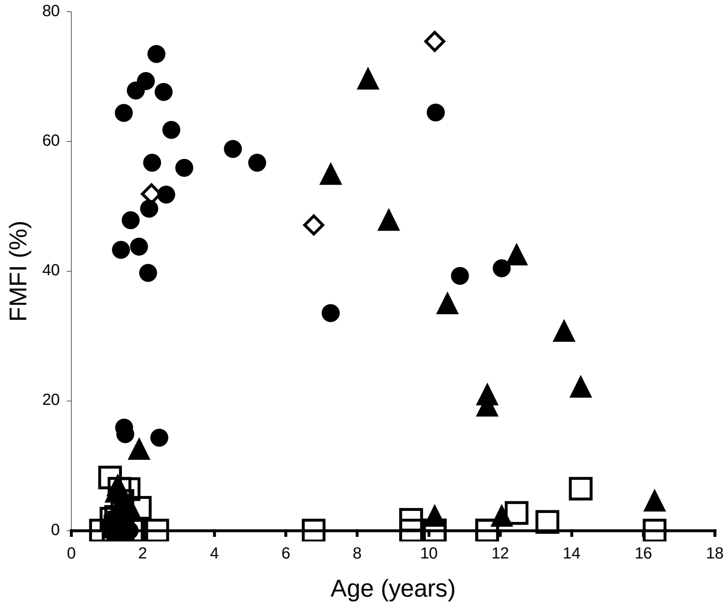


Figure 6.6: Percent of fat in femur marrow of eastern grey kangaroos killed by known causes, as a function of age. ● = road kills; ◊ = killed by storm at Googong; □ = 'starved'; ▲ = dingo kills.

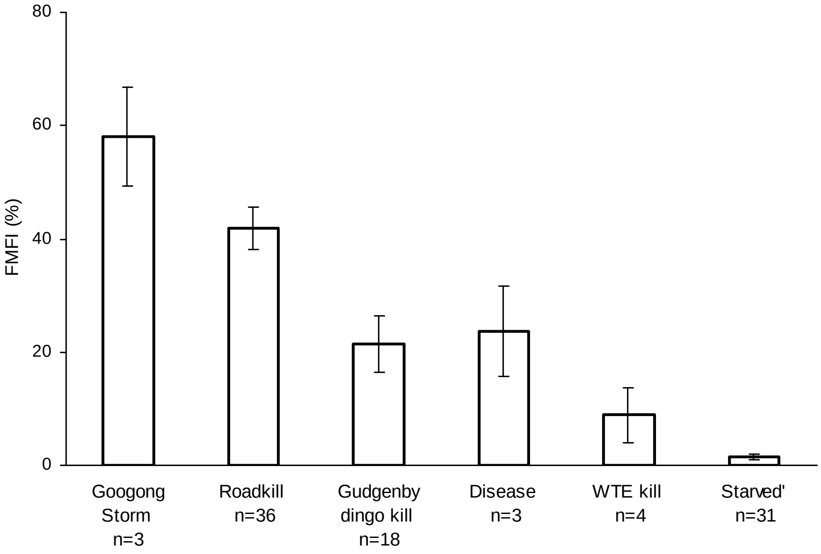


Figure 6.7: Percent of fat in femur marrow (± SE) of eastern grey kangaroos found dead from various causes on the study sites and from motor vehicle accidents on roads between the study sites. WTE kill = possibly killed by wedge-tailed eagle.

Whereas the KFIs of dingo-killed kangaroos and road kills were not significantly different (above), the FMFs were. The dingo-killed kangaroos (Figure 6.7) were in significantly poorer body condition (lower FMF) than either of the living populations (Road kill t-test; t= 3.21, df= 19, p=0.009, Storm t-test; t= 2.89; df=52, p=0.002). However, the kangaroos killed by dingoes were in significantly better condition than the 'starved' kangaroos found dead from non-predation causes (t test; t= 5.29, df= 47, p<0.001). The latter difference was also distinguishable in the KFI result.

6.3.2 Seasonality of deaths

Infected foot wounds or damaged lungs killed some kangaroos at Tidbinbilla in the weeks following the bush fire of January 2003, but the carcasses recorded in April 2003 (Figure 6.8) were mainly kangaroos that had died from starvation in the subsequent months. Some still had stomachs when they were found and these all were nearly empty, and generally contained as much charcoal and grit as greenery, suggesting their owners had been having difficulty foraging.

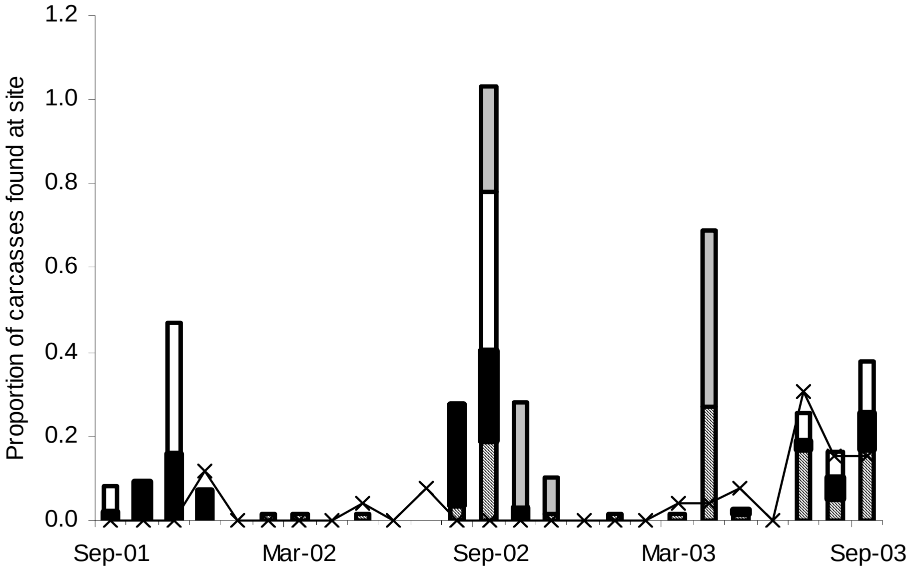


Figure 6.8: Eastern grey kangaroo carcasses found per month on each site, expressed as the proportion of the carcasses on the site. As there are three sites, bars can be >1. Shaded =Tidbinbilla (n=12); Open = Googong (n=16); Solid = Starved at Gudgenby (n=96); Hatched = Undetermined cause all sites (n=59). Line with crosses = predator kills at Gudgenby (n=26). Many additional carcasses were not recorded in September 2002 at Gudgenby for logistic reasons. Kangaroos killed directly by the bushfire at Tidbinbilla in January 2003 have been excluded, as have those killed by the storm at Googong in March 2003.

The pasture had been completely removed by the January bush fire (Chapter 4) then for two months, green shoots, which could be observed only inside grazing exclosures, were consumed completely by the remaining kangaroo population. At that time there must have been strong competition for the little food available and it is to be expected that some of the kangaroos that had survived both the bushfire and the risk of infection from burnt feet or damaged lungs, later died from starvation. It was almost invariably clear which carcasses had died (a) before the fire (burnt bones), (b) in the fire (cooked appearance, characteristic body posture, and increased resistance to decay on the upper surface), and (c) after the fire (furred, normal range of postures and normal decay).

Disregarding the carcasses recorded in April 2003 from post-bush fire starvation, there is an obvious seasonal pattern of mortality on all three sites (Figure 6.8). In the first four months of the year, few carcasses were found, (less than 2% of carcasses per site per month), and most of those were noted at the time either as predator kills or ‘unknown cause’ if they had been too much eaten, resulting in little evidence of kangaroos dying from starvation in those months. In contrast, 55% of carcasses were recorded in August and September of both years. This figure under-represents the importance of August and September because many carcasses present in September 2002 at Gudgenby were not recorded.

In contrast to the highly seasonal pattern of total mortality, the pattern of predation at Gudgenby has a persistent background level with a few peaks (Figure 6.8). The longest gap without predator kills recorded in both years is only 2 months, from January to February, but as indicated, some of the carcasses recorded as ‘unknown cause’ in those months may have been predator kills.

6.3.3 Age distribution and age-specific mortality

The age distribution of the living population of eastern grey kangaroos is derived from the shot sample taken at Tidbinbilla in May-June 1997, and from the carcasses that had been killed by the bushfire in January 2003 (Figure 6.9). For statistical comparison between these samples, and with other samples, the juveniles (mainly pouch young) were excluded, as they were not sampled effectively by either method.

The age distribution of the shot sample is not significantly different from that of the bush fire kills (χ^2 test for four age classes, ‘sub-adult’ [1 year olds]; ‘young adult’ [2 – 3]; ‘prime breeding age’ [4 – 10]; and ‘old’ [>10]; $\chi^2 = 1.33$, df = 3, p. = 0.722). A different age distribution is evident among the dead kangaroos that did not show signs of predation or fire, the ‘starved’ sample. Firstly, only 5% of the sample were 3 – 8 years old, compared to 27% and 36% from the shot and firekilled samples. Secondly, the ‘starved’ sample contains a much higher proportion of sub-adults (1 year old), 58%, compared to 18% and 24% for the shot and firekilled samples. It is likely that sub-adults are under-represented in this ‘starved’ sample, because they are easier to overlook than the larger and more durable adult carcasses. Even so the age distribution of the 'starved' sample is significantly different from both the bush fire kills and the shot sample (χ^2 test against bush fire sample, age classes as above; $\chi^2 = 32.23$, df = 3, p <0.001. χ^2 test against shot sample; $\chi^2 = 37.32$, df = 3, p <0.001). Thus the mortality episode of August – September both years was of mainly sub-adults and some older kangaroos (10 – 22 years old) with fewer kangaroos of breeding age.

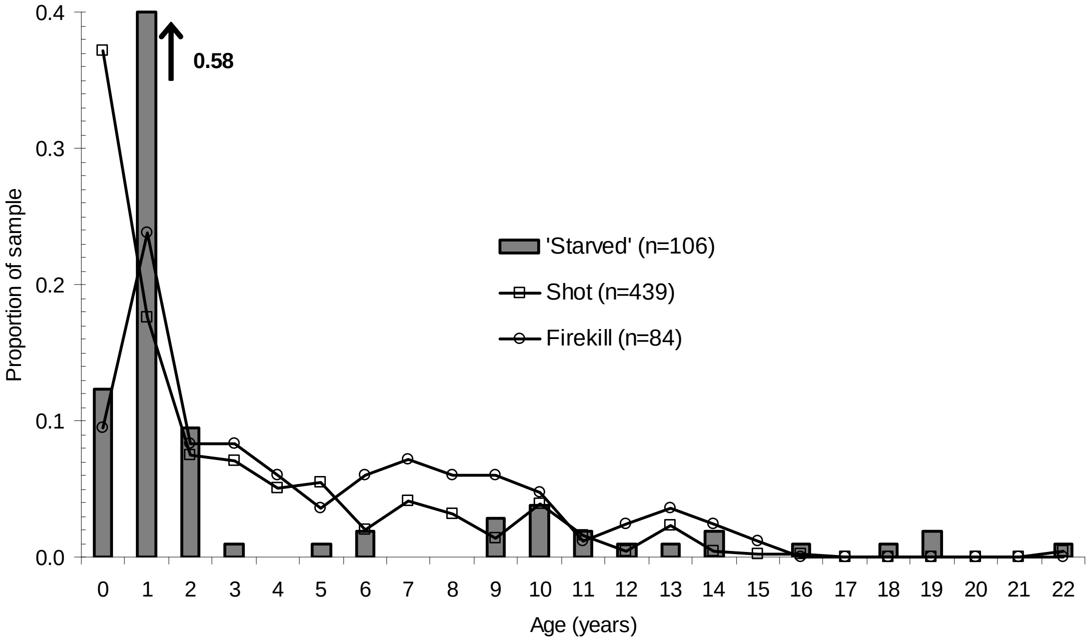


Figure 6.9: Age-frequency of kangaroos dying from different causes. Bars represent the age-frequency distribution of 106 eastern grey kangaroos not killed by storm, bushfire or predators, i.e. 'starved' on all three sites in 2002 and 2003. Circles represent the age-frequency of 84 killed by a bushfire at Tidbinbilla in 2003; and squares represent a shot sample of 439 taken in 1997 at Tidbinbilla. The bar for the 1 – 2 year old class of 'starved' animals has been shortened from its true value of 0.58.

The difference in proportion of 0 – 1 year olds between the shot and fire killed samples, and also of 1 – 2 year old sub-adults, is attributable mainly to the seasonal timing of the two samples, and to the constraints of the fire killed sample. The bushfire took place in mid-January, during the birth pulse, therefore many females would have had empty pouches, ready to receive a young about to be born, and other females would have had pouch young up to a few weeks old. The decomposition of the fire killed carcasses before they were recorded, and the activity of Australian ravens (*Corvus coronoides*), resulted in relatively few of these small pouch young being observed. A young-at-foot 12 months older would also have accompanied some females, but would have been recorded separately in a sample of this type. However, when the shot sample was taken in late May, pouch young would have been 4 – 5 months old. All would be recorded in a sample of this type. In contrast, the young-at-foot would have been becoming independent sub-adults 17 – 18 months old. They are more flighty and agile than other kangaroos and seem likely to be under-represented in shot samples from high density populations, in spite of efforts by the shooters to avoid that.

The mortality rate by age (q_x) calculated from the fire-killed kangaroos is illustrated in Figure 6.10. The age frequency (f_x) values are also illustrated. The f_x values are shown for kangaroos up to 15 years old but only those up to 13 were included in the calculation of q_x to avoid sample sizes < 5. Ages 0 and 1 were combined. The estimated mortality rate in years 0 and 1, is 785 females per 1,000 females born, based on the raw data. Thus the survival to breeding age is 215 per 1,000, i.e. a rate of 0.215, which is very close to the estimate of 0.21 calculated independently in Table 6.3 for use in the demographic sensitivity analysis from the other demographic statistics estimated in this study.

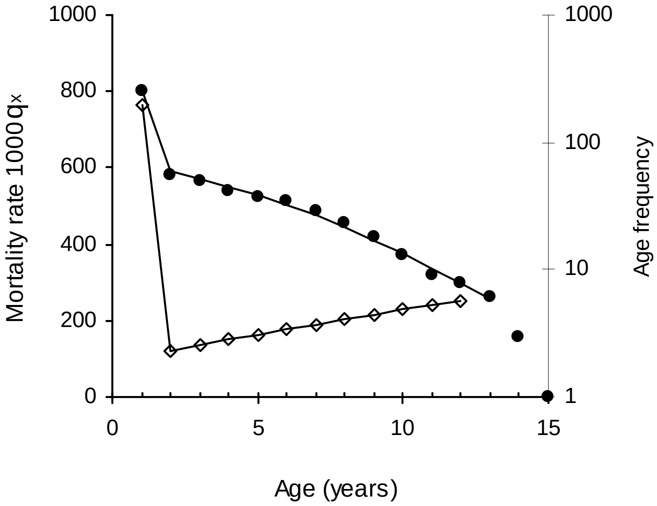


Figure 6.10: Age-frequency and mortality of an eastern grey kangaroo population at Tidbinbilla. ● = Age-frequencies on a log scale, of a shot sample of eastern grey kangaroos from the high density population at Tidbinbilla, ages 0 and 1 combined, with a quadratic curve fitted to the values from > 5 individuals, i.e. age 0 – 1 to age 13 years; —◊— = age-specific mortality rate per 1000, calculated from the fitted quadratic curve.

The dingoes selectively killed mainly older and younger kangaroos, a pattern which may appear (Figure 6.6) superficially similar to the 'starved' sample (ignoring fat levels). However, the age distributions are significantly different, due to the presence among the predated animals of several adults of breeding age (χ^2 = 13.11, df = 3, p = 0.004.). The age distribution of the kangaroos killed by dingoes was also significantly different from that of the living kangaroos (χ^2 test against bush fire sample, using same age classes as above; χ^2 = 10.36, df = 3, p = 0.016). The same is true if the living kangaroos are represented by the shot animals in place of the bush fire killed ones (χ^2 = 19.34, df = 3, p <0.001).

6.3.4 Survival of marked kangaroos

One female died at Tidbinbilla during the one year radio tracking study; 4 females and 1 male were repeatedly relocated until the bushfire near the end of the two-year period. (After the bush fire I found the carcasses of two of the ear tagged females, found the male and one other female alive, and presumed the other female to have been killed.) At Googong the carcass of one ear tagged male was found in the year after the radio tracking study; the other 6 female and 3 male kangaroos were seen alive for two years. At Gudgenby, all of the disfigured individuals I had photographed survived (one female and four males), although one male apparently moved off the site, or to where I did not see it, for two years before it was re-sighted. In combination, 11 of 12 females and 8 of 9 males survived the two years. The annual survival rates were 0.96 for females and 0.94 for males, and 0.95 for the sexes combined.

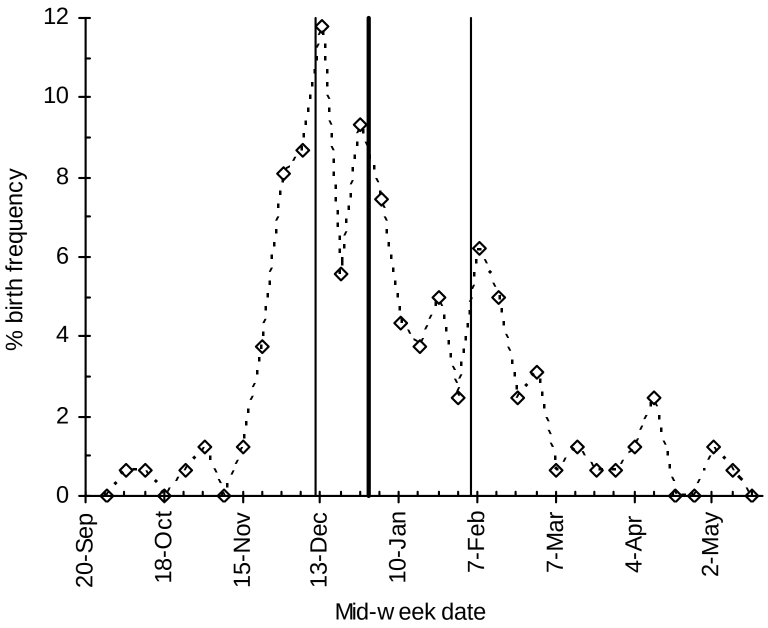


Figure 6.11: Seasonal birth pattern of eastern grey kangaroos at Tidbinbilla. ◊ = percent frequency of births per week, of 161 pouch young taken from female wild kangaroos shot in a non-selective sample taken in Tidbinbilla Nature Reserve in 1997. The bold vertical line is the median date of birth (30 December) and the light lines delimit the upper and lower quartiles (11 December and 5 February). The mean date of birth is 7 January. 84% were born in the three months starting from the third week of November. From data supplied by Dr Graeme Coulson, University of Melbourne.

6.3.5 Age-specific fecundity

Graeme Coulson's data from Tidbinbilla confirms that a seasonal breeding pattern applies to eastern grey kangaroos in the region of the study sites (Figure 6.11). At Gudgenby and Tidbinbilla in September 2002 the proportions of adult females with pouch young were 0.886 ± 0.041 SE and 0.783 ± 0.058 SE respectively. These estimates can be compared with the data from the shot sample taken at Tidbinbilla in 1997 i.e. Graeme Coulson's data. The proportion of females at least two years old which had pouch young was 0.832 in the shot sample, which lies between my estimates for Gudgenby and Tidbinbilla and within the 95% confidence intervals of both of them. Also from the shot sample, the proportion of females was 0.71 (equivalent to a sex ratio of 0.41 : 1). When multiplied together (0.832 X 0.71), these estimates suggest the number of early young-at-foot delivered onto the sites from the pouch would be approximately 0.59 times the density.

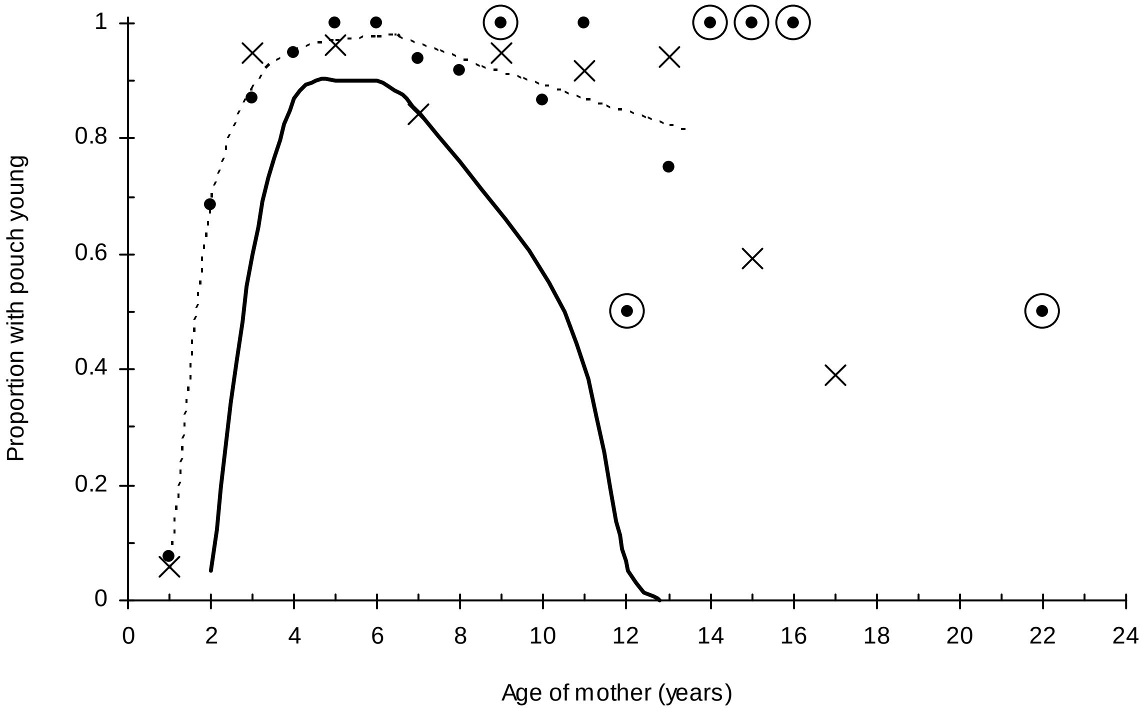


Figure 6.12: Fecundity of eastern grey kangaroos as a function of age. ● = eastern grey kangaroos at Tidbinbilla, from sample shot in May-June 1997 (n = 193). Circled values are based on less than five animals and were ignored for curve fitting; - - - = fitted function described in text; X values copied from Kirkpatrick (1965) minus one year from the age (see text); —— = estimate for western grey kangaroos north east of Perth in Western Australia, copied from Arnold *et al.* (1991) for comparative purposes. Data on age and breeding status of Tidbinbilla kangaroos supplied by Dr Graeme Coulson.

Age-specific fecundity, as the proportion of females with pouch young, expressed in relation to the age of the mothers, was obtained from Graeme Coulson's data and illustrated in Figure 6.12. The 2-part fecundity rate curve fitted by non-linear least squares regression is defined by Equation 6.4 for ages up to six and Equation 6.5 for age six or older. Data points based on less than five animals were excluded from the estimation but are shown circled in Figure 6.12. (Eqn 6.4, F = 1382, df = 2,5; $p < 0.001$; $R^2 = 0.986$; Eqn 6.5, F = 202; df = 3,3; $p < 0.001$; $R^2 = 0.443$)

[For ages 1 – 6 years] $m_x = 0.979 \{1 - \exp[-1.18 (x - 1)]\}$ Eqn 6.4

[For ages 6 – 13 years] $m_x = \exp\{0.14 - 0.026 x - 0.000123 [\exp(-11 x) - 1]\}$ Eqn 6.5

As shown in Figure 6.12, the majority of female eastern grey kangaroos at Tidbinbilla (68%) are breeding as 2-year olds, i.e. approximately half a year after the mean age of weaning. Figure 6.12 also presents values copied from Kirkpatrick (1965, Figure 2) for comparison. Kirkpatrick (1965) presents values for every second year of age. One year has therefore been subtracted from his ages to correspond to the median age of his sample. This correction makes Kirkpatrick's (1965) fecundity data for 1 – 2 year olds compatible with his estimated mean age of primiparity, i.e. 1.8 years (his Table 4).

The data presented in Figure 6.13 illustrate that young females breeding for the first time tend to do so later in the breeding season (t test; t = 3.21, df = 135, p = 0.002).

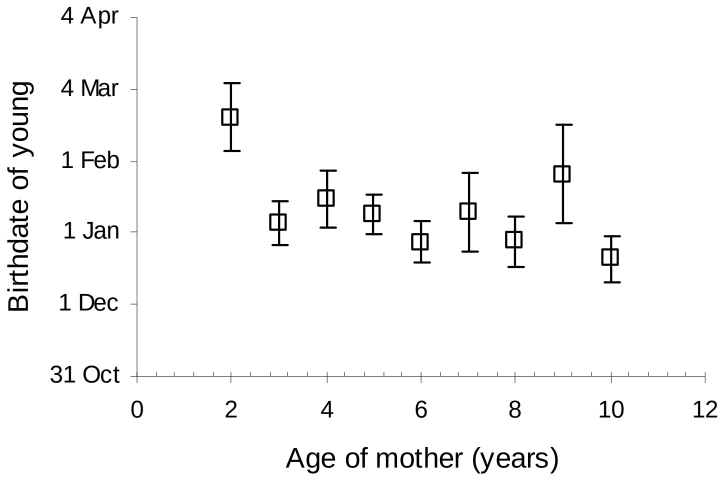


Figure 6.13: Mean birth date (± SE) of 115 eastern grey kangaroos at Tidbinbilla in relation to age of their mother. Two year olds give birth significantly later in the season than older mothers.

6.3.6 Demographic sensitivity analysis

From Table 6.3, population growth rate is most sensitive to annual adult survival; it is about 22% as sensitive to the next most sensitive demographic rate, survival to first reproduction. (As mentioned in sub-section 6.2.7, sensitivity is defined as the change in finite population growth rate (λ) caused by a unit change in a demographic rate, and it can be calculated using equations given by Lande (1988).)

Table 6.3: Demographic parameters required for input to the sensitivity analysis, how they were obtained, and the sensitivity value resulting from the calculation.

Parameter	Definition	Value	Source of input value	Sensitivity
λ	finite rate of increase	1.00	Assume population stable	NA
α	age at 1st reproduction (years)	1.9	The age at which 50% of females have young, from the Tidbinbilla shot sample. (Linear regression of fecundity on age for 1 – 3 year olds, in ten age classes).	–0.002
b	production of females per female per year	0.42 or (0.47)	Proportion of females producing an early young-at-foot (by observation in September on two sites) X 0.5 for equal sex ratio. Proportion of females aged 2 – 10 with pouch young in shot sample X 0.5 for equal sex ratio.	0.2 (0.1)
s	adult annual survival	0.95	From marked adult kangaroos	1.01
l_α	probability of survival to first reproduction	0.21	Difficult to estimate accurately from animals taken in the field. Estimated here by balancing Eqn 2 of Lande (1988) using the values given above for the other four parameters.	0.22

Two values from different sources are given for the birth rate b, the lower one (0.42) having been used. Using the higher estimate from the shot sample (0.47) makes insufficient difference to alter any conclusions reached in the Discussion.

6.4 Discussion

6.4.1 Population limitation

Table 6.1 defined how the limitation hypotheses were to be tested. Table 6.4 shows the result. Providing that the condition of the living population on the study sites is approximated by either the storm kills or the road kills, or both, the predator limitation hypothesis can be rejected because the animals killed by dingoes were in significantly poorer condition than the living animals. The dingo-predated kangaroos had significantly more marrow fat (higher FMF) and kidney fat (higher KFI) than the non-predation carcasses (the ‘starved’ sample), so the surplus/ food hypothesis can also be rejected. Thus, the kangaroo population at Gudgenby meets the criteria set up by Sinclair and Arcese (1995) for the predator sensitive food hypothesis.

No predator kills were seen on the other two sites and dingoes are absent or uncommon. Foxes were being poisoned on the other sites but were continually present as demonstrated by the bait takes (Chapter 1). Banks *et al*. (2000) showed that fox predation can limit high-density kangaroo populations. Was the fox baiting enough to prevent this, so that the

Googong and Tidbinbilla populations were food limited, as intended by the research design? Foxes take mainly young-at-foot (Banks 1997, 2000), remains of which would be unlikely to be found during pasture surveys, so I do not have evidence from carcasses to evaluate this question. However I return to the question of the effect of fox predation in Chapter 8.

Table 6.4: Relative femur marrow fat (FMF) level of living, predator killed and starved animals under three limitation hypotheses, based on Sinclair and Arcese (1995). The tick marks show conditions that were fulfilled, and crosses the opposite.

Hypothesis	FMF of living animals	FMF of predator kills	FMF of non-predation ('starved') deaths
Predation	High ✓	High X	Not applicable or Low✓
Predator sensitive food	High✓	Intermediate✓	Low ✓
Surplus / Food	High✓	Low X	Low✓

The hypothesis that dingoes could affect kangaroo density or pasture availability at Gudgenby may seem implausible at first sight because the absolute density of dingoes at Gudgenby was low relative to that of eastern grey kangaroos. I was aware of nine different individual dingoes, while the number of kangaroos was about 6,500 (Chapter 7). Obviously the number of dingoes may be an underestimate, but more importantly, their effect on the pasture-herbivore system may be magnified by non-lethal effects, by causing kangaroos to adopt costly defensive strategies. In a review of predation research across all taxa, Preisser *et al.* (2005) estimated the non-lethal effects of predation to be greater than the lethal effects. They estimated the non-lethal effects of predation on the density of the food base of the prey to be 85% of the total predator effect. That is a magnification effect of 5.6 times the estimate that would be obtained by considering the kill rates of the predators. Therefore the ratio of dingoes to kangaroos may be no guide to the power of predation to alter the density of the prey population or its food supply. McNamara and Houston (1987) state that where there is an interaction between predation and starvation, the number of deaths due to each cause is not an indicator of its importance, and it is also inappropriate to consider either on its own as a cause of limitation. An experiment would be needed. A management implication of the results of this chapter is that at Gudgenby and other sites with a significant dingo presence, management decisions should not be made separately about either dingoes, kangaroos or pastures.

The kangaroos killed by dingoes tended to be in poor condition and most were old ones and young ones, the same demographic groups of kangaroos targeted by the dingoes studied by Oliver (1986) on the Fortescue River in Western Australia. However three of the 18 predated kangaroos from which fresh bone marrow was obtained were seven to nine years old and had high FMF levels. Thus the dingoes were taking a mixture of animals, neither exclusively ones in poor condition, nor just the oldest and youngest, but also prime age adults in good condition, a demographic group which appears almost immune from other causes of natural mortality, and to whose mortality the population growth rate is more sensitive than it is to any other demographic rate.

The road killed kangaroos in Figure 6.6 show that sub-adult kangaroos are capable of developing high fat levels in their marrow. Limitations applying in some species restricting the use of FMF to adults, because only adults develop marrow fat (Hanks *et al.* 1976; Torbit *et al.* 1988; Adams 2003) do not appear to be a concern for eastern grey kangaroos. Therefore the absence of high FMF values among the sub-adults recorded in the field as ‘starved’ is legitimate evidence which confirms starvation as the probable cause of death, just as it would if they had been mature animals of most ungulate species (Caughley and Sinclair 1994). The similar FMF values of the three kangaroos killed by the storm at Googong to that of the kangaroos killed on roads is important. It supports the use of the FMF of road killed animals as a substitute for a hypothetical shot sample from the living animals on the study sites.

KFI values similar to those recorded in this study, or higher, and parallel bodyweight data, enabled Shepherd (1987, p. 141) to conclude that kangaroo deaths during the drought at Kinchega were due to starvation. Compared to Shepherd’s (1987) evidence, the evidence from this study is stronger that starvation was the cause of death as it comes from FMFs, not KFIs.

Carcass samples are likely to be biased because small carcasses tend to be more completely consumed and to decay more rapidly, and larger carcasses are more visible. Compared to a systematic monthly survey, the bimonthly site-visits in this study and the informal search method, make bias more likely (most carcasses were detected from a vehicle driving between pasture assessment locations). However the presumed bias against small carcasses did not prevent juvenile kangaroos (sub-adults) being by far the dominant age class recorded. Of necessity, the dingo predation data result mainly from surplus killing, i.e. they represent mainly kangaroos that the dingoes killed but did not eat. If the dingoes were more likely to eat the fatter kangaroos of those they had killed, then the FMF estimate of predator kills will be an underestimate, and there is a risk of having failed to identify predator limitation when it is operating. Evidence that this is not the case is the similarity between the herbage mass at Gudgenby and the other sites where there are no dingoes (Chapter 4). If kangaroos were predator regulated at one site, food availability would be predicted to be higher at that site (Sinclair and Arcese 1995). Although herbage mass was highest at Gudgenby at the beginning of the study, it declined during the study to a similar level as on the other sites (Chapter 4).

Dingo predation can have powerful effects on kangaroo density, even to the point of working to the detriment of the dingoes (Thompson 1992) and the local extinction of the kangaroos (Robertshaw and Harden 1989). A hypothesis which may account for the difference between results of this study and those cited is the predator pit hypothesis. This would mean that dingo predation can prevent kangaroo density increasing at low kangaroo densities (Robertshaw and Harden 1989; Thompson 1992), but once kangaroo density passes a threshold (escapes from the pit), dingo predation would be incapable of reducing it to the low density state (the Gudgenby site). Results compatible with that hypothesis have been reported for a number of other predator-prey systems (Pech *et al.* 1992, 1995; Sinclair *et al.* 1998; Sinclair and Krebs 2003). If that hypothesis is correct, there is potential for the dingo-kangaroo system at Gudgenby to respond to sufficient perturbation by moving rapidly between the two stable states, and then to vary only within one stable state until the next large perturbation. That possibility supports the suggestion that dingoes, kangaroos and pastures should not be managed in isolation, and would be managed best as a single system.

The conclusions which may be drawn from the two condition indexes are circumscribed by the scarcity of other information about condition in kangaroo populations, especially FMF measurements. Mean FMF values as low as the ones reported in this study would be unusual in north American ungulate populations, for example Mech *et al.* (2001) considered a mean FMF value of 70% in elk (*Cervus elaphus*) killed by wolves to be evidence the moose had low body fat and were in marginal condition, yet their ‘low’ fat level is higher than all of the mean values in this study. Measurement of FMF and KFI in kangaroo populations experiencing a wider range of levels of food restriction is desirable to establish a basis from which the significance of any particular value can be inferred. Determining body condition is essential for a more complete understanding of demographic processes (Huot *et al.* 1995; Boos *et al.* 2005).

6.4.2 Fecundity

The estimates of annual production of late pouch young (0.886 ± 0.041 SE per female at Gudgenby and 0.783 ± 0.058 SE per female at Tidbinbilla) are consistent with the shot sample, and similar rates have been reported previously for kangaroos outside the semi-arid zone. Over a five year period on a site with a Mediterranean climate, Arnold *et al.* (1991) recorded 83% of adult female western grey kangaroos with pouch young, and Banks *et al.* (2000) reported similar proportions of eastern grey kangaroo females with pouch young on four sites in the same region as this study. Such high fecundity shows that the *per capita* food shortage associated with these high density kangaroo populations is not affecting either adult fertility or survival of pouch young to a degree which might limit the population. Poole (1975) reported 17% of pouch young died in captive trials when less than a month old. However eastern grey kangaroo mothers rapidly replace these early losses due to their 30.5 day gestation (plus a few females may be carrying a diapaused embryo). Because of the short gestation, 17% neo-natal mortality is unlikely to greatly diminish the proportion of females with large pouch young in late September. In stable populations (Chapter 8) such high fecundity means that equal mortality must occur at later stages of life.

Caughley (1977a) observed that in wild mammals the proportion of females of each age which have a young (hereafter ‘fecundity’) rises rapidly with increasing age to a plateau which has little curvature. The shot sample from Tidbinbilla (Figure 6.11) conforms to that pattern. It is also typical in having few data for old animals, which is reflected in the lower R^2 value for the descending part of the curve (Equation 6.5) for six to 13 year olds and too few samples to estimate the curve for females older than 13 years.

The mean fecundity of prime female eastern grey kangaroos two to nine years old (0.90) is substantially higher than the mean value for ungulates reported by Gaillard *et al.* (2000) (0.818; CV = 0.125). In particular, the plateau of fecundity in Figure 6.11 is high for a wild population. It is high compared to that estimated by Arnold *et al.* (1991) for western grey kangaroos and it is higher compared to the more rigorously devised estimates of Eberhardt (1985) for wild horses, white-tailed deer, and seals.

The fecundity reported here for eastern grey kangaroos in high-density food-limited populations is so high there is little scope for it to be any higher in more favourable circumstances. Stewart *et al.* (2005) demonstrated experimentally that fecundity of elk declines in a density dependent manner, but there appears little scope for such a finding for eastern grey kangaroos in temperate grasslands. This is a difference to red kangaroos and western grey kangaroos in arid and semi-arid areas in which up to 85% of females have been found anoestrus in drought conditions (Shepherd 1987). And it is different to many ungulate populations which display density dependent reduction of fecundity, e.g. in red deer (Clutton-Brock and Albon 1989), black-tailed deer (*Odocoileus hemionus)* (Gilbert and Raedeke 2004), and elk (Stewart *et al.* 2005).

Female eastern grey kangaroos at Tidbinbilla breed younger than the pattern surmised for western grey kangaroos by Arnold *et al.* (1991). At Tidbinbilla, in their first possible breeding season, 68% of female eastern grey kangaroos gave birth, and 87% a year later. The equivalent values from the sketch drawn by Arnold *et al.* (1991) for western grey kangaroos are approximately 5% and 60%. Arnold *et al.* (1991) say their figure is not based on data, so the Tidbinbilla result is not necessarily indicative of true differences, it may just be a better estimate. The Tidbinbilla estimate is similar to that of Kirkpatrick (1965) in southern Queensland, after a year of age has been subtracted from Kirkpatrick's (1965) values for the reasons given in Results. Kirkpatrick gives scant details (e.g. the sample size is not stated) leaving us to guess why and how he combined his values into 2-year age classes. The subtraction of one year seems to make sense, but it may be a mistake. Perhaps because of the ambiguity about how to interpret Kirkpatrick's (1965) data, later authors (Dawson 1995, Witte 2005) have copied the fecundity curve of Arnold *et al.* (1991) in spite of the reservation expressed by its authors. It is suggested that Equations 6.4 and 6.5, based on Graham Coulson's data, are a more reliable representation.

Primiparity and reproductive senescence

The mean age of primiparity, 1.9 years by regression from the Tidbinbilla shot sample (Table 6.3), translates to a mean age at first conception of 1.8 years, gestation having a mean of 30.5 days in eastern grey kangaroos (Poole 1975). This result for mean age at first conception is the same as reported by three other studies (Table 6.5), and a similar estimate, i.e. 2.0 years was obtained by Poole (1973). The exception, from Stuart-Dick (1987), repeated by Dawson (1995), gives the mean age of first conception in the Wallaby Creek study population as 3.3 years. However this was revised to 1.8 years in time for the publication of Stuart Dick and Higginbottom (1989). Therefore all five source populations represented in Table 6.5 had a mean age at first conception of 1.8 to 2.0 years.

Table 6.5: Mean age of first conception reported for five populations of eastern grey kangaroos.

Reference	Mean age of first conception (years)	Source population
Kirkpatrick (1965)	1.8	South eastern Queensland
Poole (1973)	2.0	Mt Hope in central New South Wales (NSW), plus captive kangaroos
Poole and Catling (1974)	1.8	Captive kangaroos in Canberra
Stuart-Dick (1987), cited by Dawson (1995)	3.3 3.0 – 3.5	Wallaby Ck in north eastern NSW
Stuart-Dick and Higginbottom (1989)	1.8	Wallaby Ck in north eastern NSW
This study (Table 6.3)	1.8	Tidbinbilla

Density dependent delay of primiparity has been reported for many herbivores (Clutton-Brock and Albon 1998, their Fig. 7.2; Gaillard *et al*. 2000). Dawson (1995, p. 89) states that density dependent delay of primiparity also applies to kangaroos, however there is scant support from the Tidbinbilla data, which come from the highest density wild kangaroo population known (Chapter 7).

Poole (1983) observed kangaroos born late in the season had a lower survival rate, even in captive colonies. The same is generally true in other herbivore species. In many species, births are highly synchronous, timed to maximise offspring survival by reducing *per capita* predation risk and by matching seasonal food availability (Gaillard *et al*. 2000), e.g. Gregg *et al*. (2001) found pronghorn antelope (*Antilocapra americana*) born outside the peak period suffered higher mortality from predation and Festa-Bianchet (1988) found birthdate affected survival of bighorn sheep (*Ovis canadensis*) due to nutritional stress. The same was true of mountain goats (*Oreamnos americanus*) (Cote and Festa-Bianchet 2001) and red deer (Clutton-Brock and Albon 1989). Primiparous eastern grey kangaroos bred significantly later than the peak of the season (Figure 6.12 and associated text), probably as a consequence of developmental immaturity, as some of these mothers might themselves still have been suckling (Poole 1975). Based on the research quoted above, the later birthdate would be expected to reduce the survival of the offspring of the younger mothers.

In practice, the early primiparity may be having little effect in the high density populations on the study sites if it is offset by high mortality of sub-adults. Rather it can be inferred to enable eastern grey kangaroo populations to be capable of a faster response when *per capita* food supply is greater, such as during a run of good years, and also in low density populations where the *per capita* food supply exceeds requirements, such as populations reduced to low density by predation or harvesting.

The eastern grey kangaroos at Tidbinbilla persist in breeding longer into old age (Figure 6.12) than surmised by Arnold *et al*. (1991) for western grey kangaroos. Young were found in the pouches of 17 of the 21 shot females that were more than 10 years old (81%). Gaillard *et al*. (2000) state that many studies of fecundity in mammal populations combine the prime and senescent females, although compared to prime females, breeding by senescent females is more affected by variation in food supply, environmental conditions, and body size. Only seven of 198 studies reviewed by Gaillard *et al*. (2000) recorded fecundity of senescent females, providing a mean = 0.783 (CV = 0.134, n = 6). That means the data presented for eastern grey kangaroos in Figure 6.12 are exceptional, having separated the prime and senescent females. More interestingly, the fecundity of senescent eastern grey kangaroos is also exceptional. Taking the definition of senescence suggested by Gaillard *et al*. (2000), i.e. females at least ten years old, the senescent eastern grey kangaroos had a fecundity of 0.83, which, compared to the seven studies reported by Gaillard *et al*. (2000), is outside the 95% confidence interval of their mean (0.783). By breeding longer the Tidbinbilla kangaroos can be inferred to increase their output of young, and potential population growth rate. However this would have only a small effect on population growth rate because female kangaroos more than 10 years old are a small proportion of the population.

6.4.3 Survival

The age distributions of both the shot sample and of the kangaroos killed by the 2003 bushfire are of the typical pattern for wild mammals (Caughley 1966; Eberhardt 1985), namely (a) a rapid initial drop from a high proportion of young animals, (b) a ‘flat’ phase due to high survival in the ‘prime’ ages and (c) a drop into senescence, tailing off to a persistent group of old animals.

The higher annual female survival rate (0.96) compared to males (0.94) is typical of kangaroo species (Dawson 1995, p. 88) and other large herbivores (Gaillard *et al*. 2000; Patterson *et al*. 2002). Like many other large herbivores, once kangaroos reach sexual maturity they enjoy a relatively high survival rate. Eberhardt (2002) tabulates published survival rates for 41 populations of large marine and terrestrial mammals in varied environments. They range from 0.7 to 0.995, and Eberhardt (2002) concludes that populations with little human interference normally experience female survival of at least 0.95. The estimate here for eastern grey kangaroos conforms with that general pattern. In particular, compared to the 41 populations listed by Eberhardt (2002), the estimate given here of the adult female survival rate for eastern grey kangaroos on the study sites lies above that for red deer on Rhum (Sibly and Smith 1998) and between the estimates for two fenced populations of roe deer (Gaillard *et al*. 1993).

Longevity

The two oldest females in the Tidbinbilla shot sample are of unusual age for wild eastern grey kangaroos, with a molar index of 5.0, equivalent to almost 23 years, (and they also exemplify the trend of high fecundity persisting into old age, because one of them had a pouch young). At least one kangaroo older than this has been reported, i.e. a male red kangaroo 26 years old (Robertson 1986) but kangaroos so old are uncommon. Male kangaroos older than ten years are considered rare in the wild (Dawson 1995, p. 88) yet males more than ten years old comprised 3.5% of the sample shot at Tidbinbilla and one estimated to be 22 years was found at Gudgenby. The finding during this study of carcasses of three kangaroos whose ages (based on molar index) are 20 to 23 years, suggests even older kangaroos would be likely to be encountered if larger samples were taken from these sites. It might be hypothesised that kangaroo populations such as the ones on the study sites experiencing low levels of predation and culling, might contain a higher proportion of old kangaroos. Robertson's (1986) 26 year old kangaroo (above) also originated from an unculled population in Kinchega National Park. The Tidbinbilla shot sample can be contrasted to that of Wilson (1975) who published the ages of 4,623 kangaroos taken by professional shooters. Wilson's (1975) data from three temperate districts where the 'grey kangaroos' were almost certainly eastern grey kangaroos, shows 5.7% were at least ten years old and 0.9% were at least fifteen years old (kangaroos up to one year old were excluded from these calculations because commercial shooting would under-represent them). The corresponding Tidbinbilla values, 21% at least ten years and 2% at least fifteen years, are sufficiently different from Wilson's (1975) to suggest the hypothesis may be correct, i.e. that eastern grey kangaroos on my study sites live longer than kangaroos in heavily culled or predated populations, although differences in the sampling preclude a firmer conclusion based on statistical tests.

6.4.4 Mortality

Winter die-offs

The mortality of eastern grey kangaroos on the study sites was concentrated into late winter and early spring. Sub-adults were affected disproportionately (58% of carcasses compared to 18% and 24% in samples of the living population), whereas the kangaroos of breeding age were relatively protected from starvation-related mortality (5% of carcasses compared to 27% and 36% of living animals). This is consistent with a common pattern in mammals of the temperate zone, e.g. in Soay sheep (Clutton-Brock and Pemberton 2004), and white-tailed deer (DelGiudice *et al*. 2002). DelGiudice *et al.* (2002) recorded 84% of mortality in two winter months, with the oldest animals and ones 0.6 years old at greatest risk.

Winter mortality of such proportions is said by national parks staff to be not unusual at Gudgenby (M. Muranyi, personal communication). It has been documented at Tidbinbilla (ACT Kangaroo Advisory Committee 1997) and it is probably characteristic of a range of sites. Heavy winter mortality of eastern grey kangaroos has been reported to occur repeatedly at Yan Yean, near Melbourne (Quin 1989; Coulson *et al*. 1999a, b) and one year near Blowering Dam in the southern highlands of New South Wales (Jaremovic 1984). As in this study, the mortality was biased toward sub-adults and older kangaroos (Jaremovik 1984; Quin 1989; Coulson *et al*. 1999a, b).

Cause of winter mortality

The cause of winter mortality at the Blowering Dam site was diagnosed by Jaremovik (1984) as pneumonia but the explanation was ‘multi-layered’ according to Dawson (1995). Stress, cold, and food shortage were mentioned.

Parasites are also involved. Some of the ‘starved’ kangaroos on the study sites were being eaten from within by the nematode *Globocephaloides trifidospicularis*, which consumes intestinal mucosa and blood, and the same parasite was assessed to be the cause of the Yan Yean mortality by Quin (1989). Three other harmful nematodes were also common in dying sub-adult kangaroos at Yan Yean, *Rugopharynx rosemariae*, *Strongyloides* sp. and *Labiostrongylus* sp. among the usual diversity of benign species (Arundel *et al*. 1990). Quin (1989) attributed the prevalence of *Globocephaloides trifidospicularis* to high kangaroo density in confined conditions, leading to high concentrations of parasite eggs in the soil.

Demonstrations that helminth parasites are capable of having a substantial impact on mammal populations are rare (Sinclair 1989; McCallum 1995). However, by applying anthelmintic drugs to a natural population, Stein *et al*. (2002) showed that gastrointestinal nematodes affect host condition and fecundity. Wilson *et al*. (2004) showed parasites reduced over-winter survival in one winter when 44% of sheep died but not in another winter when 70% died. The possibility of population level effects of parasites in eastern grey kangaroos has not been disproved and should not be dismissed. However a consensus for mammalian herbivores seems to be as described by Murray *et al*. (1997) for snowshoe hares and by Speare *et al*. (1989) for macropods, that parasitism and food limitation are likely to synergistically affect survival. Furthermore, starvation is probably a necessary precursor for high parasite levels across a population, but not the reverse, because mortality by starvation is not necessarily accompanied by high levels of parasites. Evidence for the former is that Houdijk and Athanasiadou (2003) reviewed literature, and presented experimental data, to argue that increased levels, and effects, of gastrointestinal parasites depend on scarcity of protein in the diet. Evidence for the latter is the apparent absence of gastrointestinal parasites in some of the starved kangaroos at Gudgenby (Will Andrew, ACT Government Veterinarian, personal communication, 2003).

Predators are involved too. Some of the kangaroos at Gudgenby that were killed but not eaten by dingoes (surplus-killed) in the months leading up to the late winter episodes of high mortality had such a low level of fat in their femur marrow it is doubtful they could have survived the winter if they had not been killed by predators. Rather than parasites being the cause of winter mortality as previously described (Jaremovik 1984; Quin 1989), or predators, hypothermia, or stress, the evidence is more compatible with the hypothesis that the ultimate cause of most winter mortality on these sites is starvation. Parasites, hypothermia, pneumonia, other diseases, and predation, are merely alternative proximal causes.

This conclusion is contrary to the view of Banks *et al*. (2000) that there is little evidence that food stress affects young kangaroos, and death by starvation is rare. However they noted that a proportion of sub-adults not recruited into the population were not accounted for by predation, and that some other factor may also have been involved. That other factor may have been starvation. In part, this conclusion by Banks *et al*. (2000) may have been reached because they found no carcasses of sub-adult kangaroos. My experience was that, although some carcasses of large kangaroos lasted up to two years, most carcasses of sub-adults appeared in a brief interval, disappeared rapidly, and could be missed easily. At Gudgenby, only a small fraction were found (less than 1%) even in favourable circumstances. Compared to my sites, the sites used by Banks *et al.* (2000) were relatively unfavourable narrow valleys with fringing woodlands where fewer carcasses would have been visible. Robertson (1986) searched for kangaroo carcasses on the much more favourable inland plains, during a drought which he said had the greatest impact on sub-adults, yet even in that case, few of the 827 carcasses found were sub-adults.

On the study sites, declining internal reserves apparently become critical at the end of winter, as occurs with other food limited mammal populations outside the wet-dry tropics (Clutton Brock and Albon 1989; Sinclair 1996). At this time the kangaroos may also be combating the influence of either cold, parasites, disease, risk of predation, or combinations of these, as were the kangaroos in southern Australia studied by Jaremovik (1984), Quin (1989), Dawson (1995), Coulson *et al.* (1999a 1999b), and Banks *et al.* (2000). The pouch young appear to have a degree of protection, but not the sub-adults. The energy needs of sub-adults are high. Sub-adult red kangaroos have 1.8 times higher digestible energy intakes than mature non-lactating females, on high quality food (641 ± 26 kJ $kg^{-0.75}$ day^{-1}, compared to 385 ± 37 kJ $kg^{-0.75}$ day^{-1}; Munn and Dawson 2003). Yet sub-adults probably process food less efficiently than the adults due to their smaller size (Hume 1999), especially if the food is of the lower quality typical in natural pasture, further increasing their dependence on pasture quality and on maintaining a high intake rate. The difficulty of meeting this demand in competition with other members of the population, results in a disproportionately high death rate of this demographic class when food is short.

Munn and Dawson (2001) show that kangaroo young-at-foot have higher water needs than adults, and suggest that in arid areas this restricts their ability to forage far from water sources to reach the less eaten out country further from water. Local conditions are different. Water was readily available but during my study, I never saw a kangaroo drink water. Eastern grey kangaroos have water conserving capacities equivalent to similar sized arid-zone-inhabiting placental mammals (Blaney *et al.* 2000) and it is likely that most of their water needs in temperate sites are met from the vegetation. In any case, surface water was rarely more than one kilometre away. In temperate sites like these, sub-adults are likely to be relatively unaffected by this mortality factor. In view of the importance of sub-adult mortality to population growth rate, here is an additional reason which may contribute to the difference in density of kangaroos between semi-arid and temperate areas, as described in Chapter 3.

Age-specific mortality

The q_x curve is of the typical mammalian form (Caughley 1966) with most mortality before reproductive age, low mortality in the first year of reproductive age, and a gradually increasing mortality rate thereafter. The lack of a significant difference between the age structure of the kangaroos killed by the bush fire and the age structure of the sample shot for research, indicates that the sampling bias of the fire kills is probably low. That increases the confidence in the estimate obtained from the q_x values of the probability of survival to first reproduction (l_α). Also, the latter is very close to the estimate calculated by balancing the equations of Lande (1988) using the estimates made in this study for adult survival (s), production of female young (b), age at first reproduction (α), and finite rate of increase (λ).

Mortality before reproductive age can be divided into juvenile and sub-adult components. High mortality acting on the juvenile class is normal in ungulate populations in all climatic zones (Sinclair 1996; Gaillard *et al.* 1998, 2000). Using the same definition of 'juvenile' and 'sub-adult' as applied to ungulates by Gaillard *et al.* (1998), the eastern grey kangaroos differed from the ungulate pattern. The high percentages of females observed with late pouch young in spring implies that the eastern grey kangaroos experienced low juvenile mortality. Therefore most of the mortality before reproductive age must have been sub-adult mortality. Subtraction of an allowance for the difference between eutherian and marsupial reproduction does not change the pattern. Eastern grey kangaroos are born at a rudimentary stage after a mean gestation of 30.5 days (Poole 1975) and remain in the pouch beyond the stage when they begin foraging on grass. There is no stage in their development physiologically equivalent to eutherian birth (Tyndale-Biscoe and Janssens 1988) contrary to Russel (1982) who defines it as the time when homeothermy commences. However there is a marked acceleration in growth after the development of fur, and completion of nephrogenesis, which occur in eastern grey kangaroos at about six to seven months of age, which is also the time when homeothermy develops (Janssens and Rogers 1989). If half a year was subtracted from the age of a young kangaroo for the purpose of ecological comparison with ungulates, the sub-adult mortality would still fall into the one to two year old sub-adult class. So perhaps this difference between eutherian juvenile mortality and marsupial sub-adult mortality should be respected as genuinely another difference between kangaroos and ungulates, within an overall pattern of ecological similarity. High mortality of sub-adults as recorded on my study sites, is typical of kangaroo populations (Shepherd 1987; Arnold *et al.* 1991; Dawson 1995). Arnold *et al.* (1991) hypothesised it to be the factor which determines kangaroo density on their Baker's Hill site, a view which was repeated by Dawson (1995) for kangaroo populations generally. Clancy and Croft (1992) identified a lack of information on survival and movements of sub-adults as a significant gap in the understanding of kangaroo population dynamics.

Demographic importance of sub-adult mortality

Demographic sensitivity analysis indicated finite population growth rate (λ) to be most sensitive to a change in annual adult survival (s), and 38% as sensitive to change in the rate of survival to first reproduction (1_α). That relativity (about one third) is typical of large herbivores (Gaillard *et al.* 2000). However the proportion of carcasses found on the sites indicates mortality in the sub-adult year to be many times higher than annual adult mortality, (58% of found carcasses were one year old, compared to an average of 1.8% in each year of age from two to fifteen.) This pattern supports the hypotheses of Arnold *et al.* (1991), and Dawson (1995) that sub-adult mortality is the main determinant of population growth rate in grey kangaroos. Although the population growth rate was most sensitive to survival of adults, the adults were buffered from starvation mortality, and in practice it was the second most sensitive demographic rate, survival to breeding age, which had most potential to alter population growth rate from year to year, due to the potentially high mortality rate of sub-adults. This appears to be a common pattern for herbivore populations, at least for ones at high density limited by food. Gaillard *et al.* (2000) and Loison *et al.* (1999) found survival to breeding age had greatest effect on population growth rate in modelled populations using data for five populations of three species for which high quality, long-term data exists. Gaillard *et al.* (2000) concluded that observed differences in temporal variation in a demographic rate may be more important than elasticity or sensitivity in affecting population growth rate. This appears the case with the eastern grey kangaroo populations on the study sites.

Eberhardt (1977, 2002) proposed the negative effects of increasing density (declining *per capita* resources) on population growth rate would occur in a particular order. Juvenile survival should change first, then age at first reproduction, fecundity, and finally adult survival. The kudu (*Tragelaphus strepsiceros*) populations studied by Owen-Smith (1990) are examples. They were resilient to drought due to high survival of prime females, and fluctuated in size according to variations in annual juvenile survival, which was a function of rainfall the year before. The review of density dependent limitation in large herbivores by Gaillard *et al.* (1998) reported that results of most long-term studies confirmed Eberhardt's

(1977) proposal, and that survival of breeding age females varies little, but high variability in juvenile survival between years and between populations may play a predominant role in population dynamics.

With a review encompassing many more studies, Sinclair (1996) also makes observations about the life-stages at which density dependent mechanisms apply to mammal populations, pointing out (his Table 1) that for large terrestrial herbivores, 52 of 109 studies (48%) reported density dependence acting through fecundity, 43 (39%) found it acting through mortality of early juveniles and none found it operating through mortality of late juveniles or sub-adults. The eastern grey kangaroos on the study sites are an exception to the general pattern described by Sinclair (1996) in that the most important mortality occurs at the sub-adult stage and there is no evidence of an effect on fecundity.

The episodes of winter mortality of kangaroos witnessed in places such as the study sites, can be considered an important part of the mechanism of population limitation. Interestingly, this mechanism is more visible to the public and management staff than many other ecological mechanisms.

6.4.5 Motor vehicles and predation

Unlike starvation, dingo predation is liable to affect the prime breeding females, to whose mortality the population growth rate is most sensitive. Female eastern grey kangaroos with young-at-foot tend to forage alone, or in smaller groups (Stuart-Dick and Higginbottom 1989; Jarman and Coulson 1989). Banks (2000) demonstrated experimentally that this behaviour increases when predation risk is reduced, therefore presumably it is done in spite of predation risk, in order to reduce the costs of group foraging. Whether female eastern grey kangaroos with young also increase their risk taking behaviour in inverse proportion to food availability has not yet been researched. The expectation of a negative relationship between food and risky behaviour is encouraged by the FMF results which support the predator-sensitive food hypothesis on the Gudgenby site. For this study, foxes were poisoned on all sites, and the only significant predators were the dingoes at Gudgenby, but the predator sensitive food hypothesis may have general application to high density kangaroo populations where foxes are uncontrolled.

Motor vehicles killing herbivores have the potential to reduce population growth rates and were compared to predators by O'Gara and Harris (1988). Kangaroo road kills are typically male biased (Coulson 1982, 1989b, 1997; Lintermans and Cunningham 1997) and road kills may also be selective for immature kangaroos (Lintermans and Cunningham 1997). The results presented here do not support a hypothesis that motor vehicles were selective for kangaroos in poor condition, because the majority of those killed were in good condition and the mean FMF was significantly higher than that of predator kills. This contrasts with the situation described by O'Gara and Harris (1988) for white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemonius*) killed by motor vehicles, which were mainly fawns and old animals in poor condition. Animals killed by predators in the area studied by O'Gara and Harris (1988) were prime aged animals in good condition. O'Gara and Harris (1988) observed that on their research site, injured deer and ones in poor condition tended to move downhill and occupy the road, especially in winter when it was the only snow-free area. The main predator (mountain lion *Felis concolor*) was a sit and wait predator, which may be less selective for condition than dingoes which mostly hunt kangaroos by chasing (Thompson 1992; Jarman and Wright 1993).

This chapter considered kangaroo demographic issues and whether the populations on the study sites were indeed food-limited, as required by the experimental design in order to estimate the numerical response. The next chapter (Chapter 7) is focused on the challenge of estimating the density of high-density kangaroo populations as a prelude to estimating the numerical response in Chapter 8.

CHAPTER 7

ESTIMATING KANGAROO DENSITY

Maximum kangaroo density obeys the same rules as maximum flood level, and for the same reasons; you have not seen the maximum yet. (Graeme Caughley and Ann Gunn).

Line transect method using red light. Some macropods are insensitive to red light.

CHAPTER CONTENTS

7 ESTIMATING KANGAROO DENSITY

This chapter deals with that ubiquitous challenge in ecology, the estimation of animal abundance. There are three reasons this chapter is a necessary precursor to the estimation of the numerical response in Chapter 8, firstly because the challenges facing the estimation of density of eastern grey kangaroos on the study sites include some difficulties that are not shared with other kangaroo populations, secondly because strong claims have been made previously about extreme kangaroo densities on the sites (Fruedenberger 1996; Nelson 1997; ACT Kangaroo Advisory Committee 1997) and thirdly because my estimates disagreed with the estimates given in those studies. The chapter begins by reviewing kangaroo counting methods. Next, a preliminary trial is described, of three variations on the ground line-transect method. Based on the results of the trial, I selected for the study a vehicle-based, nocturnal, line-transect method, which involved development of novel apparatus to increase the data recording rate. Because the density estimates produced by this method were higher than the previous estimates from the same and similar sites (references given above), independent density estimates were also made, using the so-called ‘drive count’ method. All of these estimates are discussed in this chapter.

7.1 Introduction and literature review

7.1.1 Review of the national program for estimating kangaroo density

Harvesting is the dominant form of management of eastern grey kangaroos (Chapter 1). To determine sustainable annual harvest levels for each kangaroo species requires estimates of absolute density, rather than density indexes (Caughley and Sinclair 1994; McCallum 1999). Methods of estimating kangaroo density on a large scale, as described by Gilroy (1999) and Grigg *et al*. (1999), have a long history and are reasonably well understood. Strip counts from fixed-wing light aircraft were first used for kangaroos as long ago as the 1960s (Southwell 1989) and were expanded in the 1970s based on the application of a regression method (Caughley 1974, 1977b) to correct for effects of the height and speed of the aircraft and width of the counting strip, which have an inverse influence on the proportion of animals sighted. Initial evaluation (Caughley *et al*. 1976) appeared mainly to support the use of the regression method. As aerial strip counts of kangaroos became more widely used, further visibility corrections were advocated including corrections for temperature (Bayliss and Giles 1985), cloud cover (Short and Bayliss 1985), time of day (Hill *et al*. 1985; Short and Hone 1988), and habitat (Short and Bayliss 1985, Short and Hone 1988; Choquenot 1995; Pople *et al*. 1998; Gilroy 1999). A system of national estimates was developed (Caughley *et al*. 1983; Pople and Grigg 1999; Grigg 2002) covering much of inland Australia. The commercial kangaroo industry was originally confined to the same area. In this national system there are agreed visibility correction factors for each kangaroo species and habitat type (Grigg and Pople 1999), and an agreed training standard for observers (Beard 1999; Grigg and Pople 1999).

However Hone (1986) had demonstrated by both simulated and real counts that the regression method used to develop correction factors was flawed, greatly overestimating when true density was high, and with the effects of strip width and density differing from linear to quadratic. Such problems were openly acknowledged (Seber 1992; Pople *et al*. 1998) but ignored, based on the arguments that there are long series of data obtained by the same method and only fixed-wing surveys are cheap enough to apply on a continental scale. The decision to retain the *status quo* prioritised consistency ahead of accuracy, contrary to the edicts in Caughley's (1974) original paper on the use of the regression method to correct kangaroo aerial survey, that accuracy must take precedence over either repeatability or precision. Consequently, there have been ongoing calls for more research on correction factors including by Pople *et al.* (1998), and kangaroo researchers and managers periodically revise the correction factors, e.g. Grigg and Pople (1999). An obvious and superior approach to the regression method, is double sampling (Seber 1992 p133) i.e. calculating visibility correction multipliers as the ratio to the number of animals recorded in a more accurate counting method applied over a representative sample of the area. For example, Bayliss and Yeomans (1990) used photography to correct counts of magpie geese made by airborne observers. Aerial strip counts of kangaroos have been compared with drive counts (Short and Hone 1988) and with helicopter line transect counts (e.g. Pople *et al.* 1998; Cairns 1999; Pople 1999). Alternatively the mark–recapture or ‘double count’ method could also be used in low density kangaroo populations where visibility is good (Choquenot 1995).

The visibility correction multipliers that result from double sampling vary greatly between years and sites, e.g. those estimated for eastern grey kangaroos in central Queensland by Pople *et al.* (1998) ranged from 3.7 to 10.2. McCallum (1999) recommended a departure from the established approach of adopting continent-wide standard correction factors, and advocated routine use of double sampling, meaning a selection of the fixed-wing transects would be reflown using the helicopter line transect method. This would enable visibility correction multipliers for each kangaroo species and habitat type to be specific to each survey, which is the approach strongly recommended by Seber (1992) who advised that in reality, the visibility correction factor would change even when aerial surveys were repeated on the same site. McCallum (1999) acknowledged the need to reduce the fixed-wing component to enable double sampling to be done at equal cost.

The sites used in this study are too small for aerial strip counts to be effective, and the terrain is too unfriendly to low level operation of fixed-wing aircraft, but the history of the development of the national system of estimating kangaroo density, as outlined above, is relevant to this study in two ways. At a detailed level, it suggests potential sources of bias, and at a strategic level it highlights the difficulty of estimating populations. Even when a relatively large group of scientists have worked with a particular method for decades, there may still be substantial uncertainties.

7.1.2 Line transect

Following the 1989 review of methods of estimating macropod density (Southwell 1989) there has been increasing use of walked line transect methods in the forested and dissected eastern highlands, which have not been within the part of the continent regularly covered by aerial strip counts. Compared to the development of aerial strip counts, the development of line transect methods for kangaroos was, and is, more able to draw on international experience. Among the hundreds of publications available, Buckland *et al.* (1993, 2000) in particular provide comprehensive theoretical and practical explanations; and Thomas *et al.* (1998) provide a software program to simplify the data analysis. Recent examples of the use of the walked line transect method to estimate density of terrestrial mammals other than kangaroos include Focardi *et al.* (2002) and Jathana *et al.* (2003) for large herbivores, Ruette *et al.* (2003) for foxes and Dique *et al.* (2003) for koalas.

Coulson (1979) and Coulson and Raines (1985) made pioneering use of a walked line transect method to estimate kangaroo density, taking advantage of a kangaroo population isolated on a small island (266 ha) to compare line transect estimates to the results of a drive count, pellet counts, and other density estimation methods specifically intended for small areas. Southwell and Fletcher (1990) confirmed that biased estimates of macropod density resulted from using roads and tracks as an alternative to cross-country transects. Hone (1988) compared various strip and line transect analytical methods in a realistic manner using a helicopter to count carcasses where a known number of animals had been shot. His density estimates were not significantly different from true density using all of seven line transect estimators attempted, and two of four strip widths. The most accurate estimate was obtained with a Fourier series estimator – referred to hereafter as the uniform function, following Buckland *et al.* (1993). Line transect analytical methods were also evaluated by Southwell and Weaver (1993), Southwell (1994), and Anderson and Southwell (1995) using kangaroo data. Line transect methods were tested on kangaroo populations of known size (Southwell 1994) followed by application to wild populations (Southwell *et al.* 1995a, b, 1997), including nocturnal surveys (Southwell 1994; le Mar *et al.* 2001). Helicopter line transect methods were also developed (Hone 1988; Clancy *et al.* 1997; Clancy 1999). Application of helicopter line transect counts to the larger, more open parts of the southern tablelands has commenced concurrently with this study (Pople *et al.* 2003, Cairns 2004). However helicopter line transect surveys can underestimate density of kangaroos compared to walked line transect counts, e.g. by 33% ± 9 for eastern grey kangaroos (Clancy *et al.* 1997).

7.1.3 Selection of a density estimation method for this study

A variation of one of the methods referred to above was required to estimate the density of eastern grey kangaroos on the study sites. The accuracy of helicopter surveys is likely to be lower in areas of high relief (Southwell and Sheppard 2000), but in any case helicopter-based methods appeared unsuitable because the sites are too small and too much enclosed by steep hills for satisfactory aircraft operations, particularly if the transects follow the conventional east-west orientation. Even if aircraft could overcome these limitations, the high density of kangaroos (approximately 500 km^2), combined with the fact that large groups of kangaroos fluidly merge and divide continuously when flushed by aircraft, would make it extremely difficult to apply the more robust aerial survey methods, i.e. line transect or mark-recapture. Instead, a ground line transect method was sought for this study.

Walked line transect surveys have been used repeatedly to estimate the density of eastern grey kangaroos and other macropods in the eastern highlands (Coulson and Raines 1985; Southwell 1989, 1994; Southwell *et al.* 1995a, b, 1997; le Mar *et al.* 2001) and of western grey kangaroos in woodland areas in south–western WA (Arnold and Maller 1987). However it can prove difficult to achieve desired levels of precision in a limited time. In small woodland remnants with only 2.1 – 4.8 km of transects in parallel lines only 140 – 280 m apart, Arnold and Maller (1987) walked 64 hours per survey per site to estimate density of western grey kangaroos with an error of ± 15%. The ACT Kangaroo Advisory Committee (1997, Appendix B) reported fourteen walked line transect surveys for eastern grey kangaroos in the ACT, including two of the present study sites, which required 96 hours of walking on average, and achieved a mean coefficient of variation of 20%. The rate of progress is generally about 1 km hr^{-1} (Southwell *et al.* 1994, 1995; personal observation). To achieve the same precision in this study at the same rate, the equivalent of 7.6 weeks of work would have been needed in every eight-week monitoring cycle (at 40 hours per week), leaving insufficient time for pasture assessment and other work. Similar amounts of time have been required for line transect surveys by other authors working in the ACT region (Freudenberger 1996; Nelson 1996; Muranyi 2000).

Like many other herbivores, eastern grey kangaroos are more dispersed when feeding than when resting (Jarman and Coulson 1989). Preliminary observations suggested that the eastern grey kangaroos on the Gudgenby site were more evenly dispersed in smaller groups at night than in daytime, as described by Freudenberger (1996). Freudenberger (1996) thought it would make no difference to count at night, but his focus was on whether it would alter the density estimate. The aspect of interest for this study was that a less clumped distribution of kangaroos would reduce the survey effort required to achieve a given level of precision, which was important to the time–budget problem. The kangaroos were also more approachable at night, so reactive movement seemed likely to be a problem. Lastly, research design considerations also made night counting more attractive for the reasons outlined below.

Eastern grey kangaroos are well known for moving from daytime rest areas to grassy feeding areas at night (Kirkpatrick 1967; Frith 1973; Taylor 1980; Hill 1982; Dawson 1995, p14). There is also good evidence to the contrary. Southwell (1987a) at Wallaby Creek in north eastern New South Wales and Moore *et al*. (2002) at Yan Yean near Melbourne in Victoria, found the preference of eastern grey kangaroos for open grassy areas did not change with time of day, and Clarke *et al*. (1989) reported eastern grey kangaroos continuing to graze at low intensity all day rather than moving into more sheltered habitats. It was my impression that there was little kangaroo movement on my study sites between the open grassy areas and nearby areas of forest and woodland, even on hot summer days. However, if that appearance was false, and kangaroos were moving between feeding areas and sheltering areas to a greater extent than I appreciated, daytime surveys would underestimate the feeding density of kangaroos. This added to the reasons for preferring to estimate kangaroo density at night.

Therefore, three ground line transect methods were evaluated in May-June 2001 to select one for continued use throughout the remainder of the study. These were (a) the standard walked line transect method in daylight, (b) the line transect method at night using a white spotlight from an off-road vehicle driven along predefined cross-country transects, and (c) using a red spotlight from the off-road vehicle. Using red light was an attempt to exploit the inability of some macropod species to detect this wavelength (Hemmi, RSBS, ANU, personal communication). If this reduced the response of kangaroos to the passage of the survey vehicle, it would reduce the problem (described below) of kangaroos flushing ahead, and may also result in an improved detection function. In addition, drive counts were carried out at Googong in August 2001 and Gudgenby in April 2002 as an independent check on the chosen method.

7.2 Methods

7.2.1 Line transect trials

The diurnal walked line transect method was similar to line transect methods used for eastern grey kangaroos by Southwell *et al*. (1995b, 1997), Freudenberger (1996), Nelson (1996), ACT Kangaroo Advisory Committee (1997), Muranyi (2000), and le Mar *et al*. (2001).

However my survey began soon after first light, a time of day when eastern grey kangaroos are active, and finished at the second occasion on any transect when a kangaroo was seen lying down. This generally occurred after about 1.5 to 2 hours. Counts were done in fine weather, and were abandoned if mist was observed.

Radial distances were measured to the kangaroo at the centre of a group, or interpolated between kangaroos, using a Bushnell 1000 laser rangefinder accurate to ± 1 m. Direction (± 0.5^{o}) to the apparent centre of mass of each group was measured with a Suunto prismatic night compass. Groups were defined as kangaroos no more than 15 m apart, except that occasional large clusters which met this criterion were subdivided into manageable 'groups', each of which could be counted without traversing the beam of the spotlight. Group size was checked with binoculars in most cases. Observations were spoken into a tape recorder, transcribed, and analysed in program Distance 3.5 (Thomas *et al*. 1998).

In the night counts, an open-backed vehicle was driven cross-country on straight lines marked with posts bearing small reflectors. Contrary to the experience of le Mar *et al*. (2001), the laser rangefinder and night compass worked just as well as in daylight, or better. However the rangefinder operated satisfactorily only after the instrument had been trained on the target animal or group. In the high density populations with large numbers of groups that had to be recorded quickly, unacceptable delays occurred when using the rangefinder in the normal hand-held manner, while aligning the field of view with each new target animal or group. Therefore the spotlight, rangefinder and compass were attached together in such a way that a kangaroo at the centre of the spotlight beam would be aligned with the crosshair sight of the rangefinder. The compass was aligned with the azimuth of the rangefinder where it met the horizon. The three instruments were mounted on a freely moving ball-and-socket device attached to the vehicle. The only item that remained hand held was the binoculars (8 X 56 designed for low light conditions), which were necessary for correctly counting group size. Observations were spoken into a motorcycle intercom then keyed into a database by the vehicle driver. Observations were sometimes also tape recorded to check for data entry errors. The red light method was the same as the white spotlight method except that the vehicle headlights and spotlight were covered with red filters.

After commencing the trial at one site, it was discovered that magnetic interference from the vehicle, the spotlight, and other equipment, had biased the compass bearings in a manner too complex to be readily corrected, with most angles to the transect having been reduced by between 6° and 25°. This would reduce the variance and inflate the density. The compass was therefore replaced with a compass rose, i.e. a disc engraved with degree markings, attached to the ball and socket device, (Figure 7.1). A red laser beam was projected onto the compass rose in a vertical band to define the plane where the bearing was to be read, which was a simple way to retain freedom of movement of the ball and socket joint in all directions, necessary when the vehicle travelled up, down and across hills. The small reflectors along each transect enabled the drivers to keep the vehicle closely aligned with the transect. Only data from Googong, the second site used in the methods trial, where the compass rose was used, were used to select between line-transect methods.

Each method was carried out for 6 hours per site. This choice was based on a preliminary two–hour night count for which the coefficient of variation (CV) was 27%. Error tends to decline in proportion to the square root of the number of samples, so considering hours as sampling units, in six hours, the mean CV should decline to about 15% but it would decline only slowly thereafter, reaching 10% after 12 hours and 7.5% after 25 hours. Six hours of counting per site appeared likely to be achievable for the three sites in six to nine nights per bimonthly sampling cycle. It would have been impractical to plan for a much greater counting effort considering the predicted availability of assistants to drive the survey vehicle. During the study, 48 people drove the survey vehicle and keyed in the observations on the 91 nights of counting.

Figure 7.1: Line-transect equipment. To increase the rate of recording observations at night, the spotlight, laser rangefinder and compass rose were mounted on a commercially available ball and socket device (seen here with grip handle and locking lever) in such a way they could be finely adjusted to co-align. A red laser beam (not visible) marked the ‘zero’ point where the bearing on the compass rose was read, with the aid of a small light to illuminate the engraved digits. A white plastic cover protected the rangefinder from light rain or snow. Twelve coil springs (visible below the compass rose) insulated the equipment from both engine vibration and shocks due to the vehicle bumping over rocks.

I sought the survey method which could provide the most precise estimate (lowest CV) in the time I had available. The precision of any line-transect survey depends on the number of encounters, the number of transects, the consistency of encounter rate between transects, and the variation in group size. The differences in precision between the line-transect methods that I trialled are a consequence of the intersection of those factors, with the kangaroo behaviours and visibility conditions characteristic of each of the methods under trial - transects walked in daytime, transects driven at night with a red spotlight, and transects driven with a white spotlight. In other words, the standard factors that determine precision of line-transect estimates are, in this case, the mechanism underlying my primary criterion, precision of each method per unit of my time. For the purpose of the methods trial, I assumed I was using each of the methods optimally. From Table 7.1 it can be seen that the white spotlight method met the criterion of lowest CV per unit of my time. This was an unexpected, but convenient, result because the visibility reduction entailed by the red light method placed greater demands on the drivers, especially on transects traversing steep rocky areas. The white spotlight method was therefore used for the study, on set transects that required six hours over two nights to traverse at Googong, the same at Tidbinbilla, and nine hours over three nights at Gudgenby. The additional effort was applied at Gudgenby because of its larger size, and because results of the initial six–hour counts there generated higher CVs than the other sites.

Counts were scheduled close to the new moon date as a precaution to minimise any variation due to effects of moon phase. Suspicion that such an effect may exist is encouraged by the correlation between moon phase and the rate that eastern grey kangaroos are killed on roadways (Coulson 1982; Lintermans and Cunningham 1997). Also, like rabbits, eastern grey kangaroos are predation-sensitive foragers (Banks 2001; Chapter 6) and like rabbits (Kolb 1992), may change their nocturnal movements according to the moon phase, when predators are present.

Table 7.1: Comparison of results from three kinds of line transect count. A six-hour trial of each method was used to estimate density of eastern grey kangaroos at Googong.

Method	Number of kangaroo groups recorded	Density estimate (No. ha^{-1})	CV (%)
White spotlight (driven at night)	177	5.3	14
Red spotlight (driven at night)	131	3.0	17
Daytime, walked	71	6.1[(a)]	31[(a)]

(a) Additional daytime survey reduced both the density estimate and the CV for this method until they approached those obtained for the white spotlight but about three times as many hours were required. See Results.

Due to the constraints of the terrain, transects were neither systematic nor random, but followed negotiable straight-line routes marked out in advance across country, away from roads and tracks. Roads and tracks were avoided because they are more likely than cross country transects to be a biased selection of the terrain and to result in biased estimates of macropod density as found by Southwell and Fletcher (1990). Minor deviations were required in some cases around small obstacles such as rocks or logs too large to move or drive over, but no observations were recorded while making these deviations. The lower topographic relief at Gudgenby enabled the transects there to cover most combinations of slope and aspect, but at Googong and Tidbinbilla the steepest and rockiest areas were not sampled. Until March 2002 (the fourth bimonthly count per site) there was some variation between surveys in which transects were counted, as several transects proved inadvisable for the less experienced drivers, due to loose rock, steepness, or boggy areas, but from that date, the same transects were used consistently.

Until January 2002, the driver entered data to the keyboard of a laptop computer placed on the front passenger seat. However some drivers experienced difficulty entering data in this manner, so from March 2002, a U-shaped foam board was placed around the driver supporting a numeric keypad and a trackball (but leaving free access to the vehicle controls). Together with enlarged text on the computer screen, this enabled faster data recording in reasonable comfort. From November 2002, anyone riding in the tray of the vehicle was tethered so they could not fall out. My counting proficiency must have improved with experience, as surveys at the end of the period required less time. If reactive movement was biasing the counts (see *Assumption 5* below) the increased speed would presumably have reduced this bias.

7.2.2 Assumptions underlying the line transect method

Buckland *et al.* (1993 pp 30 – 37) prominently list three assumptions underlying the line transect method (Assumptions 1 – 3 below). Reports of line transect surveys often compare their methods to these (e.g. Southwell and Sheppard 2000; le Mar *et al.* 2001; Dique *et al.* 2003). However there are other assumptions given less prominence by Buckland *et al.* (1993), (Assumptions 4 – 6 below) some of which may also be critical in certain cases, including this study.

Assumption 1: Objects on the line are detected with probability close to 1.0.

The assumption that objects lying on the survey line are all recorded is important for certain types of surveys. The observers in many helicopters or light aircraft cannot see the flight line, for example, and there is an obvious issue when surveying animals which spend time below the surface, such as cetaceans or rabbits (Chapter 3). However a kangaroo which remained stationary on the transect line would not be missed by a ground based survey, so in my study this assumption was met.

Assumption 2: Objects are detected at their initial location before any movement in response to the observer.

The assumption that objects are detected at their initial location before moving is a challenge for any survey of mobile objects and for surveys of animals that are cryptic. Eastern grey kangaroos are highly mobile. In open habitat at night they are generally obvious but may be cryptic at times, e.g. when they are at long range, facing away from the observer and feeding without lifting their heads. On the study sites there were always some kangaroos on the move independent of disturbance by the researcher. However the kangaroos were more approachable at night than in daylight and most were recorded while stationary, before they moved off. Their tolerance of the survey vehicle enabled me to adopt the practice of not recording stationary kangaroos at long range ahead of the survey vehicle. Waiting until they were 50 – 100 m away, or showing signs that they may be about to take flight, enabled me to estimate the group size more accurately. The sighting histograms do not generally have a data spike at a distance from the transect, which is often indicative of animals moving away from the transect before being detected (Buckland *et al.* 1993). Reactive movement parallel to the transect and away from the vehicle would not be detectable from the histograms. It would cause density to be underestimated (Buckland *et al.* 1993; Southwell 1994), and is mentioned further under Discussion.

Assumption 3: Perpendicular displacements are estimated accurately.

The assumption that perpendicular displacements are estimated accurately has subsidiary components. The calculation of perpendicular displacement was by simple trigonometry in program Distance 3.5 (Thomas *et al.* 1998) and can be assumed to be accurate. It is calculated from the measurements of radial distance and angular displacement of each observation. These measurements were obtained from a laser rangefinder and a compass rose respectively, both of which I consider potentially highly accurate for the purpose, following common practice in the literature. Actual accuracy depends on a human operator, and therefore in my study sources of error were observed occasionally. An underestimate of the range to a kangaroo can occur when the (infrared) laser beam of the rangefinder passes just above ground level, and is reflected by an unseen object such as a tall grass stem. The ‘grass reflection’ phenomenon was apparent when the range displayed by the range finder was implausibly low or when the range measurement increased if the aim point on the kangaroo was shifted slightly. (Optional program settings within the rangefinder can be used to reduce this problem or detect it more easily.) The elevated observation point on top of a vehicle would have reduced this source of error, compared to walked counts, and for both methods it seems likely to be a problem only with long range observations (at least in the short grass conditions of this study). Truncation of the data (see below) has removed observations at long range perpendicular to the transect. At the other extreme, for objects lying directly on the transect line (zero perpendicular distance), errors in the estimation of radial distance have no effect on the density estimate because radial distance itself has no effect. Thus the potential effect on the density estimate of inaccurately measured radial distance is greatest in regard to those objects positioned at intermediate distance from the transect (e.g. 10 – 80 m in this study) which were recorded from a long range (greater than 200 m in this study). In practice these would have been so few that I suspect any ‘grass reflection’ effect in this survey would be insignificant due to the large number of records taken at shorter range that would not have suffered from the problem.

Errors were also possible in recording the angular displacement. The vehicle was aligned with the transect whenever it stopped to make an observation. Where small detours had to be made around obstacles on the transect line, the vehicle was realigned with the transect before any more observations were recorded. A longitudinal stripe on the roof of the double-cab vehicle in front of the rangefinder was a convenient sighting aid, so that if the driver had not correctly aligned the vehicle this was readily apparent. The alignment of the equipment was checked at the commencement of every counting session and part way through most of them (i.e. that zero degrees on the compass rose was aligned with both the aim point of the rangefinder and the long axis of the vehicle). It rarely needed adjustment and is assumed to have delivered unbiased measurements. Probably the greatest potential for error in recording the angular displacement was misreading the numbers engraved on the compass rose. A light was attached to the equipment specifically to reduce this potential as much as possible. As with the measurements of radial distance, I suspect the incorrect angular displacement data would have insignificant effect among the large number of correct records.

Data reporting errors cannot be assessed but are assumed to be symmetrical i.e. reporting a reading of 11 degrees as 9 degrees is likely to have happened as often as the reverse. On about one–eighth of the nights, a second volunteer was also present on the back of the vehicle and would have been in a good position to report any large data reporting errors, but this did not occur. Limited searching for keying-in errors using the tape recordings of the intercom conversations indicated keying-in errors to be infrequent.

Assumption 4: Only objects in the area perpendicular to the transect are recorded.

The requirement to record only objects perpendicular to the transect seems obvious. However my prior experience with spotlight surveys in which all visible individuals were recorded, led me at first to count some kangaroos that were beyond the far end of the transects, before realising this was inappropriate. Having corrected my mistake I then found it was also possible to inadvertently record kangaroos that were in fact beyond the far end of the transects, and to wrongly exclude animals that were within the transect bounds when they appeared not to be. Therefore I adopted the practice of measuring the range to the final reflector on the transect for comparison. Where kangaroo groups straddled the boundary, those members outside the count area were excluded. (A better procedure would have been to include all of a group when the centre of mass of the group was inside the survey area, and exclude all of the group when the centre of mass was outside.) Future surveys of high density populations of mobile animals could benefit from the use of additional reflectors or markers placed in a line perpendicular to the end of the transect, to define the boundary of the counted area.

There is potential for an observer approaching the start of a transect to flush kangaroos onto or away from the counted area. My initial assumption was that this would be managed more easily by arranging transects with a gap between the end of one and the start of the next, but experience indicated there was no easy solution. Contiguous transects had the advantage that the kangaroos were under continuous observation. In either case, when approaching the start of a transect, careful note was taken of kangaroos flushed into or away from the counted area and they were recorded (or not) as if still in their original positions.

Assumption 5: The same objects are not counted twice in one sample

Buckland *et al.* (1993) clarify that counting the same animals twice in one survey is not necessarily a problem, e.g. transects may intersect, but that density will be overestimated if the same animals are recorded more than once per transect. In both the walked and vehicle based surveys, large groups of kangaroos would sometimes move ahead and out of sight, e.g. over a hilltop, rather than to the side. As others have done (Southwell 1994), when that occurred I judged whether kangaroos seen later in the same transect were the same ones as those already counted, or new ones, or a combination. Where possible I was guided by cues such as whether the kangaroos were mostly wary, or mostly feeding calmly, but these were inevitably somewhat arbitrary judgments. Density may have been overestimated on some occasions by double counting, and underestimated on others by excluding kangaroos that should have been counted. In theory this problem is best overcome by using a survey platform that travels faster than the maximum speed of the animals, but that is impracticable for ground line transect surveys of kangaroos. The use of a vehicle, rather than walking, should have reduced the error from this source. To reduce bias from this source, future line transect surveys in similar conditions should be conducted so as to minimise the time taken to record each kangaroo group, enabling more rapid progress along the transect. Automatic recording of range, direction and other parameters is one possibility. Bradbury *et al*. (1996) connected a rangefinder and compass to a portable computer and mapped the positions of individual Thomson's gazelles (*Gazella thomsoni*) while digitally logging the sex and posture of each animal, achieving a rate of hundreds per few minutes.

Assumption 6: Transects are located randomly with respect to the objects counted.

The requirement for transects to be located randomly with respect to the counted objects led to lay them out across country, avoiding roads. However due to the terrain, the transects at Googong especially, and also Tidbinbilla, did not sample the steep areas representatively. Such a sampling bias would be expected to positively bias the density estimates at those sites because few kangaroos were present in these steep areas at night. However the proximity of the line transect estimates to the result of the drive count at Googong (Figure 7.4) suggests this bias may have been small.

7.2.3 Line transect data analysis

Program Distance 3.5 (Thomas *et al*. 1998) was used for the analysis, except for model averaging (explained below) which was done using the formula provided by Burnham and Anderson (2002 pp 256 – 257). For each survey at each site a plot of frequency of groups sighted against distance from the transect was inspected (Figure 7.2) to decide the distance at which to truncate the furthest sightings, as recommended by Buckland *et al*. (1993 p 50). Data were truncated at mean distances of 78 m for Googong (range 60 to 105), 100 m for Gudgenby (range 80 to 120), and 80 m for Tidbinbilla (range 65 to 135). The three key functions q(x) (i.e. alternative forms of detection function) recommended by Buckland *et al*. (1993 pp 46 – 48) (i.e. uniform, half-normal, and hermite polynomial) were fitted separately to the data from each survey to choose an extension series based on minimum AIC, or no extension series, for each key function. (Extension series for the uniform function were cosine and simple polynomial, for the half-normal function were cosine and hermite polynomial, and for the hazard rate function, a simple polynomial. The uniform key function with no extension series fitted best for 20 of the total 37 surveys, uniform plus cosine expansion for 8 and uniform plus simple polynomial for 4, with half–normal and hazard rate key functions fitted to the remaining 5 surveys. More detail is given in Appendix 4.) The three density estimates for each survey from fitting the three key functions were combined by means of model averaging using the formula given by Burnham and Anderson (2002).

Thus the density estimate on each occasion at each site is the result of a weighted average between three detection functions, each with the best extension series for that function, given the data. One consequence of most of the analysis steps mentioned, is that the estimate of variance is made more realistic, i.e. larger (Burnham and Anderson 2002). The truncation particularly, and the other steps, are also likely to improve the accuracy of the estimate (Buckland *et al.* 1993).

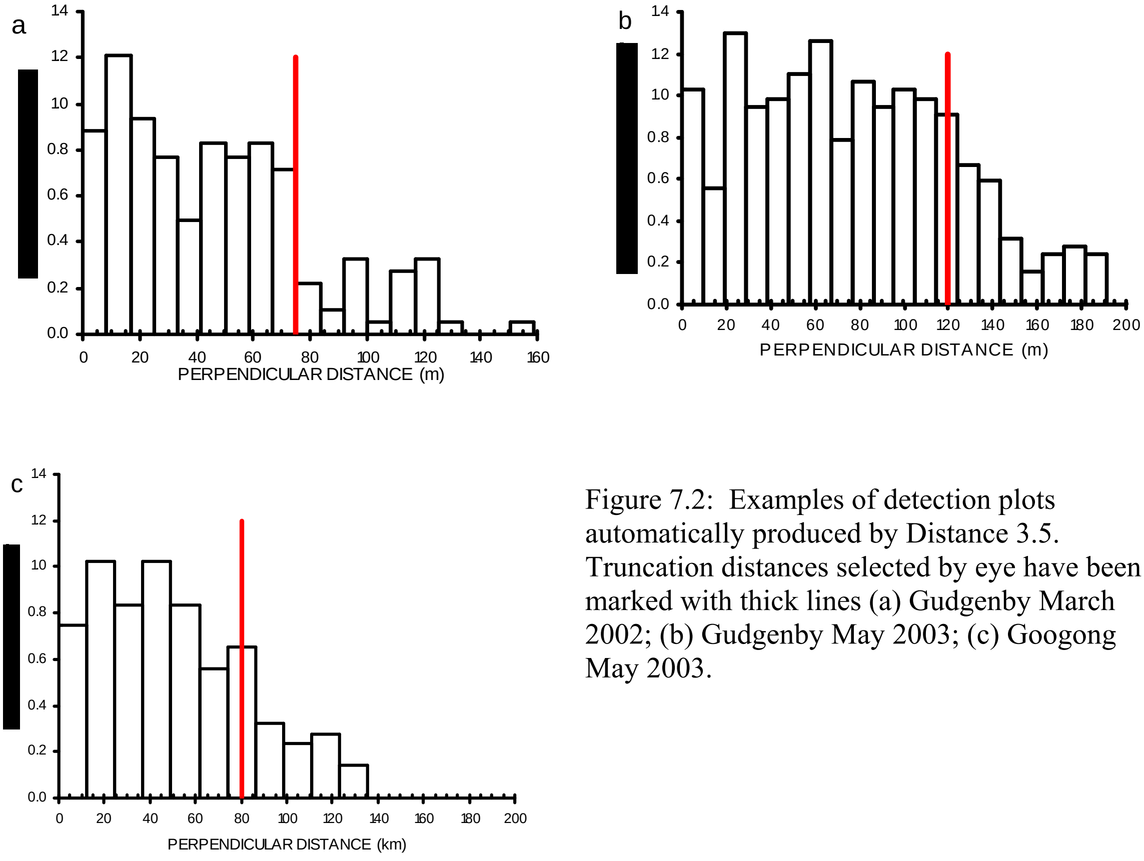


Figure 7.2: Examples of detection plots automatically produced by Distance 3.5. Truncation distances selected by eye have been marked with thick lines (a) Gudgenby March 2002; (b) Gudgenby May 2003; (c) Googong May 2003.

7.2.4 Drive count

Two ‘drive counts’ (Lancia *et al*. 1996) were conducted to obtain independent estimates for comparison with the line transect estimates at Googong and Gudgenby. Drive counts are a form of total count in which a line of people walk through a defined area counting every member of the target population that passes between them and the next person on one side. Drive counts of kangaroos have been previously used by Coulson and Raines (1985) to evaluate estimates obtained by line transect and faecal pellet count methods and by Short and Hone (1988) to correct aerial strip counts of kangaroo density. Drive counts were reviewed by Southwell (1989) for potential application to macropod species.

The areas covered by drive counts in this study were 4.5 km^2 at Googong and 9.4 km^2 at Gudgenby, which are larger than the 2.7 km^2 area counted by Coulson and Raines (1985) and smaller than the 12.1 km^{2}area counted by Short and Hone (1988). At Googong no kangaroos entered the reservoir during the drive count so it provided an effective and convenient barrier, like the water bodies defining the counted areas for Coulson and Raines (1985) and Short and Hone (1988). The Gudgenby drive count was the first in which this technique has been applied to kangaroos in an area not bounded on any side by barriers to kangaroo movement. All sides of the counted area had to be surrounded by people, either without disturbing the kangaroos, or (in reality) while recording the effect of this disturbance on the count. People, also called ‘counters’, were transported to marked vantage-points along opposite sides of an area which was roughly square. From these positions they could tally the number of kangaroos passing between themselves and the next position to one side. On the remaining two sides mobile counters then moved inward until they met in the middle and all kangaroos had been counted. The drive count at Googong involved 75 people and Gudgenby involved 105 people.

Drive counts and other forms of total count appeal intuitively because they purport to provide exact population counts (Southwell 1989) but most workers who have attempted them concede that an unknown number of animals may be missed (Lancia *et al*. 1996). McCullough (1979) is quoted by Lancia *et al*. (1996) as believing that drive counts of the George Reserve deer herd underestimated at low density and overestimated at high density with up to 30% bias.

Eastern grey kangaroos rely on speed rather than concealment to escape danger, and the vegetation in the counted areas was mainly open, so kangaroos were unlikely to remain unseen. More likely sources of error included the potential for confusion when individual kangaroos passed through the line of counters more than once, and the potential for large groups of kangaroos to be herded into confined areas if there was insufficient space between counters. (In fact the name ‘drive count’ conveys the opposite sense of what is desired, namely that the animals gradually pass back through the line of people so the animals are not driven ahead into a place from which a mass of panicked animals finally emerges.) For this study, substantial preparation and organisation was directed at minimising these and other potential sources of error (Appendix 3), and during each event special observers looked critically for sources of error and assisted in estimating their magnitude. Written material was provided for each sector boss, team leader, and counter (Appendix 3), and prior briefings. More than 25% of the participants were dedicated to supervisory and support roles, so that the counters were well coordinated and could concentrate on the counting as much as possible. For effective control, mobile teams were limited to no more than seven people and stationary teams to no more than 11. Counters were added or removed from the mobile teams from time to time (by team leaders), in order to maintain acceptable spacing. Both events were strongly supported by the ACT Parks and Conservation Service which supplied vehicles, radio communications equipment and experienced supervisors. Both drive counts were also strongly supported by the University of Canberra, whose third year wildlife students included the counts within larger exercises, and had been well briefed in advance. Other volunteers from Canberra Institute of Technology, Greencorps and elsewhere also participated. The sizes of the counted areas were estimated by mapping with a Global Positioning System (GPS) receiver, and calculation in program ArcView 3.5, a Geographic Information System (ESRI 1999).

7.3 Results

7.3.1 Line transect

The density of eastern grey kangaroos at Googong in June 2001 estimated with the nocturnal line transect method was close to the estimate obtained when the same transects were surveyed in daylight in the conventional manner (Table 7.2; Figure 7.4). The walked daytime method was then continued beyond the six-hours period used for the methods trial until its variance was approximately the same as that from the nocturnal method. This took approximately three times as many hours. It can be concluded that the vehicle as a survey platform, and the nocturnal timing, did not introduce a net bias to the density estimate; they merely enabled it to be obtained more efficiently. A separate question is whether the sampling design, i.e. transects selected so the vehicle could be driven on them, resulted in an estimate that was biased compared to true density. Results of the drive counts, discussed below, help answer that question.

Table 7.2: Comparison of results from diurnal walked and nocturnal driven line transect methods at Googong in June 2001.

	Density (EGK ha^{-1})	SE	Count time (hrs)
Diurnal walked	4.9	1.5	17
Nocturnal driven	5.3	1.5	6

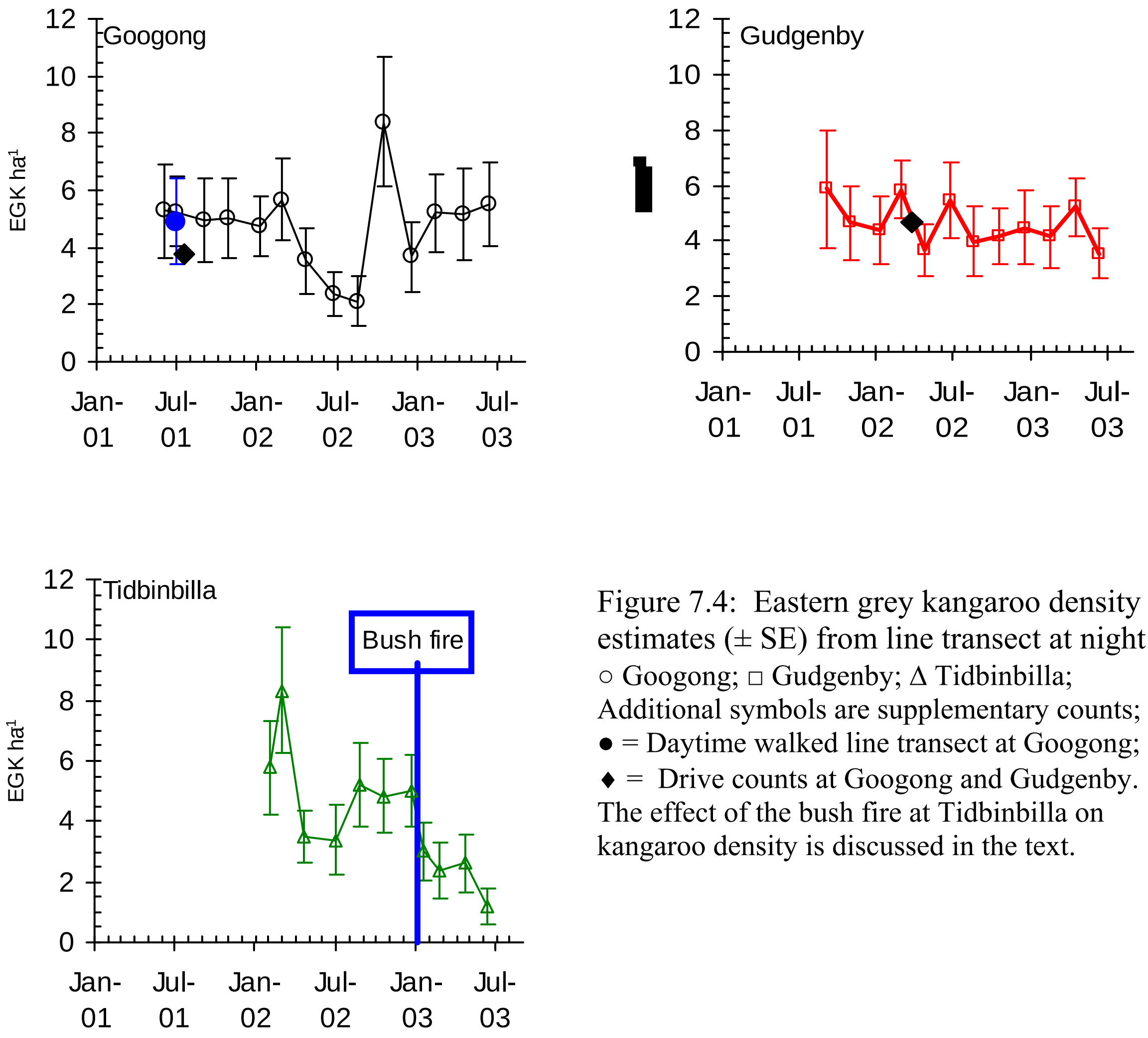


Figure 7.4: Eastern grey kangaroo density estimates (± SE) from line transect at night. ○ Googong; □ Gudgenby; Δ Tidbinbilla; Additional symbols are supplementary counts; ● = Daytime walked line transect at Googong; ♦ = Drive counts at Googong and Gudgenby. The effect of the bush fire at Tidbinbilla on kangaroo density is discussed in the text.

Summary statistics for each of the 38 line transect surveys (three sites, night and day) are at Appendix 4.

The nocturnal line transect estimates of the densities of eastern grey kangaroos at the Googong and Gudgenby sites at the end of the study period were close to what they had been at the beginning (Figure 7.4). The density estimates at Gudgenby fluctuated little, but those at Googong fluctuated improbably in the middle of the period. At Tidbinbilla the mean of the three estimates following the bushfire in January 2003 was approximately half the mean of the last three density estimates prior to the bushfire (2.7 as compared to 5.0 ha^{-1}) but not significant at the 0.05 level (t-test; $t = -2.58$, $df = 4$, $p = 0.061$). The difference between all pre-fire estimates and all post-fire estimates was greater (Figure 7.4; Table 7.3), and significant (t-test; $t = -3.16$, $df = 9$, $p = 0.012$).

Table 7.3: Mean density of eastern grey kangaroos at each site from nocturnal line transect estimates.

Site	Mean density (EGK ha^{-1})	Mean SE	Mean CV (%)
Googong	4.8	1.35	29
Gudgenby	4.5	1.19	26
Tidbinbilla pre – fire	5.1	1.35	27
Tidbinbilla post – fire	2.3	0.85	39

Because eastern grey kangaroos are strongly seasonal breeders in southern Australia (Chapter 1), permanent pouch emergence occurs in spring and summer for most animals. I also observed a die–off both years in late winter and early spring, of sub-adults and old kangaroos (Chapter 6). However no such seasonal pattern is evident from the line transect results for both years on all sites. The reasons for that are mentioned under Discussion.

The coefficient of variation of the density estimates (Table 7.3) was higher than the 15% expected from the preliminary trials. As shown in Table 7.4, little of the imprecision is due to uncertainty about the form of the detection function, or the variation in group size. Rather, the encounter rate, meaning the variation between transects, is responsible for 74% to 83% of the variance. This was evident in the field as nightly variation in where kangaroos were encountered, i.e. inability to predict which transects would have large numbers of kangaroos and which would have few.

Table 7.4: Sources of the variance in the estimates of the density of eastern grey kangaroos at each site as the mean (± SE) of all surveys.

	Googong mean (SE)	Gudgenby mean (SE)	Tidbinbilla mean (SE)
Detection probability	6.3 (2.1)	7.8 (3.2)	10.2 (3.2)
Encounter rate	82.5 (1.8)	81.6 (3.2)	74.3 (3.2)
Group size	11.2 (0.8)	10.6 (1.2)	15.5 (3.3)

7.3.2 Drive count

In the drive count at Googong, 2,012 eastern grey kangaroos were counted moving either into or out of the area, which represented 1,755 independent animals. This corresponds to 3.8 ha^{-1}. The possible error due to animals missed, or animals counted twice, was estimated to be plus 0.2 and minus 0.1 kangaroos ha^{-1}. At Gudgenby, 1,312 eastern grey kangaroos were counted moving into the area, and 5,712 moving out, resulting in a density estimate of 4.7 ha^{-1} and an uncertainty of ± 0.7 ha^{-1}. These results are illustrated in Figure 7.4 with the line transect survey results for the respective sites. Sudden rain storms occurred in the final stages of both events and at Gudgenby the uncertainty around the estimate was increased when some counters had to abandon their vantage points on rock outcrops and others had their written record destroyed. The density estimates from the drive counts are within one standard error of the density estimates from the line transect surveys carried out around the same time.

7.3.3 Seasonal pattern

The death of sub-adults and older animals in late winter and early spring would reduce population density, and density would be increased again in late spring and early summer by the permanent emergence of the pouch young into the counted population (Chapter 6). Ability to discern these patterns would depend on accuracy and precision of the bimonthly density estimates, and would also be subject to appropriate timing of the counts (which were not conducted for this purpose). These seasonal trends, coordinated between sites, are not evident in the line transect results for the individual sites. When the density estimates are combined between sites (Figure 7.5), there is the suggestion of a pattern. The wide confidence intervals around each estimate (Table 7.3, Figure 7.4) preclude significant differences between seasons.

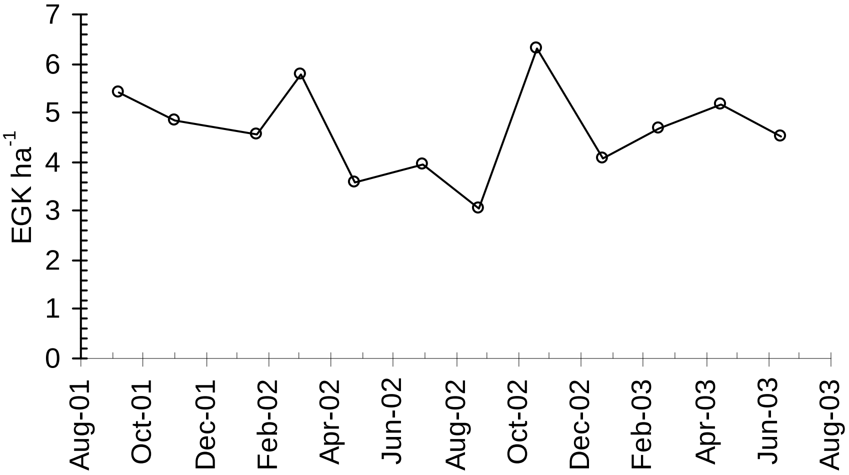


Figure 7.5: Means of bimonthly kangaroo density estimates on Googong and Gudgenby sites.

7.4 Discussion

7.4.1 Accuracy

Compared to the nocturnal line transect estimates, the two drive counts are considered truly independent, but the walked line transect estimate is not fully independent because it used the same transects. The agreement between the nocturnal line transect estimates and these three alternative estimates does not support a hypothesis that the nocturnal line transect estimates are biased. Only the drive count at Googong produced an estimate which was notably different from the nocturnal line transect estimates carried out at the same time, i.e. it was 1.3 ha^{-1} lower, but this difference was not statistically significant, as it was within one standard error of the nocturnal line transect estimates at about the same time.

The point was made under Methods, that reactive movement by kangaroos parallel to the transect and away from the vehicle would not be detectable from the histograms, and would cause density to be underestimated (Buckland *et al.* 1993; Southwell 1994). It was also pointed out that numbers of kangaroos were observed exhibiting that behaviour, and disappearing ahead, requiring judgments to be made whether to include or exclude kangaroos seen later on the same transect. This introduces the potential to bias the density estimates in either direction, by consistently making the wrong decision. The agreement between the estimates from the drive counts and the those from the nocturnal line transect surveys suggests that the nett bias was low at the time the drive counts were carried out.

Considering the evidence presented here that the nocturnal line transect estimates are realistic, what does it mean that lower density estimates have been reported for these sites in the past?

7.4.2 Comparison with density of other kangaroo populations and previous density estimates on the study sites

Fruedenberger (1996) reported that density of eastern grey kangaroos on ACT reserves, which he estimated by the walked line transect method to be 2.33 ha^{-1}, was greater than reported for any other macropod population. The density at Tidbinbilla, which is one of the ACT reserves, was considered remarkably high at 3.57 ha^{-1}. The density of the eastern grey kangaroo population at Yan Yean (Coulson *et al*. 1999a), estimated by the same method, is almost as high as the estimate for ACT reserves , i.e. 2.20 ha^{-1}. Table 7.5 presents all of the eastern grey kangaroo density estimates for the ACT region prior to this study. It includes two Tidbinbilla estimates subsequent to that of Freudenberger (1996), one close to the one reported by Freudenberger (1996), and one lower, as well as another remarkably high density estimate for a different site, namely Googong (3.6 ha^{-1}). (One estimate at Tidbinbilla has been disregarded for purposes of this comparison as it followed a small control operation.) In summary, walked line transect estimates of the density of eastern grey kangaroos at Googong and ACT reserves including Tidbinbilla, were in the range from 1.9 to 3.7 ha^{-1} between 1995 and 1999. They are all lower than the means of the density estimates from each site in the current study, except the post fire estimate at Tidbinbilla (Table 7.3).

There are notable differences in how the estimates in Table 7.5 were obtained compared to the present study. They were made throughout the day, when many kangaroos would have been resting. In order to include any kangaroos resting in adjoining bushland, many transects commenced and finished part-way up the surrounding hillsides. The surveys at Googong (Muranyi 2000) were an exception, because in that case the full length of all transects was within the habitat occupied by the high density kangaroo population. So, except for the two Googong surveys, the 'site' that was sampled in the surveys listed in Table 7.5 included large areas of habitat that the present study treats as rarely used by kangaroos. The difference in the definition of 'site' could explain much of the difference between the previous estimates and the higher estimates from the present study. The time of day may also have influenced the probability of recording kangaroos on the centerline of the transect if the kangaroos take flight in daytime when the observer is further away than they do at nighttime, as appears to be the case. However it is not possible with the line transect data available to be sure how much of the difference in density estimates is due to the definition of ‘site’ and how much is due to other factors such as technique, movement of kangaroos onto the sites at night, and genuine changes in density. In any case, the estimates from this study are within the 95% confidence intervals of the earlier estimates, and vice versa. So the estimates from this study are higher, but not significantly higher than previous estimates on the sites, and they are the highest reported densities of kangaroos. In regard to the discrepancy between previous and current estimates at Googong, the information from rangers at Googong (Bernard Morris, Googong ranger, personal communication, 2001) is that density of the eastern grey kangaroo population at Googong has been increasing consistently. In that case, a real difference in density seems the most likely explanation.

Table 7.5: Walked line transect estimates of density of eastern grey kangaroo in ACT areas normally protected from shooting, carried out prior to this study. The Tidbinbilla and Googong sites used in this study are within the sites of the same names here, and the Gudgenby site of this study is included in ‘Namadgi cleared valleys’.

Site	Date	Density EGKs ha^{-1}	CV (%)	lower 95% conf	upper 95% conf	Reference
Tidbinbilla	Nov-95	3.6	14	2.7	4.8	Freudenberger 1996
Tidbinbilla	May-96	2.2	22	1.4	3.4	Nelson 1996
Tidbinbilla	Mar-97	3.7	19	2.5	5.4	ACT KAC 1997
Tidbinbilla	Jul-97	2.3$^{\#\#}$	13	1.8	3.0	ACT KAC 1997
Namadgi - cleared valleys	Nov-95	1.9	21	1.3	2.9	ACT KAC 1997
Namadgi - cleared valleys	Nov-96	2.8	24	1.7	4.3	ACT KAC 1997
Namadgi - cleared valleys	May-97	2.7	30	1.5	4.8	ACT KAC 1997
Googong	Jun-96	2.0	27	1.2	3.3	Muranyi 2000
Googong	Aug-99	3.6	30	2.0	6.4	Muranyi 2000
ACT reserves	Nov-95	2.3	10	1.9	2.8	Freudenberger 1996
ACT reserves	May-96	2.1	17	1.5	2.9	Nelson 1996
ACT reserves	Nov-96	2.5	18	1.8	3.5	ACT KAC 1997
ACT reserves	May-97	2.4	21	1.6	3.6	ACT KAC 1997

= after shooting

Concurrent with this study, a trial was commenced by the National Parks and Wildlife Service (NPWS) of NSW, to introduce commercial harvesting of eastern grey kangaroos to south eastern NSW, which is the region including the study sites (Figure 1.4). Pople *et al*. (2003) explain the design for helicopter line transect surveys to estimate abundance of eastern grey kangaroos in the area and Cairns (2004) reports the result of the first survey. Kangaroos are shot mainly on cleared grazing land, and the design excluded large areas of heavy tree cover, areas of national park and state forest, and areas of high relief. Mean transect length was 21.6 km. The estimated density of eastern grey kangaroos across the whole of the 24,472 km^2 surveyed area was 11.95 ± 2.51 km^{-2}, i.e. 0.1 ± 0.03 ha^{-1}. This value is not only lower than those from the study sites, but it is only about one fifth of the densities estimated by the ACT Kangaroo Advisory Committee (1997), in four surveys using the walked line transect method on cleared grazing land in the ACT (Table 7.6) where kangaroos are also shot under license to reduce competition with stock. There is no obvious reason why ACT graziers would tolerate kangaroo density five times as high as their NSW counterparts. One factor responsible for the difference could be the type of underestimation reported by Clancy *et al*. (1997) in which helicopter line transects generated a density estimate 33% ± 9 lower than walked line transects. Another factor may be that the much shorter transects used by the ACT Kangaroo Advisory Committee (1997) were completely in high quality habitat, whereas the longer helicopter transects may have included patches of remnant woodland and other areas of lower quality kangaroo habitat. Thus, aside from the differences introduced by the choice of survey platforms, there is a difference of survey objectives compared to the rural study by the ACT Kangaroo Advisory Committee (1997), and the current study. Cairns (2004) reported regional density over a scale of tens of thousands of square kilometres. This study is reporting density on localised sites of several square kilometers.

The discussion above should not be read as an indication that the density estimates in this study are of feeding patches and would be lower if the full home range of the animals was sampled. As indicated in Chapter 3, there is relatively little use by eastern grey kangaroos of areas outside the defined boundaries of the grassland study sites where the line-transect surveys were carried out. The boundary of the area that is well used by kangaroos is sharpest where the neighbouring area is either steep, or where it is closed tea tree shrubland. My preliminary observations of kangaroo tracks and droppings indicated that at Tidbinbilla eastern grey kangaroos infrequently penetrate more than about 80 m into steep, dense tea tree. Even on hot days the kangaroos near the centre of the Gudgenby site appeared to remain where they were, rather than moving a kilometre or two into the forest on the steep surrounding hillsides. As mentioned in Chapter 3, some other studies (eg Moore *et al*. 2002), also have reported eastern grey kangaroo populations which do not make much use of areas covered in woody vegetation. Thus the densities of eastern grey kangaroos given in this chapter are probably a valid representation of these populations, but they are not regional densities (eg averaged across a shire, state or territory), which will depend on the frequency and extent of such grassy islands in the region.

Table 7.6: Estimates of density of eastern grey kangaroos by walked line transect surveys on ACT rural lands, from ACT Kangaroo Advisory Committee (1997).

Date	Density (EGK km^{-2})	CV (%)	Total length of transects (km)
Nov 1995	50	19.7	195
Apr/May 1996	59	16.9	163
Nov 1996	48	30.5	172
Apr/May 1997	39	21.8	195

7.4.3 Precision

Precise density estimates of kangaroo populations are obtained infrequently from sampling surveys. A notable exception is the estimate by Freudenberger (1996) with a CV of 10% (Table 7.5), but aside from noting that such precision was unusual, Freudenberger (1996) did not suggest an explanation. Similar surveys by Nelson (1997) and ACT Kangaroo Advisory Committee (1997) produced less precise estimates (Table 7.5), including surveys of the same sites, using the same personnel and equipment. Other surveys reporting similar precision to that of Freudenberger (1996) include Southwell (1994) and Cairns (2004). Many factors can contribute to imprecision, including model-selection uncertainty for the detection function, and variable group size. In this study, ‘group size’ in the sense used for recording the line transect data, was only a minor source of variance and so was model-selection uncertainty. The main source was variation between transects. That relates to kangaroo grouping on a different scale than the one which has attracted most attention in the literature.

Eastern grey kangaroos are gregarious (Southwell 1984a) and occur in open membership clusters from two to hundreds. Behavioural researchers refer to kangaroo clusters of increasing size, as ‘sub-groups’, ‘groups’, ‘mobs’, and ‘aggregations’ (Jarman and Coulson 1989; Dawson 1995) but it is recognised that, except at the sub-group level, membership changes from hour to hour (Dawson 1995, p29), and that the rate of change increases exponentially with density (Southwell 1984b). Researchers have resorted to measures of absolute proximity to define some of these units, for example (Dawson 1995) defines all kangaroos within 50 m of each other being part of the same group. Group size is correlated with both population density and openness of habitat (Jarman and Coulson 1989). On the study sites, large daytime aggregations (as shown on the title page of the next chapter) could inappropriately be defined as one ‘group’ using definitions such as the 50 m proximity rule, or even the 30 m rule used by Southwell (1984a). The only study of the behaviour of kangaroos in high density conditions such as the study sites appears to be that of Banks (1997, 2001) who recorded kangaroos feeding further from cover where fox density had been reduced, and females with dependent young feeding in smaller groups.

Variance of the density estimates will be higher if the scale of the sampling unit is not much larger than the scale of aggregation. Short transects could lie entirely within an area of high density, or entirely in an empty area, whereas much longer transects would each include some areas of high kangaroo density and some of low density, thereby reducing the variance. In this study, zones containing a high density of kangaroo groups were often encountered between areas with few or no kangaroos. Transects used in this study were mostly 200 to 350 m long. The low precision of density estimates in this study may be partly because the (relatively short) transects were not much larger than the scale of nocturnal kangaroo ‘aggregations’. If that is so, then longer transects would improve the precision, but a different survey platform would be required, at least for the terrain at Googong and Tidbinbilla.

7.4.4 Counter saturation

Southwell (1994) found a negative density-dependent bias when estimating kangaroo populations of density greater than 0.3 ha^{-1} (30 km^2) which he attributed to counter saturation. The populations on the study sites are an order of magnitude higher so the possibility of underestimation due to saturation of the counting and recording system is one that confronts this study. That statement may seem paradoxical to the authors of the studies listed in Table 7.3, who recorded lower densities on sites of the same name, and may be more inclined to suspect overestimation than underestimation, but the difference in definitions of ‘site’ has been discussed above. In this study, the agreement between the line transect estimates and the independent estimates from the drive counts does not support a hypothesis that the line transect estimates were suffering from a negative density-dependent bias.

7.4.5 Seasonal pattern

Evening counts of eastern grey kangaroos in valleys of Namadgi National Park (Banks 1997) provided evidence of patterns of seasonal reproduction in the variable proportion of pouch young and young-at-foot. It is reasonable to expect that kangaroo density would be increased by the permanent emergence of the pouch young into the counted population in late spring and early summer. Also to be expected is a reduction in density due to mortality of sub-adults and older kangaroos in late winter and early spring. A strong test of any attempt to estimate kangaroo density bimonthly, is whether such annual patterns can be discerned. Imprecision of the individual density estimates could swamp such seasonal patterns, or the attempt could be frustrated by the extent to which the processes overlapped. There is a weak suggestion of such a pattern when the density estimates are combined between sites (Figure 7.5) but clear evidence of the presumed seasonal pattern from a single site (or evidence to refute it) remains a challenge for future attempts to estimate density in high density kangaroo populations.

In this chapter I have analysed the peculiar difficulties of applying the line transect method to highly mobile objects at high density, and I have presented the results of bimonthly surveys on each of the three study sites. In the next chapter, these data are used to estimate population growth rates which are combined with the results from the pasture chapter (Chapter 4) to estimate the numerical response of the eastern grey kangaroo populations.

CHAPTER 8

THE NUMERICAL RESPONSE

Successful applications of modelling in ecology are almost always iterative. The initial versions of the model highlight areas of uncertainty and weakness, which can then be addressed in later versions (Hamish McCallum)

Eastern grey kangaroos are gregarious. Most aggregations at Gudgenby seem to spend the full day in the open, but membership changes continually.

CHAPTER CONTENTS

8 THE NUMERICAL RESPONSE

8.1 Introduction and literature review

8.1.1 Population growth rate

The importance of population growth rate in ecology has long been recognised (Andrewartha and Birch 1954; Cole 1958; Hone 1999; Sibly and Hone 2003; Chapter 2). Whether the management objective for a population is conservation, pest management or harvesting, it is of practical importance to know how fast it is increasing or decreasing, and critical to know the factors that determine that rate (Caughley 1976a, 1977a; Sinclair and Krebs 2003).

Two representations of population growth rate are in common use in ecology. ‘Population growth rate’ here refers to the instantaneous rate of increase (r) the natural logarithm of the other representation, the ‘finite rate of increase’ or ‘proportional rate of increase’ (λ), so:

$$r = \log_e(\lambda) = \log_e(N_{t+1} / N_t) \qquad \text{Eqn 8.1}$$

where N_t = population density at time t (Caughley 1977a). By convention, r is expressed as an annual rate (i.e. the units of t are years) unless stated otherwise. The sign of r indicates whether a population is increasing or decreasing, and stability is defined as $r = 0$ (or $\lambda = 1$).

Population growth rate represents the net value of all demographic rates combined, such as birth and mortality rates. It is determined by the combined effect of all intrinsic and extrinsic forces acting on a population. The potential of the population to respond to these forces may be restricted by demographic characteristics of the population such as its age structure and sex ratio. Therefore the population growth rate is determined by previous conditions as well as current conditions.

It follows from the above that the value of r is particular to each time and each population, but there is an exception. The intrinsic rate of increase, symbolised r_m or r_{max}, is a constant for each species, determined by characteristics of the organism, not its environment, and scales allometrically between species (Caughley 1977a; Caughley and Krebs 1983; Sinclair 1996). However r_{max} will only be achieved when environmental conditions and the demographic structure are both favourable. Cairns and Grigg (1993) make the distinction between the theoretical maximum, or intrinsic rate of increase, and a 'generic' maximum rate of increase defined by the asymptote of a numerical response fitted to data from a real population. They interpret the values of r_{max} estimated by Bayliss (1985, 1987) for red kangaroos at Kinchega (0.34 – 0.58) to be the latter form and also the values 0.26 and 0.33 estimated by J. Caughley *et al.* (1984) for red kangaroos on the inland plains of western New South Wales. However the distinction made by Cairns and Grigg (1993) between two forms of r_{max} seems unnecessary providing it is accepted that numerical responses from field data are estimates that reflect both current and previous characteristics of the site and seasons, as well as measurement error, and may result in asymptotic estimates of r_{max} that are higher or lower than the intrinsic rate of increase which would be measured in a hypothetical population living in an environment that was constant and favourable.

Sibly and Hone (2003) described population growth rate as the key unifying variable linking many facets of population ecology, for example showing that it defines the niche of an organism, and that it quantifies ecological stress, such as from environmental toxins. The word 'population' in front of 'ecology' seems barely necessary in their statement, considering that ecology is defined as the scientific study of the interactions that determine the distribution and abundance of organisms (Krebs 2001). The distribution of an organism can be defined in relation to the mean and variance of its population growth rate (Caughley *et al.* 1988; Vucetich and Waite 2003) while its abundance is determined by its population growth rate acting on its previous abundance. Thus, because population growth rate determines distribution and abundance, it can be regarded as the key unifying variable in ecology. Population growth rate also links evolution and ecology (Godfray and Rees 2003), selection favouring genotypes associated with positive values of *r*, and extinction likely for those genotypes that experience net negative population growth rate.

Behavioural ecology also lies within this framework defined in relation to population growth rate. As a result of evolutionary processes, an animal's behaviour is assumed to optimise constraints imposed by factors such as its own inherent limitations, and its imperfect knowledge of its environment (Krebs and Davies 1993; Sibly *et al*. 2003). This has both evolutionary and ecological aspects, which are linked by the idea that behaviours incapable of influencing population growth rates cannot have evolutionary effects. To consider animal behaviours in relation to their effects on population growth rate may not only enrich population dynamics (Krebs 2003) but also lead to more meaningful ways to study animal behaviour. An example is that the experimental, population dynamics-oriented approach taken by Banks *et al*. (2000) and Banks (2001) enabled the correction of a false idea about kangaroo behaviour, as the following account shows. Chapter 6 discussed the dilemma of a prey animal faced with the choice between obtaining higher food intake rates by foraging alone or in places that risked predation, and safer but less profitable foraging within a group, or closer to cover. Solitary foraging by females with young-at-foot had been wrongly inferred from behavioural studies to be undertaken in order to reduce predation risk. But, as a result of the research method used by Banks *et al*. (2000) and Banks (2001), solitary foraging turns out to be undertaken in spite of predation risk, most likely to reduce costs of group foraging (Banks 2001). Sibly *et al*. (2003) suggested that the addition of relevant features of an animal's behavioural ecology to mechanistic analysis of population growth rates appears to resolve problems of understanding relationships between population growth rate and environment. Sutherland and Norris (2003) give examples including the empirically based model of Stillman *et al*. (2000) for oystercatchers (*Haematopus ostralegus*). Their behaviour-based model predicts mortality from the impact of competition on the energy budget of individual birds. It successfully predicted mortality at much higher density than the range of density at which the model had been parameterized, and it was used also to predict the impact of environmental change, in the form of increased levels of human harvesting of edible bivalves on which the oystercatchers feed (Stillman *et al*. 2001, 2003). Thus even behavioural ecology can be seen to lie within the framework of ecology and evolution defined by population growth rate.

8.1.2 The numerical response

The history of changes to the definition of 'numerical response' is given by Sibly and Hone (2003). Two main forms of numerical response are recognised. In the 'Caughley' or 'demographic' numerical response (Choquenot and Parkes 2001; Sibly and Hone 2003; Bayliss and Choquenot 2003), instantaneous population growth rate (r) is expressed in relation to food availability (Figure 8.1a). Food may be represented as either total food density, e.g. pasture mass (kg ha^{-1}) or as *per capita* food density, e.g. pasture density per kangaroo (kg ha^{-1} EGK^{-1}). The effect of exploitation competition is implicit in both forms.

With the so-called 'Solomon', 'Holling' or 'isocline' numerical response (Sibly and Hone 2003; Sinclair and Krebs 2003; Bayliss and Choquenot 2003), density, rather than r, is expressed in relation to food availability (Figure 8.1b). A reservation expressed by Sinclair and Krebs (2003) about the demographic numerical response is overcome by the isocline numerical response, namely the implication that at high food availability the population continues to grow without limit. This reservation is not relevant for most herbivore populations (and Caughley was explicitly referring to ungulates in his 1976 paper where the demographic numerical response was elaborated in an interactive model, following May 1973). Most herbivore populations are food limited (Sinclair 1996) and grow rapidly when food is abundant (as implied by the demographic numerical response) until they reduce the food supply and their population growth rates decline as a consequence. The difficulty arises with territorial species such as many mammalian predators. Their population growth rate may be determined by food availability at low density but at high density their populations have the potential to remain constant in the presence of abundant food because they are also limited by the number of territories. The relationship between the two forms of numerical response is explained graphically by Sinclair and Krebs (2003).

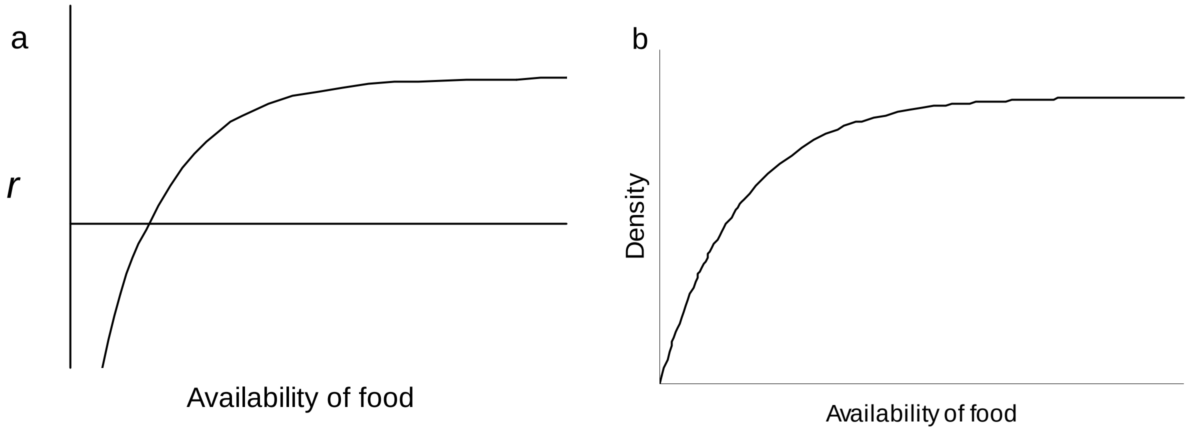


Figure 8.1: (a) ‘Caughley’ or ‘demographic’ numerical response in which the response variable is instantaneous rate of increase (*r*); (b) ‘Solomon’, ‘Holling’ or ‘isocline’ numerical response in which density is the response variable.

Caughley and Lawton (1981) classified the demographic numerical response as either ‘laissez faire’ (no interference competition – as described previously) or ‘interferential’. To incorporate interference competition Caughley and Lawton (1981) replaced the Ivlev numerical response used in their laissez faire model with the widely used ratio form of numerical response which includes terms for herbivore density as well as food (Equation 8.11). Barlow (1985) pointed out that that approach implies interference somehow acts directly on reproduction and mortality and recommended instead the model used by Caughley and Krebs (1983) in which the effect of consumer density is a separate term, an approach adopted by Pech *et al.* (1999), and Bayliss and Choquenot (2003) with Eqn 2.9 from the latter reference copied here as Equation 8.2, as follows:

$$r = - a + c(1 - e^{-dV}) - gH \qquad \text{Eqn 8.2}$$

where gH is the density term referred to. The other part of Equation 8.2 is an ‘inverted exponential’ (sometimes called ‘inverse exponential’) in ‘Ivlev’ form (Ivlev 1961), which was used to represent the numerical response of red kangaroos by Bayliss (1987) and McLeod (1997), of feral pigs by Choquenot (1998), and of mice by Pech *et al.* (1999), among others. Other forms of numerical response are given under Methods. The addition of the gH term to provide for effects of interference competition or consumer aggregation is considered by Bayliss and Choquenot (2003) to bridge between two paradigms, the density paradigm and the mechanistic paradigm.

Until the last two paragraphs, this chapter has related density or population growth rate exclusively to an extrinsic factor such as food availability, thereby making it apparent that this study falls within the ‘mechanistic paradigm’ of Krebs (1995, 2003) and Sibly and Hone (2003). Aside from the mathematical ‘bridge’ mentioned above, the numerical response is linked to the density paradigm, and in particular to density dependence, by the concept that at higher population densities *per capita* resources are reduced, thereby potentially reducing *per capita* natality and survival, and hence population growth (Krebs 2003). Also, a number of (mainly recent) publications that exemplify the density paradigm explain density dependence as a surrogate for reduction in availability of (unmeasured) resources, e.g. Saether *et al.* (2002).

Population growth rate is determined in all vertebrate populations by food supply, unless overridden by predation, disturbance, or social interactions (Caughley and Krebs 1983; Sinclair and Krebs 2003). (The latter is an intrinsic factor; the others, extrinsic.) The bushfire on the Tidbinbilla site in January 2003 was an example of a disturbance which affected the population growth rate. Chapter 6 examined the possibility that the study populations were limited by predation rather than food, and found food was the limiting factor at Googong and Tidbinbilla. The Gudgenby population was limited by the effect of dingoes on kangaroo foraging (the predation sensitive food hypothesis). Because the mean kangaroo density at Gudgenby was similar to those at Googong and Tidbinbilla (Chapter 7), the effect of dingo predation on kangaroo density at Gudgenby was considered likely to be small, and is here treated as insignificant. (Experimental evaluation at Gudgenby was impractical due to logistic constraints.)

8.1.3 Kangaroo density and food

The relationship between herbivore density and food can be represented as a power relationship

$$H = a\,V^{b} \qquad \text{Eqn 8.3}$$

where H and V are the density of herbivores and food respectively and a and b are parameters to be estimated. The relationship has a sound theoretical basis and can be derived from the Gompertz model of population dynamics (J. Hone, 2005, personal communication). In spite of appearance, it is not an isocline because there is no assumption that $r = 0$.

8.2 Methods

8.2.1 *Density dependence*

The simplest test of density dependence is whether population growth rate (r) decelerates with increasing density. Three relationships (Equations 8.4, 8.5, 8.6) were fitted to examine this, namely logistic, theta logistic and Gompertz equations respectively. Fitting a theta logistic relationship (Gilpin *et al*. 1976; Barlow and Clout 1983; Equation 8.5) is considered a more adequate test of density dependence by Saether *et al*. (2002) than a logistic. A Gompertz equation may be preferable to a theta logistic because it has similar properties when theta is less than 1, yet has two parameters rather than three.

$$r = r_{max}\,(1 - H/K) \qquad \text{Eqn 8.4}$$

$$r = r_{max}\,[1 - (H/K)^{\theta}] \qquad \text{Eqn 8.5}$$

$$r = r_{max}\,\log_e(K/H) \qquad \text{Eqn 8.6}$$

where H = herbivore density, and K = its equilibrium value, also labelled ‘carrying capacity’.

8.2.2 *Kangaroo density and food*

The relationship between kangaroo density and food (Equation 8.3) was estimated in two steps. First, $\log_e$ (a) was obtained as the intercept of a linear regression of the logged values of H and V (bimonthly estimates of H, and the previous bimonthly estimate of V). Substituting the value of (a) into Equation 8.3 enabled (b) to be estimated by non-linear least squares regression in Statistica 6.1 (Statsoft 2004).

8.2.3 *Population growth and food – the demographic numerical response*

The estimates of the density of eastern grey kangaroos (H, EGK ha^{-1}) at each survey time on each site were given as results in Chapter 7. Values of r to use in estimating the numerical response were calculated from the values of H using Equation 8.1. To test alternative numerical response equations against the data, values of r were represented in five ways (a) between density estimates two months apart, and 12 months apart, and (b) as the average of the two-monthly estimates for periods of 12, six, and four months. The corresponding estimates of food (V, kg ha^{-1}) for use in estimating the numerical response are the means of the estimates of green herbage mass over periods of corresponding length. In addition, r was regressed against green herbage mass at lagged intervals of two, four, six and eight months.

The estimates of *per capita* food are the food estimates divided by mean kangaroo density at the same time or over the same time period. Because of the bush fire which reduced the kangaroo density at Tidbinbilla, only one valid 12 monthly estimate of r was obtained from Tidbinbilla, for the 12 month period ending a few days before the bush fire. The number of estimates of r over shorter time periods was also reduced by the bush fire.

Table 8.1: Numerical response relationships examined in this study.
V = green herbage mass (kg ha^{-1}); H = herbivore (kangaroo) density (EGK ha^{-1}); a, b, c, d, g = parameters to be estimated

Name	Equation	Reference
Linear	$r = -a + b V$	Eqn 8.7
Ivlev	$r = -a + c (1 - e^{-dV})$	Eqn 8.8
Mitscherlich	$r = a - b e^{-dV}$	Eqn 8.9
Michaelis	$r = -a + c [V / (d+V)$	Eqn 8.10
Ratio	$r = r_{max} (1 - a H / V)$	Eqn 8.11
Additive	$r = a V - b H$	Eqn 8.12
Ivlev + H	$r = -a + c (1 - e^{-dV}) - gN$	Eqn 8.13
Michaelis + H	$r = -a + c [V / (d+V) - gN$	Eqn 8.14

The Ivlev form of inverted exponential numerical response used in Equation 8.2 is repeated here in Equations 8.8 and 8.13 (the difference is the lack, or inclusion, of the herbivore density term used to represent interference competition). The Ivlev form has been widely used to represent numerical responses (references given previously). Equation 8.9 represents an alternative inverted exponential, the Mitscherlich form used by Bayliss (1985) and Cairns and Grigg (1993), among others. Mathematical alternatives which do not include e (Euler) raised to a power, but which have the necessary property of ‘saturating’ (becoming asymptotic) at r_{max} include the Michaelis-Menten numerical response (Equation 8.10; Bayliss 1985; Cairns 1989; Cairns and Grigg 1993), and ratio forms (Equation 8.11; Caughley and Lawton 1981; McCarthy 1996; Turchin and Hanski 1997; Barlow and Norbury 2001; Walter 2002). The simple additive numerical response (Equation 8.12 Krebs *et al.* 2001) is also included. Lastly, as an alternative to the method of representing interference competition by addition of a herbivore density term to an Ivlev equation (i.e. Equation 8.13 mentioned above) the same effect is represented in a different mathematical form using the Michaelis-Menten equation (Equation 8.14). Michaelis-Menten is referred to hereafter as ‘Michaelis’ following Noy-Meir (1975).

These are all ‘consonant’ models in which the individual terms, as well as the predictive behaviour of the equation, are biologically meaningful and should agree with reality (Caughley 1981). Definitions are as given in the source papers (referenced above). An interesting difference between the Ivlev and Mitscherlich forms of inverted exponential is apparent by considering what happens as V increases without limit. In the Ivlev form, r approaches (c-a) which is therefore defined as r_{max} (Caughley 1976a, 1987; Bayliss 1987), whereas in the Mitscherlich form r approaches the term (a) which is therefore $r_{max.}$ Thus in the Mitscherlich form the population growth rate is represented as a positive value reduced by a resource function. That is analogous to saying population growth rate equals fecundity reduced by a mortality whose magnitude depends on resource availability. That description corresponds well to the situation described in Chapter 6 for kangaroos in these temperate study sites. The relationships are not as clear cut for the Ivlev form, with the term (a) defined as the maximum rate of decrease in the absence of food (Caughley 1976a; Bayliss 1987). Following the same analogy, population growth rate in the Ivlev form might be described as a resource-related form of mortality ameliorated by fecundity. Finally, the Michaelis form is similar to the Ivlev; as $V \rightarrow \infty$, $r \rightarrow$ c-a, so r_{max} = c-a.

The Michaelis equation was found to be unduly sensitive to outlying data points by Bayliss (1985) and Cairns and Grigg (1993) compared to the Mitscherlich equation. Bayliss (1987 p 127) preferred the Ivlev equation over all others stating it was least sensitive to outlying points.

The numerical responses in Table 8.1 were confronted with the data from this study using non-linear least squares regression in Statistica 6.1 (Statsoft 2004). Logistic, theta logistic and Gompertz growth were also modelled.

Many populations of large mammals are confronted with brief periods of food shortage and can endure them without declining much; stores of body fat must be depleted first (Chapter 6). Neither can they instantly increase when briefly faced with surplus food, for example eastern grey kangaroos in southern Australia are apparently constrained to a seasonal breeding pattern (Chapter 6). Even the mortality is seasonal (Chapter 6). Therefore the numerical response would ideally be estimated from independent annual measurements of food availability and kangaroo density, rather than bimonthly data. That would require a long-term project preferably including periods of high and low density and high and low population growth rate. This study was based on bimonthly surveys during two years of field work. Independent annual estimates of herbage mass per kangaroo are presented in the Results for comparative purposes but no more than six such data points would be possible from two years of fieldwork on three sites. Therefore, following the practice of Bayliss (1987), the annual population growth rates used here were obtained as the difference between the logged estimates of density at the same time of year in consecutive years on each site. This provided an estimate of r over a 12-month period every second month. Hence the estimates of r used to test each numerical response equation by non-linear regression are not independent because each estimate overlaps ten months with the one before. However by measuring between the same times of year the potential for seasonal bias is removed.

A potential design limitation confronting this study from the beginning was the possibility that density would vary insufficiently in the temperate environment to estimate a numerical response by non-linear regression. Sinclair (1977) indicated the need for a sufficient 'perturbation' to estimate a numerical response, such as the natural drought and recovery period that occurred during the Kinchega study (Caughley *et al.* 1987) or recovery following an artificial population reduction. It was hoped that the drought conditions that commenced in 2001 would provide a sufficient perturbation, but the density estimates presented in Chapter 7 show density at the end of the study was close to the commencing values at Googong and Gudgenby, and most of the change at Tidbinbilla was due to the bushfire and a partly artificial food shortage during the ensuing five months (Chapter 4). Natural perturbations of sufficient magnitude may be infrequent in temperate regions, and culling is undesirable in some populations, e.g. endangered species. The issue was discussed in more detail in Chapter 1, including a method of resolving it. The method uses the ratio model of numerical response (Equation 8.12; Caughley and Lawton 1981; McCarthy 1996; Turchin and Hanski 1997; Barlow and Norbury 2001; Walter 2002).

$$r = r_{max} (1 - \mathrm{a\,H} / \mathrm{V}) \qquad \text{Eqn 8.15}$$

where r_{max} is the intrinsic rate of increase, H is density, and V is food availability.

It has been pointed out (J. Hone, 2001 personal communication) that if density is unvarying, $r = 0$, so from Equation 8.12,

$$a = V / H \qquad \text{Eqn 8.16}$$

and both V and H can be measured, while the intrinsic rate of increase (r_{max}) is obtainable by allometric scaling, or from the scientific literature, as follows.

The value of r_{max} estimated allometrically for all kangaroo species by Bayliss (1985) using the bodyweight formula of Caughley and Krebs (1983) is 0.44 for populations with stable age distribution and mean male and female bodyweight of 30 kg, [which is acceptably close to my estimate of 29 kg for eastern grey kangaroos at Tidbinbilla (Chapter 6)]. But some kangaroo populations have a female biased sex ratio, which would increase r_{max}, and the data examined in Chapter 6 indicated eastern grey kangaroo populations on the study sites to be strongly biased to females. Banks *et al.* (2000) estimated the annual growth of a population of eastern grey kangaroos adjacent to the ones on the study sites as $r = 0.55$. Therefore I have selected $r = 0.55$ as an appropriate assumption for r_{max} for eastern grey kangaroos in temperate grasslands (i.e. the value that r could assume when a population with the optimum demographic structure is confronted with conditions favourable for population growth). The selected value is higher than the value 0.4 chosen by Caughley (1987) for his interactive population model of red kangaroos, but lower than several other estimates, e.g. those made by Bayliss (1985, 1987). Using hypothetical life tables with uneven sex and age distribution, Bayliss (1985) estimated r_{max} to be 0. 67 for red and 0.53 for western grey kangaroo populations that were biased to females. In the process of estimating the numerical response in relation to pasture availability, Bayliss (1987) made field estimates of r_{max} for western grey kangaroos at Kinchega National Park and the adjoining Tandou sheep station of 0.42 and 0.66 respectively. Thus the chosen value 0.55 is within the range of estimates of r_{max} from other kangaroo studies and supported by an estimate made in local conditions.

8.3 Results

Kangaroo density (H) at the end of the period was similar to its starting value, except at Tidbinbilla (Chapter 7). However green herbage mass (V) declined significantly on all sites throughout the study period (Chapter 4). Figure 8.2 illustrates these relationships using independent annual mean values for density of kangaroos and pastures. In Figure 8.2 the pasture decline is indicated by the leftward movement between years. Unchanging kangaroo density is indicated by the lack of corresponding vertical movement.

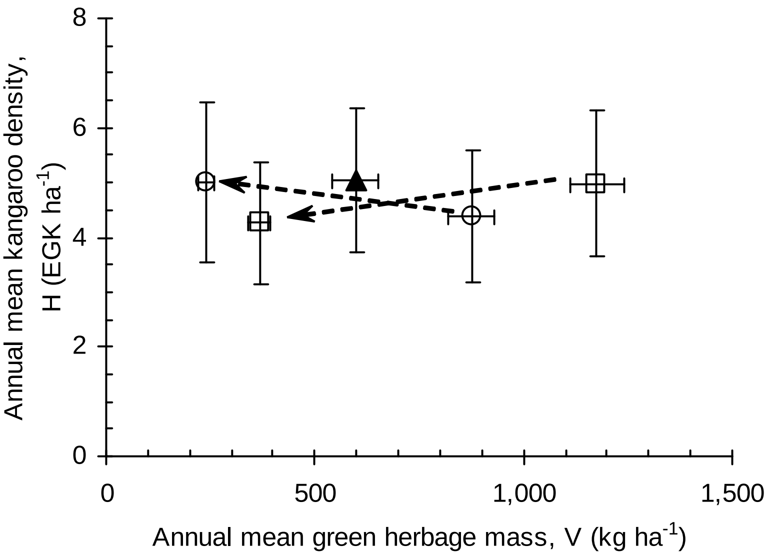


Figure 8.2: Annual means of density of eastern grey kangaroos ± SE (EGK ha^{-1}) on each site in relation to means of green herbage mass over the same period ± SE (kg ha^{-1}); ○ = Googong; □ = Gudgenby; ▲ = Tidbinbilla. The values for Googong and Gudgenby are the means of six bimonthly surveys during the year to July, in 2002 and again in 2003. The one value for Tidbinbilla is the mean of six surveys during the year to January 2003, the time of the bushfire on that site. Arrows indicate the direction of change from the first to the second year.

The reduction in herbage caused a decline from the first to the second year of the study in the estimate of food available per kangaroo (mass of green herbage per kangaroo, kg ha^{-1} EGK^{-1}) (Figure 8.3). A regression using the five points illustrated in Figure 8.3 was highly significant (Equation 8.17; SE = 25; F = 37; df = 1, 3; p = 0.009; $R^2 = 0.924$)

$$V/H = 213 - 0.415\,T \qquad \text{Eqn 8.17}$$

where T = the number of days after 15 September 2001.

At the finer temporal scale of the individual bimonthly estimates, there were rapid fluctuations in the food available per kangaroo. For example, the sharp fluctuations in the summer of 2001 (Figure 8.4) were mainly due to a flush of late spring growth followed by the sudden onset of warm dry weather which killed the green pasture before kangaroos could consume it.

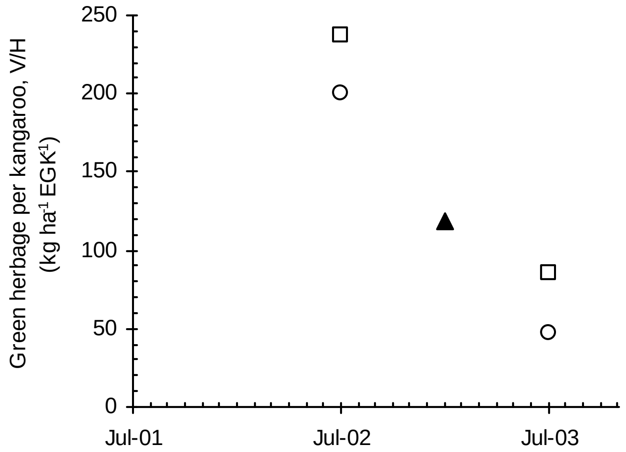


Figure 8.3: Green herbage mass per kangaroo, V/H (kg ha^{-1} EGK^{-1}). The annual mean values shown are explained in the caption for Figure 8.2.

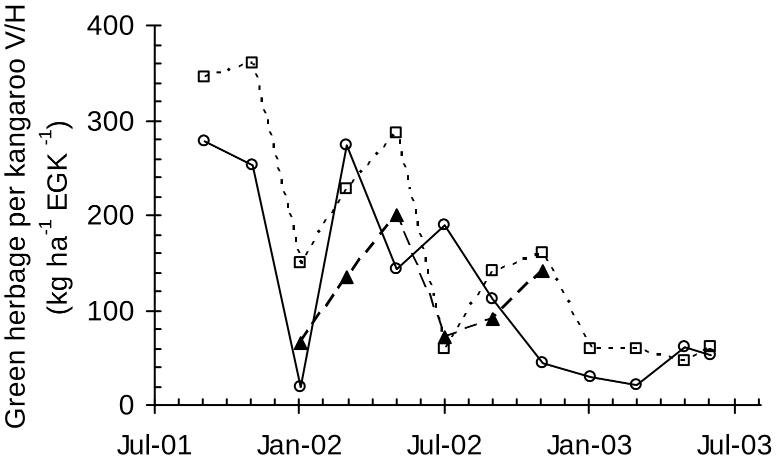


Figure 8.4: Green herbage mass per kangaroo, V/H (kg ha^{-1} EGK^{-1}) from bimonthly estimates of herbage mass given in Chapter 4 and kangaroo density in Chapter 7. ○ = Googong; □ = Gudgenby; ▲ = Tidbinbilla. The data from the Tidbinbilla site has been truncated at the time of the bushfire which killed many of the kangaroos and destroyed fences, thereby admitting a herd of cattle onto the site.

8.3.1 Density dependence

The plot of population growth rate (*r*) between surveys 12 months apart against density at the beginning of that interval appears as a scattered cluster (Figure 8.5a). All of the three growth equations used to test for density dependence (logistic, theta logistic and Gompertz, Equations 8.4, 8.5, and 8.6) provided a negative regression when fitted to those data, consistent with density dependence. However none were significant. The ΔAICc value of the Gompertz equation was lowest, indicating it to provide the best explanation, given the data (Table 8.3). The logistic equation was also supported to a lesser degree (ΔAICc less than 2). The theta logistic equation provided as good a fit to the data as the Gompertz (R^2 value equal to that for the Gompertz equation) but was penalised in the calculation of F value, p value and AICc because of its additional parameter (and fewer regression degrees of freedom). The regression estimates of r_{max} and K for the logistic and Gompertz equations are within a plausible range of values (Table 8.3), those for r_{max} being 17% and 34% higher than the value 0.55 assumed here, and those for K being 14% to 21%lower than the mean estimated density of kangaroos at Googong and Gudgenby. The regression estimate for K from the theta logistic equation is the same as that from the Gompertz equation but the estimate of r_{max} from the theta logistic equation is not realistic.

Table 8.3: Estimates of r_{max} and K (equilibrium density or carrying capacity), and regression statistics for equations used to test density dependence, fitted to the estimates of r between surveys 12 months apart and estimates of H at the start of that interval.

Name	Equation	r_{max}	K	k	DF	F value	p value	R^2	AICc	ΔAICc
Logistic	Eqn 8.4	0.6	3.9	3	2, 12	1.47	0.27	0.166	–9.83	0.97
Theta Logistic	Eqn 8.5	1566.3	3.8	4	3, 11	1.28	0.33	0.231	–7.77	3.04
Gompertz	Eqn 8.6	0.7	3.8	3	2, 12	2.10	0.17	0.231	–10.80	0.00

The scatter of points evident in Figure 8.5a can be markedly reduced to that in Figure 8.5b by averaging values of r and H between consecutive bimonthly surveys (i.e. smoothing them over periods of 2 surveys, or 4 months). Logistic, theta logistic and Gompertz equations regressed against these data generate significant positive results, which is an implausible outcome implying population growth accelerating with density in an unlimited way (Table 8.4). Thus, taking the results of both approaches into account (negative but non-significant result with unsmoothed data, and positive result with smoothed data), density dependence is not supported by these data.

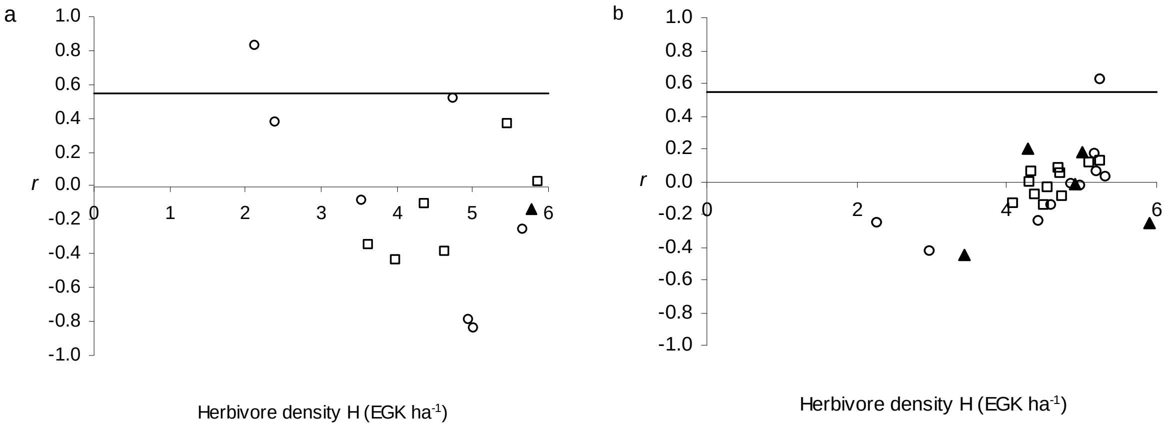


Figure 8.5: Population growth rate *r* as a function of kangaroo density H. ○ = Googong; □ = Gudgenby; ▲ = Tidbinbilla. The horizontal line marks the intrinsic rate of increase (r_{max}) assumed elsewhere in this study for eastern grey kangaroos on the study sites. (a) Values of *r* are between surveys 12 months apart, and are plotted against the estimate of kangaroo density at the beginning of the interval; (b) Values of *r* and H have been averaged between pairs of consecutive bimonthly surveys.

Table 8.4: Estimates of r_{max} and K, and regression statistics for equations used to test density dependence, fitted to the bimonthly estimates of *r* and H averaged over two surveys (four months).

Name	Equation	r_{max}	K	k	DF	F value	p value	R^2	AICc	ΔAICc
Logistic	Eqn 8.4	–0.77	4.7	3	2, 25	6.94	0.004	0.354	–78.48	0.00
Theta Logistic	Eqn 8.5	–0.86	4.7	4	3, 24	4.44	0.013	0.355	–71.12	7.36
Gompertz	Eqn 8.6	–0.64	4.7	3	2, 25	6.62	0.005	0.355	–78.06	0.42

8.3.2 Kangaroo density and food

The power function (Equation 8.3) fitted to the bimonthly estimates of kangaroo density plotted against the food density 2 months previously (Figure 8.6) resulted in Equation 8.18 (SE = 0.012; F = 184; df = 1,29; $p<0.001$; $R^2 = 0.01$), as follows:

$$H = 1.33\ V^{0.186} \qquad \text{Eqn 8.18.}$$

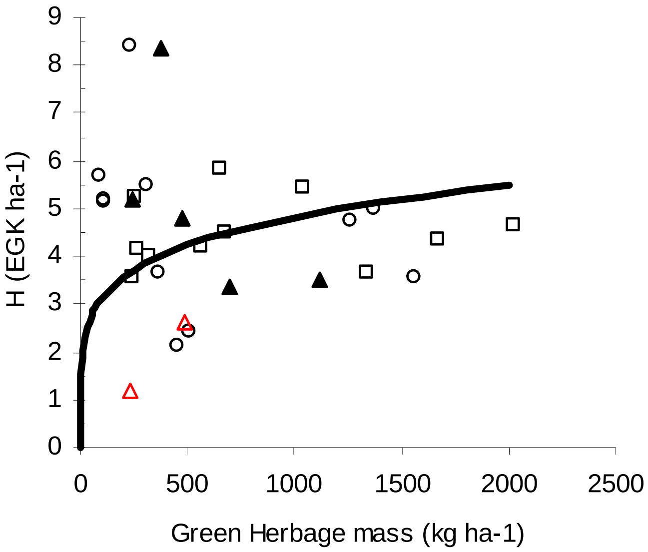


Figure 8.6: A power function fitted to the bimonthly estimates of kangaroo density (EGK ha^{-1}) plotted against density of green herbage two months previously (kg ha^{-1}). ○ = Googong; □ = Gudgenby; ▲ = Tidbinbilla; △ = Tidbinbilla post fire.

Neither Ivlev nor linear equations fitted well to these data, providing respectively a degenerate solution and a negative regression.

8.3.3 The demographic numerical response

The values of *r* between surveys 12 months apart were related to the density of green herbage (V, kg ha^{-1}) to estimate a numerical response. V can reasonably be represented either as the value at the beginning of the year (Figure 8.7a) or the mean over the year (Figure 8.7b) because mortality and fecundity might respond to food availability in either the preceding period or the current one, or both. Numerous other plausible representations of the data were also tested, as summarised in Table 8.5, including representations of *r* between the bimonthly surveys, and lagged effects of herbage density. All were tested against the eight mathematical forms of numerical response listed in Table 8.1, however only those indicated by table numbers are reported here.

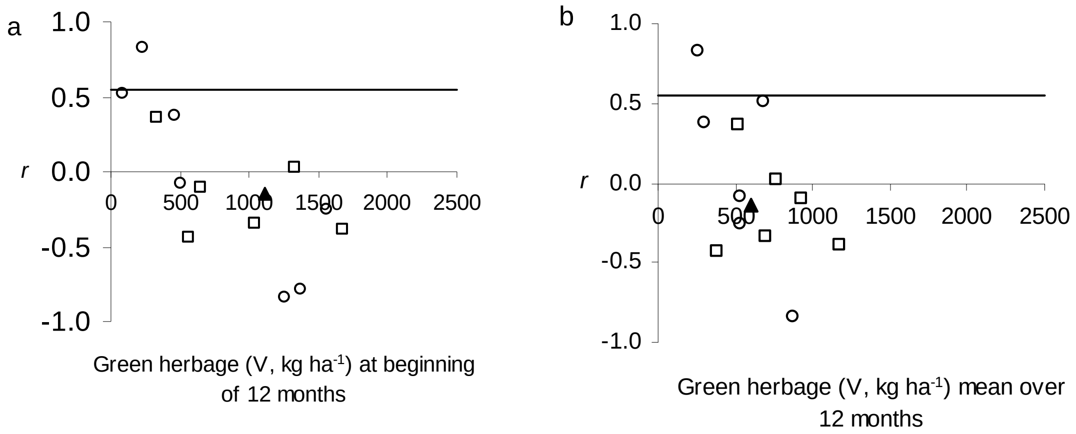


Figure 8.7: Population growth rate (r) of the kangaroo population on each site, between bimonthly surveys 12 months apart, plotted as a function of green herbage mass (a) at the commencement of the 12 month period and (b) as the mean during the 12 month period; ○ = Googong; □ = Gudgenby; ▲ = Tidbinbilla. The horizontal line marks the intrinsic rate of increase (r_{max}) assumed elsewhere in this study for eastern grey kangaroos on the study sites.

Table 8.5: Combinations of data tested against the eight forms of numerical response listed in Table 8.1. Numbers = table in which result is reported below. X = not reported below. NA = not applicable.

	V_{mean}	V_{begin}	V_{lag4mo}	V_{lag6mo}	V_{lag8mo}	V/H_{mean}
$r_{12\ months}$	8.6	8.7	X	NA	NA	8.8
$r_{2\ months}$	NA	8.9	8.10	X	X	8.11
$r_{4\ months}$	8.12	X	X	NA	NA	X
$r_{6\ months}$	X	X	X	NA	NA	X

The plot of population growth rate r between surveys 12 months apart, on green herbage mass (Figure 8.7 a, b) has a negative slope and clustered distribution. The regression method of determining a numerical response produced either degenerate solutions with unreliable parameter estimates, or unreasonable estimates that were negative, included discontinuities, or were concave up and non-significant (Tables 8.6, 8.7).

Table 8.6: Results of linear (1st row) and non-linear regressions of r between surveys 12 months apart against the mean of green herbage mass (V, kg ha^{-1}) from six surveys within the 12 months. P1, P2, etc = parameters to be estimated, in same order as given in equations.

Name	Eqn No.	P1	P2	P3	P4	k	DF	F value	p value	R^2	AICc	ΔAICc
Linear	Eqn 8.6	–0.094	$-1.6x10^{-4}$			3	2, 11	2.31	0.15	0.29	–50.16	1.39
Ivlev	Eqn 8.7					Degenerate solution						
Mitscherlich	Eqn 8.8					Degenerate solution						
Michaelis	Eqn 8.9	0.067	0.026	–231		4	3, 10	2.44	0.12	0.42	–39.21	12.34
Ratio	Eqn 8.10	92.11				2	1, 12	–11.25			–23.22	28.33
Additive	Eqn 8.11	–0.00017	–0.02346			3	2, 11	3.35	0.07	0.37	–51.55	0.00
Ivlev + H	Eqn 8.12					Degenerate solution						
Michaelis + H	Eqn 8.13	0.997	–0.002	–591	0.223	5	4,9	3.39	0.06	0.60	–22.08	29.47

Table 8.7: Results of linear (1st row) and non-linear regressions of *r* between surveys 12 months apart against the green herbage mass (V, kg ha^{-1}) recorded at the commencement of the 12 months. P1, P2, etc = parameters to be estimated, in same order as given in equations.

Name	Eqn No.	P1	P2	P3	P4	k	DF	F value	p value	R^2	AICc	ΔAICc
Linear	Eqn 8.7	0.200	–0.00022			3	2, 11	0.47	0.64	0.08	–4.86	0.00
Ivlev	Eqn 8.8	0.73	0.73	0.011		4	3, 10	0.09	0.96	0.02	6.12	10.97
Mitscherlich	Eqn 8.9	–0.004	0.72	0.011		4	3, 11	0.09	0.96	0.02	6.12	10.97
Michaelis	Eqn 8.10	300	299.52	0.0		4	3, 10	0.03	0.99	0.01	6.29	11.15
Ratio	Eqn 8.11	3.5				2	1, 12	–4.69	1.00	0.00	–4.79	0.06
Additive	Eqn 8.12	–0.001	$3x10^{-6}$			3	2, 11	0.00	1.00	0.00	–3.97	0.89
Ivlev + H	Eqn 8.13	5.94	0.09	0.009	1.31	5	4, 9	2.78	0.10	0.58	23.64	28.50
Michaelis + H	Eqn 8.14	17.5	11.6	–0.10	1.32	5	4, 9	3.39	0.10	0.58	23.65	28.51

Alternatively, the values of *r* between surveys 12 months apart, can reasonably be regressed against green herbage mass per kangaroo (V/H, kg ha^{-1} EGK^{-1}) (Table 8.8).

Table 8.8: Results of non-linear regressions of *r* between surveys 12 months apart against the mean of green herbage mass per kangaroo (V/H, kg ha^{-1} EGK^{-1}) during the 12 months. P1, P2, etc = parameters to be estimated, in same order as given in equations.

Name	Eqn No.	P1	P2	P3	P4	k	DF	F value	p value	R^2	AICc	ΔAICc
Linear	Eqn 8.7	0.73	–0.0066			3	2, 11	6.05	0.02	0.48	–15.57	0.00
Ivlev	Eqn 8.8					Degenerate solution						
Mitscherlich	Eqn 8.9					Degenerate solution						
Michaelis	Eqn 8.10	13	12	–5.1		4	3, 10	4.03	0.04	0.42	–7.39	8.19
Ratio	Eqn 8.11					Not Applicable						
Additive	Eqn 8.12	0.0014	0.0084			3	2, 11	3.35	0.07	0.14	–8.68	6.90
Ivlev + H	Eqn 8.13					Degenerate solution						
Michaelis + H	Eqn 8.14					Degenerate solution						

As well as examining population growth between surveys 12 months apart (above), the change between consecutive surveys was considered in relation to food availability at the beginning of the two-monthly period (Table 8.9) and at lagged intervals (Table 8.10).

Table 8.9: Results of non-linear regressions of *r* between surveys two months apart against green herbage mass (V, kg ha^{-1}) at the beginning of the two months. P1, P2, etc = parameters to be estimated, in same order as given in equations.

Name	Eqn No.	P1	P2	P3	P4	k	DF	F value	p value	R^2	AICc	ΔAICc
Linear	Eqn 8.7	–0.10	–0.00022			3	2, 28	1.11	0.34	0.07	–39.70	0.00
Ivlev	Eqn 8.8	–0.20	–0.47	0.0013		4	3, 27	0.77	0.52	0.07	–34.38	5.32
Mitscherlich	Eqn 8.9	–0.28	–0.48	0.0013		4	3, 27	0.77	0.52	0.07	–34.38	5.32
Michaelis	Eqn 8.10	–0.27	–0.63	485		4	3, 27	0.78	0.52	0.07	–34.41	5.29
Ratio	Eqn 8.11	23				2	1, 29	–17.34	1.00	0.00	–16.29	23.41
Additive	Eqn 8.12	–0.00037	–0.090			3	2, 28	5.38	0.02	0.04	–19.62	20.08
Ivlev + H	Eqn 8.13	0.32	–0.8	0.0	0.11	5	4, 26	0.72	0.59	0.10	–24.68	15.02
Michaelis + H	Eqn 8.14	84	84	–0.47	0.059	5	4, 26	0.54	0.71	0.07	–24.03	15.67

Table 8.10: Results of non-linear regressions of *r* between surveys two months apart against green herbage mass (V, kg ha^{-1}) four months previously. P1, P2, etc = parameters to be estimated, in same order as given in equations.

Name	Eqn No.	P1	P2	P3	P4	k	DF	F value	p value	R^2	AICc	ΔAICc
Linear	Eqn 8.7	0.045	0.000073			3	2, 11	0.11	0.90	0.01	–29.80	36.01
Ivlev	Eqn 8.8	0.53	0.60	0.0073					0.78		–24.82	41.00
Mitscherlich	Eqn 8.9	0.07	0.60	0.0073					0.78		–24.82	41.00
Michaelis	Eqn 8.10	10.97	11.07	2.8		4	3, 10	0.31	0.82	0.42	–24.67	41.14
Ratio	Eqn 8.11	0.0				2	1, 12	–11.25	1.00		–29.37	36.44
Additive	Eqn 8.12	0.034	0.00024			3	2, 11	3.35	0.05	0.23	–65.81	0.00
Ivlev + H	Eqn 8.13	1.18	0.68	0.0070	0.13				0.79		–18.99	46.82
Michaelis + H	Eqn 8.14	8.8	8.4	4.28	0.116	5	4,9	3.39	0.83	0.07	–18.77	47.04

Table 8.11: Results of non-linear regressions of *r* between surveys two months apart against the mean of green herbage mass per kangaroo (V/H, kg ha^{-1} EGK^{-1}) during the two months. P1, P2, etc = parameters to be estimated, in same order as given in equations.

Name	Eqn No.	P1	P2	P3	P4	k	DF	F value	p value	R^2	AICc	ΔAICc
Linear	Eqn 8.7	0.237	–0.002			3	2, 11	3.97	0.03	0.23	–42.42	6.06
Ivlev	Eqn 8.8	0.06	0.04	1							–30.02	18.46
Mitscherlich	Eqn 8.9						Degenerate					
Michaelis	Eqn 8.10						Discontinuous					
Ratio	Eqn 8.11						Not applicable					
Additive	Eqn 8.12	0.059	0.0017			3	2, 11	3.35	0.07	0.39	–48.47	0.00
Ivlev + H	Eqn 8.13						Degenerate					
Michaelis + H	Eqn 8.14						Degenerate					

None of these approaches resulted in an acceptable estimate of a numerical response (Tables 8.6 to 8.12).

The *ad hoc* method used by Bayliss (1987) also could not be used. Bayliss (1987) estimated r_{max}, then estimated the term -a in the Ivlev numerical response (Equation 8.7) as the intercept of a linear regression through the values of r not close to the asymptotic value. However in this study the linear regression through the cluster of points (Figure 8.7a) has a negative slope which would result in a biologically meaningless (positive) value for the term -a, (indicative of kangaroo populations which could never decline, and which grew even in the absence of food).

Table 8.12: Results of non-linear regressions of r over four months against four month mean of green herbage mass (V, kg ha^{-1}). P1, P2, etc = parameters to be estimated, in same order as given in equations.

Name	Eqn No.	P1	P2	P3	P4	k	DF	F value	p value	R^2	AICc	ΔAICc
Linear	Eqn 8.7	0.008	–0.00008			3	2, 11	0.33	0.72	0.01	–33.67	35.36
Ivlev	Eqn 8.8						Degenerate					
Mitscherlich	Eqn 8.9						Degenerate					
Michaelis	Eqn 8.10	0.08	0.01	–233		4	3, 10	0.59	0.63	0.42	–29.30	39.73
Ratio	Eqn 8.11	54				2	1, 12	–11.25			–38.10	30.93
Additive	Eqn 8.12	0.020	0.00013			3	2, 11	3.35	0.07	0.06	–69.04	0.00
Ivlev + H	Eqn 8.13						Degenerate					
Michaelis + H	Eqn 8.14	2.7	2.2	–3.19	0.096	5	4,9	3.39	0.90	0.03	–20.37	48.66

8.3.4 Ratio numerical response

Therefore the method using the ratio numerical response model was applied, as described in Methods. The mean of the parameter a = V/H is 138 (± 18 SE) kg ha^{-1} EGK^{-1} (mean of all surveys on all sites) which gives the following estimate of the numerical response:

$r = 0.55\ (1 - 138\ \mathrm{H} / \mathrm{V})$ Eqn 8.19

where the value 0.55 (intrinsic rate of increase, r_{max}) was obtained as described in Methods, H = kangaroo density (EGK ha^{-1}) and V = green herbage mass (kg ha^{-1}). Equation 8.19 is illustrated in Figure 8.8.

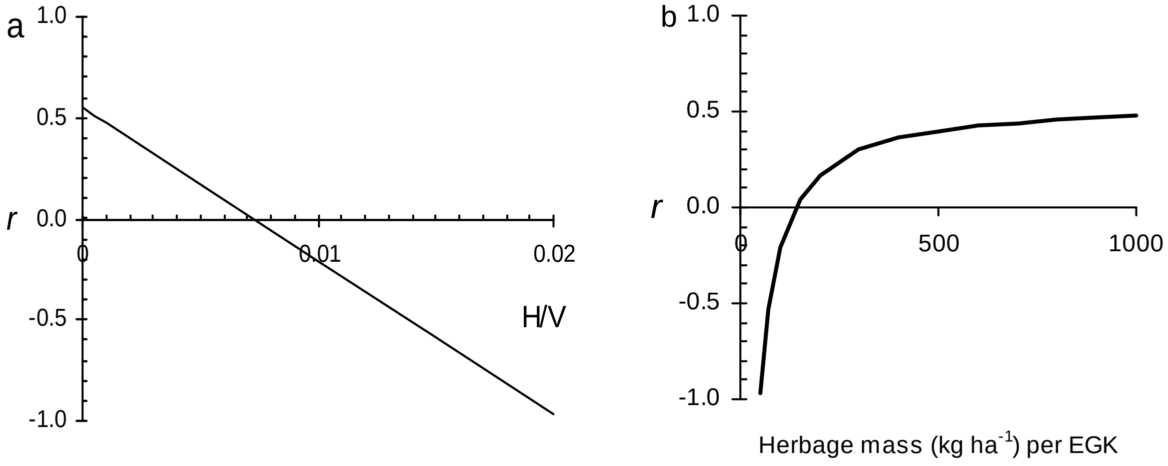


Figure 8.8: (a) Estimated numerical response (Equation 8.19) showing r as a function of H/V; (b) showing r as a function of herbage mass per kangaroo (kg ha^{-1} EGK^{-1}).

8.3.5 Kangaroo density and groundcover

At this point it is possible to add to the comment made in Chapter 4 about percentage groundcover. The results from the study as a whole indicate that unmanaged kangaroo populations did not necessarily result in unacceptably low levels of ground cover. The regression of cover on kangaroo density (Equation 9.1) was positive and not significant (SE = 1.3; F = 1.76; df = 1, 31; p = 0.19; $R^2 = 0.05$)

$\%\ \mathrm{cover} = 77.6 + 1.7\ \mathrm{H}$ Eqn 9.1

where H is kangaroo density (EGK ha^{-1}). Possibly this relationship is due to the importance of weather in influencing ground cover. High ground cover occurred at the wettest site where kangaroo density was highest.

8.4 Discussion

The drought experienced during this study greatly reduced the kangaroos’ food supply without much effect on the estimates of kangaroo density. Resistance to drought is in contrast to the picture of kangaroo population dynamics that has emerged from previous research on kangaroo population dynamics in arid and semi-arid environments, such as the Kinchega study (Caughley *et al*. 1987). The most likely explanation for the difference appears to be simply that the food reduction was much less drastic during this study. At Kinchega (Robertson 1987a) there was a more sudden decline in herbage mass than experienced in this study (Chapter 4), and at Kinchega, herbage mass remained less than 100 kg ha^{-1} for almost a year, and its lowest level was 7 kg ha^{-1}, whereas in this study the pasture declined below 300 kg ha^{-1} for only one bimonthly survey on one site, reaching a minimum of 163 kg ha^{-1} (excluding the period following the bushfire at Tidbinbilla). Adult kangaroos may be capable of bridging the troughs in food availability that occur in temperate areas (such as the one recorded in this study) by utilising internal reserves such as fat deposits (Chapter 6), and external 'reserve' food sources (see below), whereas the droughts and food shortages occurring in arid and semi-arid regions are liable to exceed the capacity of adult kangaroos to survive by those mechanisms. While this relative stability is an interesting result, its consequence was that the hoped for perturbation of density did not occur, so that the regression method of estimating a numerical response was not useful.

The ratio model of numerical response that was estimated in this study is partly an indirect estimate, as obtained for wild horses by Walter (2002), in that a value was provided for r_{max}. A desirable task for the future is to obtain regression estimates of the numerical response entirely from field data. For the regression method to be successful, a perturbation needs to be great enough, and the estimates of herbivore and pasture density need to be sufficiently accurate and precise.

The negative slope of the regression of population growth rate (r) on kangaroo density (H) (Table 8.3, Figure 8.5a) is equivalent to the results reported by Sinclair and Krebs (2003, their Figures 6 and 8), for prey experiencing Type 2 or Type 3 predation. This result suggests the data on fox baiting (Figure 3.7) and fox sightings (Section 3.4.1) should be interpreted cautiously. Foxes were present on all my sites throughout the study, and perhaps they were affecting kangaroo population growth rates, in spite of the fox poisoning carried out in the hope of preventing this. (In fact there were substantial gaps in the fox control, especially at Tidbinbilla, as described in Section 3.4.1). This implies the possibility that not only was the eastern grey kangaroo population at Gudgenby limited according to the predation sensitive food hypothesis, due to dingoes, but also the kangaroo populations at Tidbinbilla and Googong may have been limited in the same way, by foxes.

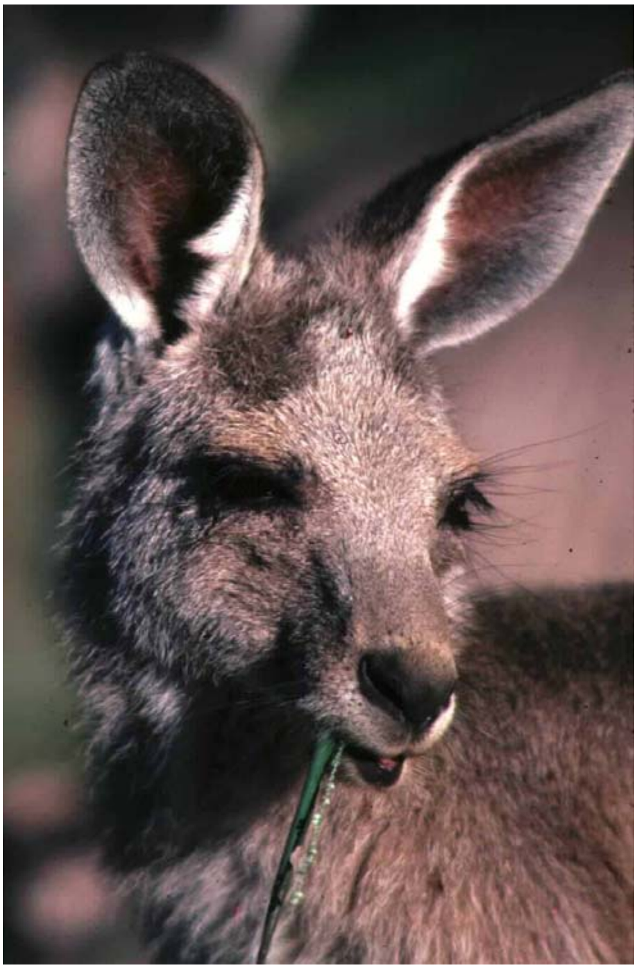
As opposed to the situation in semi-arid Australia (Caughley *et al*. 1987), natural droughts in temperate areas appear from this study to be unlikely to be a sufficient or reliable cause of the necessary perturbation. Droughts that have a more severe effect on plant growth than the one experienced during this study are infrequent on the southern tablelands. Rainfall during the study was classed by the Bureau of Meteorology as 'severely deficient' (i.e. in the lowest 5% of records) for lengthy periods (Bureau of Meteorology 2003) even though the statistical deficiency was offset by occasional severe storms such as in February 2002 and March 2003 (Chapter 4). A rainfall deficiency is also likely to vary considerably between years and sites, for example streams which had stopped flowing during the 1982 drought at Gudgenby (Peter Hann, personal communication, 2002) continued to flow during this study, but the opposite occurred on the Tidbinbilla site. Therefore an alternative approach would be to measure the density of pastures and eastern grey kangaroos in rapidly increasing populations, e.g. where kangaroo populations have been released into new sites, or are recovering from large reductions in density. Even this improvement would not encompass all the variation occurring in reality. Re-analysis by Bayliss and Choquenot (2003) of the Kinchega numerical response data (Bayliss 1987; Caughley 1987) and their argument for hysteresis (two domains of attraction, due to the system behaving differently when recovering from drought than when entering it) indicates the desirability of measurement during a decline phase as well as during an increase phase. Stable and declining populations are expected to contain a higher proportion of females and adults (e.g. Caughley 1976a; Chapter 6), compared to increasing ones, and therefore will have a higher population growth rate (i.e. a different numerical response to food availability). Strictly, the estimation of population growth rate in this way from time series of count data is only applicable if population size is known exactly. The question of how best to analyse data when both environmental stochasticity and sampling error are important has not yet been answered satisfactorily (McCallum 2000).

Previous chapters included estimates of both a pasture response (Chapter 4) and a functional response (Chapter 5), and an examination of the assumption of food limitation that underlies the method of estimating the numerical response (Chapter 6). Also, a quick method for estimating kangaroo density was detailed in Chapter 7. Finally, this chapter contained an estimate of the numerical response. It now remains to draw these parts together into the following concluding chapter.

CHAPTER 9

GENERAL DISCUSSION

Perfection of means and confusion of aims seem to characterize our age (Albert Einstein)



This is the kind of image many people associate with 'kangaroos', a sub-adult eastern grey. This one is eating seeds and blades of green grass of a length rarely seen in the natural populations on the study sites. In high-density populations, nutritious grass is in short supply by the end of winter and the sub-adult life-stage is one that few kangaroos survive. Even some nature conservation managers are disturbed when confronted with the mortality of such appealing animals on the scale that occurs naturally and seek immediate solutions. A greater awareness of herbivore ecology might assist in clarifying management aims.

CHAPTER CONTENTS

9 GENERAL DISCUSSION

9.1 Introduction

In accordance with the aim (Chapter 1) this study has increased the knowledge of population dynamics of eastern grey kangaroos in temperate areas, including estimation of the pasture response, functional response and numerical response equations for Caughley's (1976a, 1987) interactive model. In this chapter I integrate the earlier material, suggest some management implications, and identify some gaps.

9.2 Pasture growth, herbivore offtake, and groundcover

9.2.1 The pasture response model

The typical pattern of sigmoid (logistic-like) pasture growth (Crawley 1983) was not observed in this study. The negative, concave-up pattern of density dependence is similar to that reported for New Zealand pastures (Chaco 1997; Chaco *et al*. 1999). When there was sufficient moisture and warmth, the pastures grew, and the relationship of pasture growth with rainfall was close to linear. This is consistent with the models of Miller (1979), Robertson (1987a), and Choquenot *et al*. (1998). My study showed that temperature was an important predictor of pasture growth, in contrast to the finding by Choquenot *et al*. (1998) for pastures on the central tablelands, an area which has a similar climate to the area of my study.

However the pattern of growth I recorded was significantly different from the strongly seasonal (temperature influenced) pattern predicted by Vere *et al*. (2001) for pastures on the central and southern tablelands. In particular, the normal pattern of most growth occurring in spring (Vere *et al*. 2001) was not observed in the drought conditions. The best model of pasture growth (in terms of AICc) included negative terms for herbage mass, rainfall over the previous two months, and temperature, and a positive term for the interaction between rainfall and temperature. It accounted for 13% more of the variation in the data than did the simpler model as used by Robertson (1987a), Caughley (1987) and Choquenot *et al*. (1998). However this was only 63% of total variation. Re-evaluation of the model based on measurements of pasture growth in more typical (non-drought) conditions is recommended. An alternative would be to resort to more complex models.

9.2.2 Herbage mass, herbivore offtake and groundcover

The greatest contrasts between the results of this study and those of the study described by Caughley *et al*. (1987), are the higher densities of both pastures and herbivores in this study. A further contrast to the Kinchega results (Caughley 1987) is the finding of large and persistent effects of grazing on herbage mass. This finding is common to the temperate grazing studies of Neave and Tanton (1989), and Croft *et al*. (2002). Therefore a management implication is that reduction of such kangaroo populations has the potential to increase the magnitude of herbage mass.

Compared to the Kinchega study (Robertson 1987a), less variation was recorded in herbage mass between sites and seasons. At Kinchega there was more than 100-fold change in total herbage mass (Robertson 1987a) but in my study the relative change was two-fold at Tidbinbilla (pre-bush fire), eight-fold at Gudgenby and 13-fold at Googong. This is probably due to the greater effect of grazing on herbage mass in the temperate environment, as mentioned above. Food-limited herbivore populations that tend to operate at positions on the functional response that are below the saturation level should act as a density-dependent ‘governor’ on the herbage mass, with pasture consumption increasing in response to any small increases in herbage mass, thereby partly or wholly offsetting the influence of episodes of favourable weather. (This would happen only at low and moderate levels of herbage mass. It would cease if continuing favourable weather enabled the herbage mass to reach the level resulting in herbivore satiation on the functional response.) Consistent with this hypothesis, small rainfalls were recorded on numerous occasions throughout the study but only the extreme rainfalls recorded during February 2002 resulted in pasture growth increments that are comparable with those considered typical by Vere *et al*. (2001). A management implication is that reduction of kangaroo density is predicted to lead to increased variation in herbage mass.

The offtake estimates in this study (82 – 1663 kg ha^{-1} calculated per three months) are several times greater than those recorded in the Kinchega kangaroo project (10 - 180 kg ha^{-1}, Robertson 1987a), which can be attributed to the large difference in the density of kangaroos between the two areas, and the higher biomass of pasture on my sites. The magnitude of the offtake by the kangaroo population was apparent at each survey as the difference between the estimates of ungrazed and grazed green herbage mass (kg ha^{-1}). This offtake was a positive function of herbage mass (a functional response). The offtake estimated in this way was two to three times greater than the *per capita* functional response estimated more carefully in the grazedown procedures, multiplied by the average density of kangaroos. So either (a) the offtake estimated by the cage method was an overestimate, (b) the *per capita* functional response from the grazedowns was an underestimate, (c) kangaroo density was underestimated, or a combination. The average density of kangaroos on all surveys is unlikely to be an underestimate as there are corroborating estimates from the two drive counts, therefore (c) seems unlikely. Sharrow and Motazedian (1983) claim that cage-based methods overestimate offtake so (a) seems a plausible explanation for at least part of the difference.

In general, groundcover was high, varied little, and remained above the 70% target set for the surrounding region by the Murrumbidgee Catchment Management Board (2003), presumably based on studies such as that of Jefferies (1999) which showed a threshold in the rate of water erosion at about this level of groundcover. There were two exceptions to the generally high groundcover, one following a bushfire at Tidbinbilla and the other following a storm at Googong. It is likely that the reduction at Googong is due to a combination of the storm, site characteristics, drought, and heavy grazing pressure.

The study did not provide evidence that high densities of kangaroos reduce groundcover to the levels where erosion can accelerate. Unmanaged kangaroo populations did not necessarily result in low levels of ground cover. Groundcover had a positive but not significant relationship to kangaroo density, with the highest cover at the wettest site where kangaroo density was highest. Weather has an important influence on groundcover.

9.3 The functional response

The widely used ‘Type 1, 2, 3’ classification of functional responses introduced by Holling (1959; 1965; 1966), and extended by Caughley (1981) to include Type 4 functional responses, should be extended to refer to Type 5 and 6, for ‘inaccessible residue’, and ‘power’ functional responses, respectively. The common recognition of three forms of functional response is inadequate. Both the theoretical basis, and supporting data, have been published for domed, inaccessible residue, and power forms as well (Holling 1966; Noy-Meir 1975; Hassell *et al.* 1976, 1977; Short 1986; Sabelis 1992).

The type 2 functional responses estimated for eastern grey kangaroos feeding in high quality and low quality pastures, were almost the same, and rose more gradually with green herbage mass than the functional responses to total herbage estimated for sheep, rabbits and two species of kangaroos in chenopod shrublands (Short 1985,1986; Chapter 5). Unlike the situation in the rangelands, in these temperate pastures, satiation of eastern grey kangaroos requires high herbage mass. The gradual shape of the functional response is conducive to continuous stability of the pasture herbivore system (Noy-Meir 1978; Barlow 1987; Chapter 8) which is consistent with observation and experience.

The use of a single conversion factor to enable the pasture consumption of kangaroos to be represented as dry sheep equivalents (DSE) does not represent well the real differences in their feeding. It is simplistic to represent the feeding of animals as different as cows and kangaroos in terms of DSE. However the suggestion by Grigg (2002) that grazing pressure of kangaroos should be revised from 0.7 dry sheep equivalents (used by some government departments) to 0.15 DSE for (smaller) kangaroos in harvested populations, and 0.25 for (larger) kangaroos in unharvested populations, is partly supported. Values closer to 0.4 and 0.6 are more realistic over an important part of the range of pasture availability. A management implication is that the benefit of reducing kangaroo density to obtain additional grass for sheep, is less per kangaroo than previously calculated.

9.4 Estimating high density kangaroo populations

The kangaroo density estimates reported in Chapter 7 for the three study sites (mean eastern grey kangaroo densities of 450, 480 and 510 km^{-2}) are the highest kangaroo densities reported. For comparison, the maximum density of combined red kangaroos and western grey kangaroos in the Kinchega study was less than 56 km^{-2} (Bayliss 1987) and the density of eastern grey kangaroos at Wallaby Creek (Southwell 1987b) was 41 to 50 km^{-2}. The next highest kangaroo density outside the vicinity of my study sites appears to be that of Coulson *et al*. (1999a) for eastern grey kangaroos at Yan Yean Reservoir near Melbourne, which was 220 km^{-2}.

Why are these kangaroo populations at higher density than others? The study was not designed to answer that question, but an answer would be of considerable interest. Kangaroo population growth rate is affected by the reliability of rainfall (Davis *et al*. 2003) as well as by the amount of rainfall. From an inspection of maps on the Bureau of Meteorology website (www.bom.gov.au) I hypothesise that the southern tablelands lies within a region where the mean and variance of rainfall during, and just prior to, the pasture growth season, is optimised for kangaroos.

A second explanatory hypothesis is that land managers have rarely allowed kangaroo populations to exclusively utilize grasslands long enough for the population to reach maximum density. In other words, there may be many other places where kangaroo density would be as high as on the study sites, but land managers have rarely allowed such densities to develop.

My density estimates are an improvement on the ones previously reported for the same and similar sites (Freudenberger 1996; Nelson 1997; ACT Kangaroo Advisory Committee 1997) because they are for defined sites, i.e. the grassy valley floors. That appears to be at least part of the explanation why they are higher than the previous estimates which were for undefined sites apparently including part of the steep forested valley sides, which are not habitat for eastern grey kangaroos.

Counting at night was advantageous for recording density of all kangaroos that fed in the grassland, whether the kangaroos had spent the daytime in that area or not, and it was also advantageous because the kangaroos were more evenly spread out in smaller groups, enabling a desired level of precision to be reached in less time. Longer linear transects are desirable but would not be negotiable by four wheel drive vehicles. Nocturnal counts on foot could overcome the constraint on transect length (but would have been impractical with the equipment available in this project) or else non-linear transects as used by Pierce *et al*. (2001) could be used to avoid obstacles such as areas of rock outcrops while retaining the advantages of the line-transect method operated from an off-road vehicle at night.

In the high density populations, both the nocturnal line transect method used, and the more conventional walked line transect counts in daylight (used in a preliminary trial) resulted in some kangaroos flushing ahead along the transect. This required numerous subjective decisions to be made about whether or not groups of kangaroos were ones previously counted on the transect. The same observation was reported by Southwell (1994) when estimating kangaroo densities less than one-fifteenth of the densities applicable in this study. The density estimated in a survey could be biased if the decisions whether to include such kangaroos in the count were more often wrong in one direction. Saturation of the counting system is also a possibility. Southwell (1994) found evidence of saturation at much lower density than the densities on the study sites. Although in my study bias and saturation were not supported by the independent density estimates from the drive counts, which were the same or lower than the line transect estimates, nevertheless it seems advisable to reduce the reliance of the method on subjective judgments.

9.5 Kangaroo population dynamics

9.5.1 Limitation

The eastern grey kangaroo populations were limited according to the predation sensitive food (or predation sensitive foraging) hypothesis described by Abrams (1991), Hik (1995), Sinclair and Arcese (1995), and Krebs *et al.* (1996). This was clearest at Gudgenby, associated with dingo predation. The kangaroos killed by dingoes tended to be in poor condition and most were old ones and young ones, the same demographic groups targeted by the dingoes studied by Oliver (1986) on the Fortescue River in Western Australia. However at Gudgenby, dingoes also killed kangaroos of prime age in good condition, a demographic group which appears largely immune from other causes of natural mortality, and to whose mortality the population growth rate is more sensitive than it is to any other demographic rate.

For this study, foxes were poisoned, but not eradicated, on all sites. The main predators were the dingoes at Gudgenby. In view of the findings of Banks *et al.* (2000) that fox predation limited recruitment of eastern grey kangaroos, and the finding in this study that juvenile survival is the population limiting demographic rate (below), the predator sensitive food hypothesis may have general application to high density kangaroo populations where foxes are uncontrolled. The plot of r / V suggests that even where foxes were poisoned, fox predation may have had a greater effect than expected.

The hypothesis that eastern grey kangaroo populations generally are limited according to predation sensitive foraging, implies varied effects of predator control. There are two important management implications. First, management decisions about dingoes and foxes, should regard the predator as a component of the kangaroo - pasture system. In particular, where kangaroo density is naturally low, managers should only contemplate predator control with an awareness of the possibility that interference with the predators may release the kangaroo population from a low density state.

Female eastern grey kangaroos with young-at-foot tend to forage alone, or in smaller groups (Stuart-Dick and Higginbottom 1989; Jarman and Coulson 1989). This behaviour increases when predation risk is reduced, therefore presumably it is done in spite of predation risk, in order to reduce the costs of group foraging (Banks 2000). Whether female eastern grey kangaroos with young also increase their risk taking behaviour in inverse proportion to food availability has not yet been researched but the expectation of a negative relationship between food and risky behaviour is encouraged by the marrow fat results which support the predator-sensitive food hypothesis on the Gudgenby site.

9.5.2 Demographics

The estimates of annual production of late pouch young (0.886 ± 0.041 SE per female at Gudgenby and 0.783 ± 0.058 SE per female at Tidbinbilla) are consistent with the shot sample, and with rates reported previously for kangaroos outside the semi-arid zone by Arnold *et al.* (1991) and Banks *et al.* (2000). Such high fecundity shows that the *per capita* food shortage associated with these high density kangaroo populations is not affecting either adult fertility or survival of pouch young to a degree which might limit the population. Mortality of immature animals is low, at least until after they permanently vacate the pouch.

The estimate of age-specific fecundity from Tidbinbilla (Eqns 6.4 and 6.5) appears to be a more reliable one than any previously published for kangaroos. The mean fecundity of prime female eastern grey kangaroos two to nine years old (0.90) is substantially higher than the mean value for ungulates reported by Gaillard *et al.* (2000) (0.818; CV = 0.125) and the plateau of fecundity at the peak breeding ages (five to six years) is high for a wild population. Considering that the sample was taken in conditions of food shortage (an attempt to avert further winter starvation), there appears little scope for fecundity of eastern grey kangaroo populations on similar sites being shown to be density dependent or affected by food availability. This is in contrast to findings that fecundity is density dependent in several ungulate species, such as red deer (Clutton-Brock and Albon 1989), black-tailed deer (Gilbert and Raedeke 2004), and elk (Stewart *et al*. 2005). There is no support from this study for Dawson's (1995, p 89) claim for density dependent delay of primiparity in kangaroos.

Mortality was seasonal and biased to sub-adult kangaroos. As with most large herbivores (Eberhardt 1977; Gaillard *et al*. 1998, 2000), the study populations were most sensitive to survival of adult kangaroos. However in practice, the survival of marked adults was high, except during the bushfire at Tidbinbilla. The next most sensitive demographic rate was survival to breeding age, which can be divided into the periods before and after pouch emergence. The annual production of late pouch young (above) indicates low mortality in the first of these. As for the second, sub-adult mortality was high. The proportional mortality of sub-adults, in combination with the sensitivity of survival to breeding age, indicates sub-adult mortality to be the population limiting demographic rate.

How big are eastern grey kangaroos?

The mean live weight of eastern grey kangaroos taken from the unshot population at Tidbinbilla was 29 kg – smaller than the 35 kg mean live weight assumed in the Kinchega kangaroo study (Caughley *et al*. 1987). Based on the size relationship between shot and unshot populations of kangaroos in South Australia and Queensland (Grigg 2000), the mean size of eastern grey kangaroos in equivalent shot populations was predicted to be 17 kg <u>live</u> weight. The minimum <u>dressed</u> size accepted by operators of commercial chillers is 17 kg, implying that many of the kangaroos in shot populations (on rural properties) in the ACT region are too small to attract commercial shooters.

Predation and motor vehicles

It was stated above that dingo predation was liable to affect the prime animals in good condition to whose mortality the population growth rate is most sensitive. The same is true of motor vehicle accidents. Motor vehicles killing herbivores were compared to predators by O'Gara and Harris (1988). Kangaroo road kills are typically male biased (Coulson 1982, 1989b, 1997; Lintermans and Cunningham 1997) and motor vehicles may also be selective for immature kangaroos (Lintermans and Cunningham 1997) but the inclusion in the road kills of a small proportion of prime animals is likely to be disproportionately significant. It increases the potential for motor vehicle accidents to reduce kangaroo population growth rates.

9.5.3 *Drought effect*

In marked contrast to the picture of kangaroo population dynamics that has emerged from previous research, which has been in arid and semi-arid environments (e.g. Caughley *et al*. 1987), this study shows how well the kangaroo populations resisted drought. The drought experienced during this study greatly reduced the kangaroos' food supply without much effect on the estimated kangaroo density. One explanation for the difference could be simply that the food reduction was much less drastic during this study than the studies in the semi-arid region. At Kinchega (Robertson 1987a) there was a more sudden decline in herbage mass than experienced in this study (Chapter 4), and at Kinchega, herbage mass remained less than 100 kg ha^{-1} for almost a year, and its lowest level was 9 kg ha^{-1}. In my study the pasture declined below 300 kg ha^{-1} for only one bimonthly survey on one site, reaching a minimum of 163 kg ha^{-1} (excluding the period following the bushfire at Tidbinbilla). The minimum on my temperate study sites was close to the equilibrium point of the numerical response (where r = 0) for the kangaroos in Kinchega National Park (Bayliss 1987 Fig 8.5). The equilibrium for red kangaroos at Kinchega was approximately 173 kg ha^{-1} total herbage mass (175 kg ha^{-1} for western grey kangaroos). In my study the equilibrium value for the ratio numerical response is 138 kg ha^{-1} green herbage mass per kangaroo. That corresponds to 662 kg ha^{-1} green herbage mass at a mean density of 4.8 kangaroos ha^{-1}. So the temperate equilibrium is much higher, especially after allowance is made for the difference between total herbage mass (measured at Kinchega) and green herbage mass (measured in my study).

It is not that the drought experienced during this study was a mild one. Droughts that have a more severe effect on plant growth than the one experienced during this study are rarely recorded on the southern tablelands. Rainfall during the study was classed by the Bureau of Meteorology as 'severely deficient' (i.e. in the lowest 5% of long-term records) for lengthy periods (Bureau of Meteorology 2003) despite the effect on the statistics of the exceptional rain falls in February 2002 and March 2003 (Chapter 4). But droughts are defined statistically in relation to what is usual at a place, so a 'severe' drought (like this one) in a temperate area may be associated with higher herbage mass and pasture growth than a drought in a semi-arid area that is categorised as less severe.

Droughts and food shortages in arid and semi-arid regions kill adult kangaroos (Caughley *et al*. 1985; Robertson 1986; Shepherd 1987). In other words, in the extreme circumstances of drought, the kangaroos' survival mechanisms, including the use of internal reserves such as fat deposits (Chapter 6) and external 'reserve' food sources, are not sufficient to cope with the magnitude of the food shortage. However my study suggests that in temperate areas these mechanisms may be sufficient to enable adult kangaroos to bridge many of the troughs in food availability that occur in this less extreme environment (such as the food shortage recorded in this study, and the ones apparently applying during most winters).

While the relative stability of eastern grey kangaroo populations in temperate areas is an interesting result with important management implications, another consequence was that the anticipated perturbation of density did not occur, so that the parameters of the numerical response could not be estimated by the regression method. Instead a ratio numerical response was estimated, as previously used by Caughley and Lawton (1981) for *Cactoblastis cactorum*, McCarthy (1996) for red kangaroos *Macropus rufus*, Turchin and Hanski (1997) for voles *Microtus agrestis*, Barlow and Norbury (2001) for ferrets *Mustela furo*, and Walter (2002) for feral horses *Equus caballus*. The ratio numerical response in this study depends on the value provided for r_{max}, therefore a desirable research task for the future is to obtain estimates of the numerical response entirely from field data. Long-term records of herbage mass and kangaroo density in areas where the kangaroo population is increasing, would be of use.

9.6 Conclusions

Clearly this study was a beginning, not the comprehensive study of kangaroo population dynamics that is desirable to inform the management of eastern grey kangaroo populations in temperate Australia. Like all research it has provoked many questions, as well as generating understanding not previously available. The knowledge gained also has many management implications.

Insights gained in this study range from simply knowing the density of eastern grey kangaroos in these sites (the highest reported, and much higher than previously expected - Freudenberger 1996; Nelson 1997; ACT Kangaroo Advisory Committee 1997) to quantification of the offtake of pasture by the kangaroo populations, estimates of fecundity and mortality, appreciation of the importance of dingo predation, and appreciation of the winter mortality of sub-adults as the main demographic determinant of population growth rate. Numerous management implications arise from these findings, including from the assembly of the pasture, functional and numerical responses into an interactive model. Time constraints dictate that the model and many of the management implications will be documented separately, but some management implications are stated above in this chapter, and below.

Four simple estimates made in different chapters combine to generate a picture of temperate kangaroos which may be useful to some managers. Kangaroos in these temperate grasslands are on average smaller (Chapter 6), eat less (Chapter 5), are more numerous (Chapter 7) and are more fecund (Chapter 6) than would be predicted from other studies (e.g. Caughley *et al*. 1987). Thus the benefit of shooting each kangaroo, in terms of grass production, is less, or, in other words, more kangaroos have to be shot to achieve a certain level of impact reduction, and the population will recover more quickly, than would have been predicted prior to this study.

The interactive model which can readily be assembled from the products of Chapters 4, 5 and 8, can be used to test a range of management options, and the effect of variation in weather conditions, such as increased or decreased rainfall. For example, the initial version of the model indicates that commercial harvesting (currently under trial in the region), at the maximum level allowed, results in a sustainable harvest of kangaroos, but does not increase the herbage mass, and only slightly reduces the frequency of crashes when herbage mass falls to low levels. (To demonstrate this with an ecological experiment would require an extremely large investment of research effort.) However, an alternative 'national park damage mitigation' formula, which holds kangaroo density to about 1 ha^{-1}, increases herbage mass considerably and reduces the frequency of crashes in herbage mass, but at the cost of having to shoot large numbers of kangaroos. Thus the knowledge gained in this study appears to have useful potential to illustrate to managers the dynamic properties of a resource-consumer system, the probabilistic nature of management outcomes, and the consequences of their particular management proposals**.**

The chief difficulty encountered in this study was that the estimation of a numerical response of the type used by Caughley (1976a, 1987) in his interactive model was challenged by the stability of the high-density kangaroo populations and their resistance to droughts and other potential forms of perturbation. For the future, there are several potentially fruitful responses to this situation. The simplest is the measurement of green herbage mass and population growth rate in areas where eastern grey kangaroo populations are increasing. This would be a long-term (e.g. 10 years), low-effort project. A more-intensive 'demographic' approach, estimating life-time survival and fecundity, using known-age individuals, could potentially be combined on the same site(s). To record declining as well as increasing populations, a third possibility is to take advantage of any natural reductions or declines in kangaroo density e.g. due to conversion of grassland to forest as proposed in the Namadgi National Park Draft

Management Plan (Arts, Heritage and Environment 2005 p 58). A fourth possibility, considering the importance of sub-adult mortality to population growth rate, would be to identify correlates of winter mortality such as food availability in spring, summer or autumn, and episodes of wet, cold weather – similar to the results for Soay sheep (Clutton-Brock and Pemberton 2004) and red deer (Clutton-Brock and Coulson 2003). Fifth, and notwithstanding the reservations expressed in Chapter 2, the Growth, Metabolism, Mortality (GMM) approach to modelling herbivore dynamics (Owen-Smith 2002a, b) appears to have several potentially useful features worth pursuing, such as the separate modelling of green herbage and necromass, and the separate modelling of herbivore mortality related to food availability.

REFERENCES

10 REFERENCES

Abrams, P. A. (1990). The effects of adaptive behavior on the type-2 functional response. *Ecology* **71**, 877-885.

Abrams, P. A. (1991). Strengths of indirect effects generated by optimal foraging. *Oikos* **62**, 167-176.

Abrams, P. A. and Ginzberg, L. R. (2000). The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* **15**, 337-341.

ACT Kangaroo Advisory Committee (1996). 'Living With Eastern Grey Kangaroos in the ACT - Rural Land: First Report to the Minister for the Environment, Land and Planning.' www.environment.act.gov.au. (Australian Capital Territory: Canberra.)

ACT Kangaroo Advisory Committee (1997). 'Living With Eastern Grey Kangaroos in the ACT - Public Land: Third Report to the Minister for the Environment, Land and Planning.' www.environment.act.gov.au. (Australian Capital Territory: Canberra.)

ACT Parks and Conservation Service (1995). 'A summary of the information available on the abundance of eastern grey kangaroos in the ACT and effects of their grazing: Report to the ACT Kangaroo Advisory Committee.' (Unpublished ACT Government Report to the ACT Kangaroo Advisory Committee: Canberra, ACT.)

Adams, L. G. (2003). Marrow fat deposition and skeletal growth in caribou calves. *Journal of Wildlife Management* **67**, 20-24.

Allden, W. G. and Whittaker, I. A. M. (1970). The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. *Australian Journal of Agricultural Research* **21**, 755-766.

Anderson, A. E., Medin, D. E. and Bowden, D. C. (1972). Indices of carcass fat in a Colorado mule deer population. *Journal of Wildlife Management* **36**, 579-594.

Anderson, D. R. and Southwell, C. J. (1995). Estimates of macropod density from line transect surveys relative to analyst expertise. *Journal of Wildlife Management* **59**, 852-857.

Andrewartha, H. J. and Birch, L. C. (1954). 'The Distribution and Abundance of Animals.' (The University of Chicago Press: Chicago.)

Arnold, G. W. and Dudzinski, M. L. (1967a). Studies on the diet of the grazing animal. II. The effect of physiological status in ewes and pasture availability on herbage intake. *Australian Journal of Agricultural Research* **18**, 349-359.

Arnold, G. W. and Dudzinski, M. L. (1967b). Studies on the diet of the grazing animal. III. The effect of pasture species and pasture structure on the herbage intake of sheep. *Australian Journal of Agricultural Research* **18**, 657-666.

Arnold, G. W., Grassia, A., Weeldenburg, J. R. and Steven, D. E. (1991). Population ecology of western grey kangaroos in a remnant of wandoo woodland at Baker's Hill, southern Western Australia. *Wildlife Research* **18**, 561-575.

Arnold, G. W. and Maller, R. A. (1987). Monitoring population densities of western grey kangaroos in remnants of native vegetation. *In* 'Nature Conservation: The Role of Remnants of Native Vegetation.' *Eds.* D. A. Saunders, G. W. Arnold, A. A. Burbidge, and A. A. Hopkins pp 219-225. (Surrey Beatty: Sydney.)

Arts, Heritage and Environment (2005). 'Namadgi National Park Draft Management Plan.' (Australian Capital Territory: Canberra.)

Arundel, H., Dempster, K. J., Harrigan, K. E. and Black, R. (1990). Epidemiological observations on the helminth parasites of *Macropus giganteus* Shaw in Victoria. *Australian Wildlife Research* **17**, 39-51.

Arundel, J. H., Barker, I. K. and Beveridge, I. (1977). Diseases of marsupials. *In* 'The Biology of Marsupials.' *Eds.* B. Stonehouse and D. Gilmore pp 141-154. (Macmillan: London.)

Augusteyn, R. C., Coulson, G. and Landman, K. A. (2004). Determining kangaroo age from lens protein content. *Australian Journal of Zoology* **51**, 485-494.

Ayres, J. F., McPhee, M. J., Turner, A. D. and Curll, M. L. (2000). The grazing value of tall fescue (*Festuca arundinacea*) and phalaris (*Phalaris aquatica*) for sheep production in the northern tablelands of New South Wales. *Australian Journal of Agricultural Research* **51**, 57-68.

Banks, P. B. (1997). 'Predator-prey Interactions Between Foxes, Rabbits and Native Animals of the Australian Alps.' PhD Thesis (University of Sydney: Sydney.)

Banks, P. B. (2000). Can foxes regulate rabbit populations? *Journal of Wildlife Management* **64**, 401-406.

Banks, P. B. (2001). Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. *Animal Behaviour* **61**, 1013-1021.

Banks, P. B., Dickman, C. R. and Newsome, A. E. (1998). Ecological cost of feral predator control: foxes and rabbits. *Journal of Wildlife Management* **62**, 766-772.

Banks, P. B., Hume, I. D. and Crowe, O. (1999). Behavioural, morphological and dietary response of rabbits to predation risk from foxes. *Oikos* **85**, 247-256.

Banks, P. B., Newsome, A. E. and Dickman, C. R. (2000). Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology* **25**, 283-291.

Barlow, N. D. (1985). The interferential model re-examined. *Oecologia* **66**, 307-308.

Barlow, N. D. (1987). Pastures, pests and productivity: simple grazing models with two herbivores. *New Zealand Journal of Ecology* **10**, 43-55.

Barlow, N. D. and Clout, M. N. (1983). A comparison of 3-parameter, single-species population models, in relation to the management of brushtail possums in New Zealand. *Oecologia* **60**, 250-258.

Barlow, N. D. and Norbury, G. L. (2001). A simple model for ferret population dynamics and control in semi-arid New Zealand habitats. *Wildlife Research* **28**, 87-94.

Bayliss, P. (1985). The population dynamics of red and western grey kangaroos in arid New South Wales, Australia. II. The numerical response function. *Journal of Animal Ecology* **54**, 127-135.

Bayliss, P. (1987). Kangaroo dynamics. *In* 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.' *Eds.* G. Caughley, N. Shepherd, and J. Short pp 119-134. (Cambridge University Press: Cambridge.)

Bayliss, P. and Choquenot, D. (2002). The numerical response: rate of increase and food limitation in herbivores and predators. *Philosophical Transactions of the Royal Society, London, Series B* **357**, 1233-1248.

Bayliss, P. and Choquenot, D. (2003). The numerical response: rate of increase and food limitation in herbivores and predators. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 148-179. (Cambridge University Press: Cambridge.)

Bayliss, P. and Giles, J. (1985). Factors affecting the visibility of kangaroos counted during aerial surveys. *Journal of Wildlife Management* **49**, 686-692.

Bayliss, P. and Yeomans, K. M. (1990). Use of low-level aerial photography to correct bias in aerial survey estimates of magpie geese and whistle duck density in the Northern Territory. *Australian Wildlife Research* **17**, 1-10.

Beard, L. A. (1999). Training observers. *Australian Zoologist* **31**, 287-291.

Begon, M., Harper, J. L. and Townsend, C. R. (1996). 'Ecology: Individuals, Populations and Communities.' 3rd Edn. (Blackwell Science: Oxford.)

Berghout, M. (2000). 'The Ecology of the Red Fox (*Vulpes vulpes*) in the Central Tablelands of New South Wales.' PhD Thesis (University of Canberra: Canberra.)

Black, J. L. and Kenny, P. A. (1984). Factors affecting diet selection by sheep. II. Height and density of pasture. *Australian Journal of Agricultural Research* **35**, 565-578.

Blaney, C. E., Dawson, T. J., McCarron, H. C. K., Buffenstein, R. and Krockenberger, A. K. (2000). Water metabolism and renal function and structure in eastern grey kangaroos (*Macropus giganteus*): Responses to water deprivation. *Australian Journal of Zoology* **48**, 335-345.

Blyde, D. J. (1999). Advances in treating diseases of macropods. *In* 'Postgraduate Foundation Proceedings in Veterinary Science, University of Sydney. No. 237: Wildlife in Australia: Health, Care and Management.' pp 439-445. (University of Sydney: Sydney.)

Boos, M., Thouzeau, C., Delacour, G., Artois, M., Marchandeau, S., Jean-Claude, P. and Robin, J. P. (2005). Body condition assessment and prediction of fasting endurance in wild rabbits (*Oryctolagus cuniculus*). *Wildlife Research* **32**, 75-83.

Botero, G. (1588). 'The magnificence and greatness of cities. *Translated by* R. Peterson 1606. Reprinted 1979.' (Walter J Johnston, Amsterdam: Theatrum Orbis Terrarum: Norwood NJ.)

Boutin, S. (1992). Predation and moose population dynamics:a critique. *Journal of Wildlife Management* **56**, 112-157.

Bradbury, J. W., Vehrencamp, S. L., Clifton, K. E. and Clifton, L. M. (1996). The relationship between bite rate and local forage abundance in wild Thomson's gazelles. *Ecology* **77**, 2237-2256.

Bransby, D. I., Matches, A. G. and Krause, G. F. (1977). Disk meter for rapid estimation of herbage yield in grazing trials. *Agronomy Journal* **69**, 393-396.

Brooker, M. and Ridpath, M. G. (1980). The diet of the wedge-tailed eagle, *Aquila audax*, in Western Australia. *Australian Wildlife Research* **7**, 433-452.

Brooks, P. M., Hanks, J. and Ludbrook, J. V. (1977). Bone marrow as an index of condition in African ungulates. *South African Journal of Wildlife Research* **7**, 61-66.

Bubela, T. M., Dickman, C. R. and Newsome, A. E. (1998). Diet and winter foraging behaviour of the red fox *Vulpes vulpes* in alpine and subalpine New South Wales. *Australian Mammalogy*. **20**, 321-330.

Buckland, S. T., Anderson, D. R., Burnham, K. P. and Laake, J. L. (1993). 'Distance Sampling: Estimating Abundance of Biological Populations.' (Chapman and Hall: London.)

Buckland, S. T., Goudie, I. B. J. and Borchers, D. L. (2000). Wildlife population assessment: Past developments and future directions. *Biometrics* **56**, 1–12.

Burbidge, A. A. and McKenzie, N. L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50**, 143-198.

Burbidge, N. T. (1960). The phytogeography of the Australian region. *Australian Journal of Botany* **8**, 75-209.

Bureau of Meteorology (2003). Statement on drought for the 9 and 13-month periods ending 30th December 2002. *In* 'Drought Statement - Issued 7th January 2003.' http://www.bom.gov.au/announcements/media_releases/climate/drought/20030107.shtml Edn. ACT Meteorological Office

Bureau of Meteorology (2004a). ACT sweltered in February as temperature records tumbled. *In* 'Monthly Climate Summary February 2004.' ACT Meteorological office

Bureau of Meteorology (2004b). Bone dry March for ACT as new sunshine record set. *In* 'Monthly Climate Summary March 2004.' ACT Meteorological office

Bureau of Meteorology (2004c). ACT endured a 'top 10' hot summer in 2003-04. *In* 'Monthly Climate Summary .' ACT Meteorological office

Burnham, K. P. and Anderson, D. R. (2002). 'Model Selection and Multi Model Inference: a Practical Information-Theoretic Approach.' 2nd Edn. (Springer: New York.)

Cairns, S. C. (1989). Models of Macropodid populations. *In* 'Kangaroos, Wallabies and Rat Kangaroos.' *editors.* G. C. Grigg, P. J. Jarman, and I. D. Hume pp 695-704. (Surrey Beatty: Sydney.)

Cairns, S. C. (1999). Accuracy and consistency in the aerial survey of kangaroos. *Australian Zoologist* **31**, 275-279.

Cairns, S. C. (2004). 'A report to the New South Wales National Parks & Wildlife Service on the consultancy: "Kangaroo Monitoring – South East New South Wales Helicopter Survey".' (New South Wales National Parks and Wildlife Service: Sydney, also www.nationalparks.nsw.gov.au.)

Cairns, S. C. and Grigg, G. C. (1993). Population dynamics of red kangaroos (*Macropus rufus*) in relation to rainfall in the South Australian pastoral zone. *Journal of Applied Ecology* **30**, 444-458.

Caley, P. A. and Morley, C. G. (2002). Assessing growth rates of European rabbit populations using spotlight transect counts. *Journal of Wildlife Management* **66**, 131-137.

Caswell, H. (2001). 'Matrix Population Models.' 2nd Edn. (Sinauer: Sunderland, MA.)

Caughley, G. (1962). 'The Comparative Ecology of the Red and Grey Kangaroo.' M. Sc. Thesis (University of Sydney: Sydney.)

Caughley, G. (1966). Mortality patterns in mammals. *Ecology* **47**, 906-918.

Caughley, G. (1970). Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology* **51**, 53-72.

Caughley, G. (1974). Bias in aerial survey. *Journal of Wildlife Management* **38**, 921-933.

Caughley, G. (1976a). Wildlife management and the dynamics of ungulate populations. *In* 'Applied Biology.' *Ed.* T. H. Coaker pp 183-246. (Academic Press: London.)

Caughley, G. (1976b). The elephant problem-an alternative hypothesis. *East African Wildlife Journal* **14**, 265-283.

Caughley, G. (1977a). 'Analysis of Vertebrate Populations.' (Wiley & Sons: London.)

Caughley, G. (1977b). Sampling in aerial survey. *Journal of Wildlife Management* **41**, 605-615.

Caughley, G. (1981). What we do not know about the dynamics of large mammals. *In* 'Dynamic of Large Mammal Populations.' *Eds.* C. W. Fowler and T. D. Smith pp 361-372. (John Wiley & Sons: London.)

Caughley, G. (1982). Vegetation complexity and the dynamics of modelled grazing systems. *Oecologia* **54**, 309-312.

Caughley, G. (1987). Ecological Relationships. *In* 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.' *Eds.* G. Caughley, N. Shepherd, and J. Short pp 159-187. (Cambridge University Press: Cambridge.)

Caughley, G., Brown, B., Dostine, P. and Grice, D. (1984). The grey kangaroo overlap zone. *Australian Wildlife Research* **11**, 1-10.

Caughley, G., Grice, D., Barker, R. and Brown, B. (1988). The edge of the range. *Journal of Animal Ecology* **57**, 771-785.

Caughley, G., Grigg, G. C., Caughley, J. and Hill, G. J. E. (1980). Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* **7**, 1-12.

Caughley, G., Grigg, G. C. and Short, J. (1983). How many kangaroos? *Search* **14**, 151-152.

Caughley, G., Grigg, G. C. and Smith, L. (1985). The effect of drought on kangaroo populations. *Journal of Wildlife Management* **49**, 679-685.

Caughley, G. and Gunn, A. (1996). 'Conservation Biology in Theory and Practice.' (Blackwell Science: Melbourne.)

Caughley, G. and Krebs, C. J. (1983). Are big mammals simply little mammals writ large? *Oecologia* **59**, 7-17.

Caughley, G. and Lawton, J. H. (1981). Plant-herbivore System. *In* 'Theoretical Ecology: Principles and Applications.' 2nd Edn. *Ed.* R. M. May pp 132-166. (Blackwell Scientific: London.)

Caughley, G. and Sinclair, A. R. E. (1994). 'Wildlife Ecology and Management.' (Blackwell Science: Boston.)

Caughley, G., Shepherd, N. and Short, J. *Eds* . (1987). 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.' (Cambridge University Press: Cambridge.)

Caughley, G., Sinclair, R. and Scott-Kemmis, D. (1976). Experiments in aerial survey. *Journal of Wildlife Management* **40**, 290-300.

Caughley, J., Bayliss, P. and Giles, J. (1984). Trends in kangaroo numbers in western New South Wales and their relation to rainfall. *Australian Wildlife Research* **11**, 415-422.

Cayley, J. W. D. and Bird, P. R. (1996). 'Techniques for Measuring Pastures.' 2nd Edn. (Agriculture Victoria: Hamilton, Victoria.)

Chaco, O. J. (1993). A practical equation for pasture growth under grazing. *Grass and Forage Science* **48**, 387-394.

Chaco, O. J., Bywater, A. C. and Dillon, J. L. (1999). Assessment of production risk in grazing models. *Agricultural Systems* **60**, 87-98.

Chitty, D. (1952). Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire, 1936-9. *Philosophical Transactions of the Royal Society, London, Series B* **236**, 505-552.

Choquenot, D. (1994). The dynamics of feral pig populations in the semi-arid rangelands of eastern Australia. PhD Thesis. (University of Sydney: NSW.)

Choquenot, D. (1995). Assessing visibility bias associated with helicopter counts of feral pigs in Australia’s semi-arid rangelands. *Wildlife Research* **22**, 569-78.

Choquenot, D. (1998). Testing the relative influence of intrinsic and extrinsic variation in food availability on feral pig populations in Australia's rangelands. *Journal of Animal Ecology* **67**, 887-907.

Choquenot, D., Druhan, J., Lukins, B., Packwood, R. and Saunders, G. (1998). Managing the impact of rabbits on wool production systems in the central tablelands of New South Wales: an experimental study and bioeconomic analysis. *In* 'Proceedings of the 11th Australian Vertebrate Pest Conference, Bunbury, WA.' pp 367-374. (Vertebrate Pest Research Unit. NSW Agriculture, Orange Agricultural Research Institute: NSW.)

Choquenot, D., Hone, J. and Saunders, G. (1999). Using aspects of predator-prey theory to evaluate helicopter shooting for feral pig control. *Wildlife Research* **26**, 251-61.

Choquenot, D. and Parkes, J. (2001). Setting thresholds for pest control: how does pest density affect resource viability? *Biological Conservation* **99**, 29-46.

Choquenot, D. and Ruscoe, W. A. (2003). Landscape complementation and food limitation of large herbivores: habitat-related constraints on the foraging efficiency of wild pigs. *Journal of Animal Ecology* **72**, 14-26.

Clancy, T. F. (1999). Choice of survey platforms and technique for broad-scale monitoring of kangaroo populations. *Australian Zoologist* **31**, 267-275.

Clancy, T. F. and Croft, D. B. (1992). Population dynamics of the common wallaroo (*Macropus robustus erubescens*) in arid New South Wales. *Wildlife Research* **19**, 1-16.

Clancy, T. F., Pople, A. R. and Gibson, L. A. (1997). Comparison of helicopter line transects with walked line transects for estimating densities of kangaroos. *Wildlife Research* **24**, 397-409.

Clark, S. G., Austen, E. A., Prance, T. and Ball, P. D. (2003). Climate variability effects on simulated pasture and animal production in the perennial pasture zone of south-eastern Australia. 1. Between year variability in pasture and animal production. *Australian Journal of Experimental Agriculture* **43**, 1211-1219.

Clark, S. G., Donnelly, J. R. and Moore, A. D. (2000). The GrassGro decision support tool: its effectiveness in simulating pasture and animal production and value in determining research priorities. *Australian Journal of Experimental Agriculture* **40**, 247-256.

Clarke, J. L., Jones, M. E. and Jarman, P. J. (1989). A day in the life of a kangaroo: Activities and movements of eastern grey kangaroos *Macropus giganteus* at Wallaby Creek. *In* 'Kangaroos, Wallabies and Rat-Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. Hume pp 611-618. (Surrey Beatty: Sydney.)

Clutton-Brock, T. H. and Albon, S. D. (1989). 'Red Deer in the Highlands.' (BSP Professional Books: Oxford.)

Clutton-Brock, T. H. and Coulson, T. (2003). Comparative ungulate dynamics: the devil is in the detail. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 249-269. (Cambridge University Press: Cambridge.)

Clutton-Brock, T. H. and Pemberton, J. M. *Eds*. (2004). Soay Sheep: Dynamics and Selection in an Island Population. (Cambridge University Press: Cambridge.)

Colagross, A. M. L. and Cockburn, A. (1993). Vigilance and grouping in the eastern grey kangaroo, *Macropus giganteus*. *Australian Journal of Zoology* **41**, 325-334.

Cole, L. C. (1958). Sketches of general and comparative demography. *Cold Spring Harbour Symposia on Quantitative Biology* **22**, 1-15.

Coman, B. J. (1973). The diets of red foxes, *Vulpes vulpes* L., in Victoria. *Australian Journal of Zoology* **21**, 391-401.

Cooper, S. M. and Owen-Smith, N. (1986). Effects of plant spinescence on large mammalian herbivores. *Oecologia* **68**, 446-455.

Cote, S. D. and Festa-Bianchet, M. (2001). Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* **127**, 230-238.

Coulson, G. M. (1979). Some methods for surveying kangaroo populations. *Victorian Naturalist* **96**, 184-189.

Coulson, G. M. (1982). Road-kills of macropods on a section of highway in central Victoria. *Australian Wildlife Research* **9**, 21-26.

Coulson, G. M. (1989a). Repertoires of social behaviour in the Macropodoidea. *In* 'Kangaroos, Wallabies and Rat-kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. D. Hume pp 457-473. (Surrey Beatty: Sydney.)

Coulson, G. M. (1989b). The effect of drought on road mortality of macropods. *Australian Wildlife Research* **16**, 79-83.

Coulson, G. M. (1990). Forage biomass and kangaroo populations (*Marsupialia : Macropodidae*) in summer and autumn at Hattah-kulkyne National Park, Victoria. *Australian Mammalogy* **13**, 219-221.

Coulson, G. M. (1997). Male bias in road-kills of macropods. *Wildlife Research* **24**, 21-25.

Coulson, G. M. (2001). Overabundant kangaroo populations in southeastern Australia. *In* 'Wildlife, Land and People: Priorities for the 21st Century.' *Eds.* R. Field, R. J. Warren, H. Okarma, and P. R. Sievert pp 238-242. (The Wildlife Society: Bethesda, Maryland, USA.)

Coulson, G. M., Alviano, P., Ramp, D., McLean, S. W. N. and Yazgin, V. (1999a). The kangaroos of Yan Yean: issues for a forested water catchment in a semi-rural matrix. *In* 'Nature Conservation 5: Nature Conservation in Production Environments: Managing the Matrix.' *Eds.* J. L. Craig, N. Mitchell, and D. A. Saunders pp 146-156. (Surrey Beatty: Sydney.)

Coulson, G. M., Alviano, P., Ramp, D. and Way, S. (1999b). The kangaroos of Yan Yean: history of a problem population. *Proceedings of the Royal Society of Victoria* **3**, 121-130.

Coulson, G. M. and Raines, J. A. (1985). Methods for small-scale surveys of grey kangaroo populations. *Australian Wildlife Research* **12**, 119-125.

Cowan, R. T. and O'Grady, P. (1976). Effect of presentation yield of a tropical grass-legume pasture on grazing time and milk yield of Friesan cows. *Tropical Grasslands* **10**, 213-218.

Crawley, M. J. (1983). 'Herbivory: The Dynamics of Animal-Plant Interactions.' (Blackwell Science: Oxford.)

Croft, J. D., Fleming, P. J. S. and van de Ven, R. (2002). The impact of rabbits on a grazing system in eastern New South Wales. 1. Ground cover and pastures. *Australian Journal of Experimental Agriculture* **42**, 909-916.

Croft, J. D. and Hone, L. J. (1978). The stomach contents of foxes, *Vulpes vulpes*, collected in New South Wales. *Australian Wildlife Research* **5**, 85-92.

Davis, S. A., Pech, R. P. and Catchpole, E. A. (2003). Populations in variable environments: the effect of variability in a species' primary resource. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 180-197. (Cambridge University Press: Cambridge.)

Dawson, T. J. (1995). 'Kangaroos: Biology of the Largest Marsupials.' (University of NSW Press: Sydney.)

Decruyenaere, V., Peters, M., Stilmant, D., Lecomte, P. H. and Dardenne, P. (2003). Near infrared reflectance spectroscopy applied to faeces to predict dry-matter intake of sheep under grazing, comparison with *n*-alkanes and direct biomass measurements. *Tropical and Subtropical Agroecosystems* **3**, 471-475.

DelGiudice, G. D., Riggs, M. R., Joly, P. and Pan, W. (2002). Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *Journal of Wildlife Management* **66**, 698-717.

Demment, M. W. and Greenwood, G. B. (1988). Forage ingestion: effects of sward characteristics and body size. *Journal of Animal Science* **66**, 2380-2392.

den Boer, P. J. and Reddingius, J. (1996). 'Regulation and Stabilization Paradigms in Population Ecology.' (Chapman and Hall: London.)

Dennis, B. and Otten, M. R. M. (2000). Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. *Journal of Wildlife Management* **64**, 388-400.

Department of Environment and Heritage (2003). Wild Harvest of Native Species - Kangaroos. http://www.deh.gov.au/biodiversity/trade-use/wild-harvest/kangaroo/quota-summary-2003.html Accessed November 2004 Edn.

Dique, D. S., deVilliers, D. L. and Preece, H. J. (2003). Evaluation of line-transect sampling for estimating koala abundance in the Pine Rivers Shire, south-east Queensland. *Wildlife Research* **30**, 127-133.

Distel, R. A., Villalba, J. J., Laborde, H. E. and Burgos, M. A. (1996). Persistence of the effects of early experience on consumption of low quality roughage by sheep. *Journal of Animal Science* **74**, 965-968.

Dove, H. and Mayes, R. W. (1991). The use of plant wax alkanes as marker substances in studies of the nutrition of herbivores - a review. *Australian Journal of Agricultural Research* **42**, 913-952.

Dove, H. and Mayes, R. W. (1996). Plant wax components: a new approach to estimating intake and diet composition in herbivores. *Journal of Nutrition* **126**, 13-26.

Dove, H. and Mayes, R. W. (2003). Wild and domestic herbivore diet characterization: Manual for satellite meeting . *In* 'Matching Herbivore Nutrition to Ecosystem Biodiversity: VI International Symposium on the Nutrition of Herbivores.' *Eds.* L. t'Mannetje, L. Ramirez-Aviles, C. A. Sandoval-Castro, and J. C. Ku-Vera pp 1-63. (University of Yucatan: Meridia, Mexico.)

Ealey, E. H. M. (1960). 'Biology of the Euro (*Macropus robustus cervinus* Thomas): With Emphasis on its Interaction with Sheep in the Pilbara District of Western Australia.' PhD Thesis (University of Western Australia: Perth.)

Earle, D. F. and McGowan, A. A. (1979). Evaluation and calibration of an automated rising-plate meter for estimating dry matter yield of pasture. *Australian Journal of Experimental Agriculture and Animal Husbandry* **19**, 337-343.

Eberhardt, L. L. (1977). Optimal management policies for marine mammals. *Wildlife Society Bulletin* **5**, 162-169.

Eberhardt, L. L. (1985). Assessing the dynamics of wild populations. *Journal of Wildlife Management* **49**, 997-1012.

Eberhardt, L. L. (1987). Population projections from simple models. *Journal of Applied Ecology* **24**, 103-118.

Eberhardt, L. L. (1988). Testing hypotheses about populations. *Journal of Wildlife Management* **52**, 50-56.

Eberhardt, L. L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology* **83**, 2841-2854.

Eberhardt, L. L., Garrott, R. A., Smith, D. W., White, P. J. and Peterson, R. O. (2003). Assessing the impact of wolves on ungulate prey. *Ecological Applications* **13**, 776-783.

Edwards, G. P., Dawson, T. J. and Croft, D. B. (1995). The dietary overlap between red kangaroos *(Macropus rufus)* and sheep *(Ovis aries)* in the arid rangelands of Australia. *Australian Journal of Ecology* **20**, 324-334.

Emlen, J. M. (1984). Natural selection and population density-feedback II. The evolution of functional response curves. *Theoretical Population Biology* **25**, 62-77.

English, A. W. (2004). The selection and use of projectile syringe systems. *In* 'Proceedings of First World Deer Veterinary Congress.' pp 162-164. (Deer Veterinary Association: Queenstown, NZ.)

Environment ACT (2004). 'Summary Information on the Culling of 800 eastern grey kangaroos at Googong Foreshores - July 2004.' (Unnumbered internal Report: ACT Government: Canberra.)

Erlinge, S., Goransson, G., Hansson, L., Hogstedt, G. H., Liberg, O., Nilsson, I. N., Nilsson, T., von Shantz, T. and Sylven, M. (1983). Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos* **40**, 36-52.

Errington, P. L. (1946). Predation and vertebrate populations. *Quarterly Review Of Biology* **21**, 144-177.

ESRI (1999). 'Introduction to ArcView ® GIS.' (Environmental Systems Research Institute: California.)

Eveleigh, J. (1995). The current New South Wales kangaroo management program. *In* 'Conservation Through Sustainable Use of Wildlife.' *Eds.* G. C. Grigg, P. Hale, and D. Lunney pp 186-188. (University of Queensland: Brisbane.)

Festa-Bianchet, M. (1988). Birthdate and survival in bighorn lambs (*Ovis canadensis*). *Journal of Zoology* **214**, 653-661.

Festa-Bianchet, M., Gaillard, J.-M. and Cote, S. D. (2003). Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology* **72**, 640-649.

Fitzpatrick, E. A. and Nix, H. A. (1970). The climatic factor in Australian grassland ecology. *In* 'Australian Grasslands.' *Eds.* R. M. Moore pp 3-27. (Australian National University Press: Canberra.)

Fleming, P., Corbett, L., Harden, R. and Thomson, P. (2001). 'Managing the Impacts of Dingoes and Other Wild Dogs.' (Bureau of Rural Sciences: Canberra.)

Focardi, S., Isotti, R. and Tinelli, A. (2002). Line transect estimates of ungulate populations in a Mediterranean forest. *Journal of Wildlife Management* **66**, 48-58.

Forbes, T. D. A. (1988). Researching the plant-animal interface: the investigation of ingestive behaviour in grazing animals. *Journal of Animal Science* **66**, 2369-2379.

Forsyth, D. M. and Caley, P. (2006). Testing the irruptive paradigm of large-herbivore dynamics. *Ecology* **87**, 297-303.

Fox, A. D., Kristiansen, J. N., Stroud, D. A. and Boyd, H. (1998). The effects of simulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves. *Oecologia* **116**, 154-159.

Freudenberger, D. (1995). Separating the sheep from the roos: Do we know the difference? *In* 'Conservation Through Sustainable Use of Wildlife.' *Eds.* G. C. Grigg, P. T. Hale, and D. Lunney pp 208-214. (Centre for Conservation Biology, University of Queensland: Brisbane.)

Freudenberger, D. (1996). 'Density of Eastern Grey Kangaroos on Rural Leases and Nature Reserves in the ACT During November 1995.' ACT Kangaroo Advisory Committee for ACT Parks and Conservation Service. Report to Environment ACT (CSIRO, Australia: Canberra, ACT.)

Freudenberger, D., Wilson, A. and Palmer, R. (1999). The effects of perennial grasses, stocking rate and rainfall on sheep production in a semi-arid woodland of eastern Australia. *Rangeland Journal* **21**, 199-219.

Friedel, M. H. and Bastin G. N. (1988). Photographic standards for estimating comparative yield in arid rangelands. *Australian Rangelands Journal* **10**, 34-38.

Frith, H. (1973). 'Wildlife Conservation.' (Angus and Robertson: Sydney.)

Frith, H. and Calaby, J. (1969). 'Kangaroos.' (F. W. Cheshire: Melbourne.)

Gaillard, J. M., Delorme, D., Boutin, J. M., Vanlaere, G., Boisaubert, B. and Pradel, R. (1993). Roe deer survival patterns - a comparative-analysis of contrasting populations. *Journal of Animal Ecology* **62**, 778-791.

Gaillard, J.-M., Festa-Bianchet, M. and Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* **13**, 58-63.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A. and Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**, 367-393.

Gauthier, G. and Hughes, R. J. (1995). The palatability of Arctic willow for greater snow geese: the role of nutrients and deterring factors. *Oecologia* **103**, 390-392.

Geary, N. (1932). Notes on the wedge-tailed eagle. *The Emu* **31**, 288-289.

Gibb, M. J., Huckle, C. A. and Nuthall, R. (1998). Effect of time of day on grazing behaviour by lactating dairy cows. *Grass and Forage Science* **53**, 41-46.

Gilbert, B. A. and Raedeke, K. J. (2004). Recruitment dynamics of black-tailed deer in the Western Cascades. *Journal of Wildlife Management* **68**, 120-128.

Giles, J. R. (1980). 'The Ecology of Feral Pigs in Western New South Wales.' PhD Thesis (University of Sydney: Sydney.)

Gilpin, M. E., Case, T. J. and Ayala, F. J. (1976). θ selection. *Mathematical Biosciences* **32**, 131-139.

Gilroy, J. (1999). Kangaroo monitoring in relation to kangaroo management in New South Wales. *Australian Zoologist* **31**, 306-308.

Ginnett, T. F. and Demment, M. W. (1995). The functional response of herbivores: analysis and test of a simple mechanistic model. *Functional Ecology* **9**, 376-384.

Ginzburg, L. R. and Jensen, C. X. J. (2004). Rules of thumb for judging ecological theories. *Trends in Ecology and Evolution* **19**, 121-126.

Giordanengo, J. H., Frasier, G. W. and Trlica, M. J. (2003). Hydrologic and sediment responses to vegetation and soil disturbances. *Journal of Range Management* **56**, 152-158.

Gismervik, I. and Andersen, T. (1997). Prey switching by *Acartia clausi*: experimental evidence and implications of intraguild predation assessed by a model. *Marine Ecology Progress Series* **157**, 247-259.

Godfray, H. C. J. and Rees, M. (2003). Population growth rates: issues and applications. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 285-308. (Cambridge University Press: Cambridge.)

Gong, Y., Hodgson, J., Lambert, M. G. and Gordon, I. L. (1996a). Short-term ingestive behaviour of sheep and goats grazing grasses and legumes. I. Comparison of bite weight, bite rate, and bite dimensions for forages at two stages of maturity. *New Zealand Journal of Agricultural Research* **39**, 63-73.

Gong, Y., Hodgson, J., Lambert, M. G. and Gordon, I. L. (1996b). Short-term ingestive behaviour of sheep and goats grazing grasses and legumes. II. Quantitative relationships between sets of sward and ingestive behaviour variables. *New Zealand Journal of Agricultural Research* **39**, 75-82.

Gong, Y., Lambert, M. G. and Hodgson, J. (1996c). Effects of contrasting sward heights within forage species on short-term ingestive behaviour of sheep and goats grazing grasses and legumes. *New Zealand Journal of Agricultural Research* **39**, 83-93.

Grange, S., Duncan, P., Gaillard, J. M., Sinclair, A. R. E., Gogan, P. J. P., Packer, C., Hofer, H. and East, M. (2004). What limits the Serengeti zebra population? *Oecologia* **140** , 523-532.

Green, B. (1989). Water and energy turnover in free-living macropodoids. *In* 'Kangaroos, Wallabies and Rat Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. D. Hume pp 223-229. (Surrey Beatty: Sydney.)

Green, B. (1997). Field energetics and water fluxes in marsupials. *In* 'Marsupial Biology: Recent Research, New Perspectives.' *Eds.* N. Saunders and L. Hinds pp 143-162. (UNSW Press: Sydney.)

Greentree, C., Saunders, G., McLeod, L. and Hone, J. (2000). Lamb predation and fox control in south-eastern Australia. *Journal of Applied Ecology* **37**, 935-943.

Gregg, M. A., Bray, M., Kilbride, K. M. and Dunbar, M. R. (2001). Birth synchrony and survival of pronghorn fawns. *Journal of Wildlife Management* **65**, 19-24.

Grelen, H. E. (1967). Comparison of cage methods for determining utilization on pine-bluestem range. *Journal of Range Management* **20**, 94-96.

Grigg, G. C. (2002). Conservation benefit from harvesting kangaroos: Status report at the start of a new millennium: A paper to stimulate discussion and research. *In* 'A Zoological Revolution. Using Native Fauna to Assist in its Own Survival.' *Eds.* D. Lunney and C. Dickman pp 53-76. (Royal Zoological Society of New South Wales and Australian Museum: Mosman, Australia.)

Grigg, G. C., Beard, L. A., Alexander, P., Pople, A. R. and Cairns, S. C. (1999). Aerial survey of kangaroos in South Australia 1978-1998: A brief report focusing on methodology. *Australian Zoologist* **31**, 292-300.

Grigg, G. C., Jarman, P. J. and Hume, I. *Eds* . (1989). 'Kangaroos, Wallabies and Rat-Kangaroos.' (Surrey Beatty: Sydney.)

Grigg, G. C. and Pople, A. R. (1999). Outcomes of the workshop: refining aerial survey of Kangaroos. *Australian Zoologist* **31**, 317-320.

Gross, J. E., Shipley, L. A., Hobbs, N. T., Spalinger, D. E. and Wunder, B. A. (1993). Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology* **74**, 778-791.

Hanks, J. (1981). Characterisation of population condition. *In* 'Dynamics of Large Mammal Populations.' *Eds.* C. W. Fowler and T. D. Smith pp 47-73. (Wiley: New York.)

Hanks, J., Cumming, D. H. M., Orpen, J. L., Parry, D. F. and Warren, H. B. (1976). Growth, condition and reproduction in the impala ram (*Aepyceros melampus*). *Journal of Zoology* **179**, 421-435.

Hargreaves, J. N. G. and Kerr, J. D. (1992). BOTANAL - a comprehensive sampling and computing procedure for estimating pasture yield and composition. 2. Computational package. 'Tropical Agronomy Technical memorandum No. 79.' (Division of Tropical Crops and Pastures, CSIRO: St Lucia, Qld.)

Hassall, M., Riddington, R. and Helden, A. (2001). Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. *Oecologia* **127**, 97-104.

Hassell, M. P., Lawton, J. H. and Beddington, J. R. (1976). The components of arthropod predation. I. The prey death rate. *Journal of Animal Ecology* **45**, 135-164.

Hassell, M. P., Lawton, J. H. and Beddington, J. R. (1977). Sigmoid functional responses by invertebrate predators and parasitoids. *Journal of Animal Ecology* **46**, 249-262.

Haydock, K. P. and Shaw, N. H. (1975). The comparative yield method for estimating dry matter yield of pasture. *Australian Journal of Experimental Agriculture and Animal Husbandry* **15**, 663-670.

Helm, D. J. and Mead, B. R. (2004). Reproducibility of vegetation cover estimates in south-central Alaska forests. *Journal of Vegetation Science* **15**, 33-40.

Hik, D. S. (1995). Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares. *Wildlife Research* **22**, 115-129.

Hill, G. J. E. (1982). Seasonal movement patterns of the eastern grey kangaroo in southern Queensland. *Australian Wildlife Research* **9**, 373-387.

Hill, G. J. E., Barnes, A. and Wilson, G. R. (1985). Time of day and aerial counts of grey kangaroos. *Journal of Wildlife Management* **49**, 843-849.

Hocking, G. J. and Driessen, M. M. (1996). Mammals of northeast Tasmania. *Records of the Queen Victoria Museum and Art Gallery* **103,** 163-168. *Referenced In* 'Status and Management of the Forester Kangaroo in Tasmania.' Z. Tanner and G. J. Hocking (2001). (Department of Primary Industries: Hobart.)

Hodges, K. E., Krebs, C. J. and Sinclair, A. R. E. (1999). Snowshoe hare demography during a cyclic population low. *Journal of Animal Ecology* **68**, 581-594.

Hodgson, J. (1985). The control of herbage intake in the grazing ruminant. *Proceedings of the Nutrition Society* **44**, 339-346.

Holling, C. S. (1959). The components of predation as revealed by a study of small-mammal predation on the European pine sawfly. *The Canadian Entomologist* **41**, 293-320.

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* **45**, 1-62.

Holling, C. S. (1966). The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* **48**, 1-86.

Hone, J. (1986). Accuracy of the multiple regression method for estimating population density in strip transects. *Australian Wildlife Research* **13**, 121-6.

Hone, J. (1988). A test of the accuracy of line and strip transect estimators in aerial survey. *Australian Wildlife Research* **15**, 493-497.

Hone, J. (1999). On rate of increase (*r*) patterns of variation in Australian mammals and the implications for wildlife management. *Journal of Applied Ecology* **36**, 709-718.

Hone, J. (2002). Feral pigs in Namadgi National Park, Australia: dynamics, impacts and management. *Biological Conservation* **105**, 231-242.

Hone, J. (2006). Feral pigs in Namadgi National Park: Dynamics, Impacts and Control. *In* 'Caring for Namadgi: Science and People.' *Ed.* National Parks Association of the ACT pp 169-176. (National Parks Association of the ACT: Canberra.)

Hone, J. and Sibly, R. M. (2003). Demographic, mechanistic and density-dependent determinants of population growth rate: a case study in an avian predator. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 41-54. (Cambridge University Press: Cambridge.)

Houdijk, J. G. M. and Athanasiadou, S. (2003). Direct and indirect effects of host nutrition on ruminant gastrointestinal nematodes. *In* 'Matching Herbivore Nutrition to Ecosystem Biodiversity: VI International Symposium on the Nutrition of Herbivores.' *Eds.* L. t'Mannetje, L. Ramirez-Aviles, C. A. Sandoval-Castro, and J. C. Ku-Vera pp 213-236. (Universidad Autonoma de Yucatan: Meridia, Mexico.)

Houston, D. B. (1982). 'The Northern Yellowstone Elk.' (Macmillan Publishing Co.: New York.)

Hulbert, I. A. R., Iason, G. R. and Mayes, R. W. (2001). The flexibility of an intermediate feeder: dietary selection by mountain hares measured using faecal n-alkanes. *Oecologia* **129**, 197-205.

Hume, I. D. (1974). Nitrogen and sulphur retention and fibre digestion by euros, red kangaroos and sheep. *Australian Journal of Zoology* **22**, 13-23.

Hume, I. D. (1982a). 'Digestive Physiology and Nutrition of Marsupials.' (Cambridge University Press: Cambridge.)

Hume, I. D. (1982b). Diet and nutrition of kangaroos and wallabies. *In* 'Digestive Physiology and Nutrition of Marsupials.' pp 159-199. (Cambridge University Press: Melbourne.)

Hume, I. D. (1982c). The digestive physiology of marsupials. *Comparative Biochemistry and Physiology* **71A**, 1-10.

Hume, I. D. (1989). Nutrition of marsupial herbivores. *Proceedings of the Nutrition Society* **48**, 69-79.

Hume, I. D. (1999). 'Marsupial Nutrition.' (Cambridge University Press: Cambridge.)

Hume, I. D., Jarman, P. J., Renfree, M. B. and Temple-Smith, P. D. (1989). Macropodidae. *In* 'Fauna of Australia: Vol 1B, Mammalia.' *Eds.* D. W. Walton and B. J. Richardson pp 679-715. (Australian Government Publishing Service: Canberra.)

Huot, J., Poulle, M. L. and Crete, M. (1995). Evaluation of several indexes for assessment of coyote (*Canis latrans*) body-composition. *Canadian Journal of Zoology* **73**, 1620-1624.

Husseman, J. S., Murray, D. L., Power, G. and Mack, D. M. (2003). Correlation patterns of marrow fat in Rocky Mountain elk bones. *Journal of Wildlife Management* **67**, 742-746.

Hutchinson, G. E. (1978). 'An Introduction to Population Ecology.' (Yale University Press: New Haven CT.)

Ingwersen, F. (1985). 'Vegetation Communities of Tidbinbilla Nature Reserve.' Annotated Map (Department of Territories: Canberra.)

Ingwersen, F. (2001). '"Sundry nameless ranges": The Landscape Ecology of the Naas-Gudgenby Catchment.' PhD Thesis (Australian National University: Canberra.)

Ivlev, V. S. (1961). 'Experimental Ecology of the Feeding of Fishes. ' (Yale University Press: New Haven.)

Jackson, S. (2003). 'Australian Mammals: Biology and Captive Management.' (CSIRO Publishing: Melbourne.)

Janssens, P. A. and Rogers, A. M. T. (1989). Metabolic changes during pouch vacation and weaning in macropodoids. *In* 'Kangaroos, Wallabies and Rat Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. D. Hume pp 367-376. (Surrey Beatty: Sydney.)

Jaremovic, R. V. (1984). 'Space and Time Related Behaviour in Eastern Grey Kangaroos (*Macropus giganteus* Shaw).' PhD Thesis (Uni. NSW: Sydney.)

Jaremovic, R. V. and Croft, D. B. (1991). Social organisation of the eastern grey kangaroo (Macropodidae: Marsupalia) in southeastern New South Wales. I. Groups and group home ranges. *Mammalia* **55**, 169-185.

Jarman, P. J. (1986). The red fox: an exotic large predator. *In* 'The Ecology of Exotic Animals and Plants.' *Ed.* R. L. Kitching pp 43-61. (John Wiley and Sons: Brisbane.)

Jarman, P. J. and Coulson, G. M. (1989). Dynamics and adaptiveness of grouping in Macropods. *In* 'Kangaroos, Wallabies and Rat Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. D. Hume pp 527-547. (Surrey Beatty: Sydney.)

Jarman, P. J., Johnson, C. N. and Stuart-Dick, R. (1987). Macropod studies at Wallaby Creek. I. The area and animals. *Australian Wildlife Research* **14**, 1-14.

Jarman, P. J., Jones, M. E., Johnson, C. N., Southwell, C. J., Stuart-Dick, R. I., Higginbottom, K. B. and Clarke, J. L. (1989). Macropod studies at Wallaby Creek. VIII. Individual recognition of kangaroos and wallabies. *Wildlife Research* **16**, 179-185.

Jarman, P. J. and Phillips, C. M. (1989). Diets in a community of macropod species. *In* 'Kangaroos, Wallabies and Rat-Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. Hume pp 143-149. (Surrey Beatty: Sydney.)

Jarman, P. J. and Wright, S. M. (1993). Macropod studies at Wallaby Creek. IX. Exposure and responses of eastern grey kangaroos to dingoes. *Australian Wildlife Research* **20**,

Jathanna, D., Karanth, K. U. and Johnsingh, A. J. T. (2003). Estimation of large herbivore densities in the tropical forests of southern India using distance sampling. *Journal of Zoology* **261**, 285-290.

Jefferies, R. L. (1999). Herbivores, nutrients and trophic cascades in terrestrial environments. *In* 'Herbivores: Between Plants and Predators.' *Eds*. H. Olff, V. K. Brown, and R. L. Drent pp 301-330. (Blackwell Science: Oxford.)

Jeffrey, S. J., Carter, J. O., Moodie, K. M. and Beswick, A. R. (2001). Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environmental Modelling and Software* **16**, 309-330.

Jenkins, B. R. (2000). 'Soil Landscapes of the Canberra 1:100,000 Sheet Report.' (Department of Land and Water Conservation: Sydney.)

Johnson, C. N. (1989). Dispersal and philopatry in the Macropodoids. *In* 'Kangaroos, Wallabies and Rat Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. D. Hume pp 593-601. (Surrey Beatty: Sydney.)

Johnson, C. N. and Bayliss, P. G. (1981). Habitat selection by sex, age and reproductive class in the red kangaroo, *Macropus rufus*, in western New South Wales. *Australian Wildlife Research* **8**, 465-474.

Jones, C. G., Lawton, J. H. and Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946-1957.

Kenney, P. A. and Black, J. L. (1984). Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. *Australian Journal of Agricultural Research* **35**, 551-563.

Kinnear, J. E., Onus, M. L. and Bromilow, R. N. (1988). Fox control and rock wallaby population dynamics. *Australian Wildlife Research* **15**, 435-450.

Kinnear, J. E., Onus, M. L. and Sumner, N. R. (1998). Fox control and rock wallaby population dynamics. II. an update. *Wildlife Research* **25**, 81-88.

Kirkpatrick, T. H. (1964). Molar progression and macropod age. *Queensland Journal of Agricultural and Animal Sciences* **21**, 163-165.

Kirkpatrick, T. H. (1965). Studies of Macropodidae in Queensland. 3. Reproduction in the grey kangaroo (*Macropus major*) in southern Queensland. *Queensland Journal of Agricultural and Animal Sciences* **22**, 319-328.

Kirkpatrick, T. H. (1967). The grey kangaroo in Queensland. *Queensland Agricultural Journal* **93**, 550-552.

Kirsch, J. A. W. and Poole, W. E. (1972). Taxonomy and distribution of the grey kangaroos, *Macropus giganteus* Shaw and *Macropus fuliginosus* (Desmarest), and their subspecies (Marsupialia: Macropodidae). *Australian Journal of Zoology* **20**, 315-339.

Klemola, T., Koivula, M., Korpimaki, E. and Norrdahl, K. (2000). Experimental tests of predation and food hypotheses for population cycles of voles. *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**, 351-356.

Kolb, H. H. (1992). The effect of moonlight on activity in the wild rabbit (*Oryctolagus cunicuIus*). *Journal of Zoology* **228**, 661-665.

Korpimaki, E., Brown, P. R., Jacob, J. and Pech, R. P. (2004). The puzzles of population cycles and outbreaks of small mammals solved? *Bioscience* **54**, 1071-1079.

Korpimaki, E. and Norrdahl, K. (1998). Experimental reduction of predators reverses the crash phase of small-rodent cycles. *Ecology* **79**, 2448-2455.

Krebs, C. J. (1970). Genetics and behavioral studies on fluctuating vole populations. *In* 'Dynamics of Populations.' *Eds.* P. J. den Boer and G. R. Gradwell pp 243-256. (Centre for Agricultural Publishing and Documentation (PUDOC): Wageningen, Netherlands.)

Krebs, C. J. (1995). Two paradigms of population regulation. *Wildlife Research* **22**, 1-10.

Krebs, C. J. (1999). 'Ecological Methodology.' (Addison Wesley Longman: San Francisco.)

Krebs, C. J. (2001). 'Ecology: The Experimental Analysis of Distribution & Abundance.' 5th . Edn. (Benjamin Cummings: New York.)

Krebs, C. J. (2002). Beyond population regulation and limitation. *Wildlife Research* **29**, 1-10.

Krebs, C. J. (2003). Two complementary paradigms for analysing population dynamics. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 110-126. (Cambridge University Press: Cambridge.)

Krebs, C. J., Boutin, S., Boonstra, R., Sinclair, A. R. E., Smith, J. N. M., Dale, M. R. T., Martin, K. and Turkington, R. (1995). Impact of food and predation on the snowshoe hare cycle. *Science* **269**, 1112-1115.

Krebs, C. J., Boutin, S. and Boonstra, R. (2001). 'Ecosystem Dynamics of the Boreal Forest.' (Oxford University Press: Oxford.)

Krebs, C. J., Sinclair, A. R. E. and Boutin, S. (1996). Vertebrate community dynamics in the boreal forest of north-western Canada. *In* 'Frontiers of Population Ecology.' *Eds.* R. B. Floyd, A. W. Sheppard, and P. J. De Barro pp 155-161. (CSIRO: Melbourne.)

Krebs, J. R. and Davies, N. B. (1993). 'An Introduction to Behavioural Ecology.' (Blackwell Science: Oxford.)

Kreeger, T. K., Arnemo, J. M. and Raath, J. P. (2002). 'Handbook of Wildlife Chemical Immobilization.' (Wildlife Pharmaceuticals: Fort Collins, Colorado.)

Lancia, R. A., Nichols, J. D. and Pollock, K. H. (1994). Estimating the number of animals in widlife populations. *In* 'Research and Management Techniques for Wildlife and Habitats.' *Ed.* T. A. Bookhout pp 215-253. (The Wildlife Society: Maryland, USA.)

Lande, R. (1988). Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* **75**, 601-607.

Langlands, J. P. (1987). Assessing the nutrient status of herbivores. *In* 'The Nutrition of Herbivores.' J. B. Hacker and J. H. Ternouth pp 363-390. (Academic Press: Sydney.)

Lawler, I. R., Foley, W. J., Eschler, B. M., Pass, D. M. and Handasyde, K. (1998). Intraspecific variation in *Eucalyptus* secondary metabolites determines food intake by folivorous marsupials. *Oecologia* **116**, 160-169.

le Mar, K., Southwell, C. J. and McArthur, C. (2001). Evaluation of line transect sampling to estimate nocturnal densities of macropods in open and closed habitats. *Wildlife Research* **28**, 9-16.

Leader-Williams, N. (1988). 'Reindeer on South Georgia: The Ecology of an Introduced Population.' (Cambridge University Press: Cambridge.)

Leopold, A. S. and Wolfe, T. O. (1970). Food habits of nesting wedge-tailed eagles, *Aquila audax*, in southeastern Australia. *CSIRO Wildlife Research* **15**, 1-17.

Leopold, A. (1943). Deer irruptions. *Wisconsin Conservation Bulletin* **8**, 3-11.

Leopold, A. (1949). 'A Sand County Almanac and Sketches Here and There.' (Oxford University Press: New York.)

Li, G. D., Helyar, K. R., Castleman, L. J., Norton, G. and Fisher, R. P. (1998). The implementation and limitations of using a falling plate meter to estimate pasture yield. *In* 'Growing a greener future - Proceedings of the 9th Australian Agronomy Conference.' Published at http://www.regional.org.au/au/asa/1998/3/046li.htm#P1_91 Accessed 2003, 2005 Edn. *Eds.* D. L. Michalk and J. E. Pratley

Linse, S. J., Mergen, D. E., Smith, J. L. and Trlica, M. J. (2001). Upland erosion under a simulated most damaging storm. *Journal of Range Management* **54**, 356-361.

Lintermans, M. and Cunningham, R. B. (1997). Road-kills of the eastern grey kangaroo (*Macropus giganteus*) in the Canberra area: A preliminary analysis. *In* 'Living With Eastern Grey Kangaroos in the ACT - Public Land: Third Report to the Minister for the Environment, Land and Planning – Appendix E.' ACT Kangaroo Advisory Committee pp 63-67. (Australian Capital Territory: Canberra.)

Loison, A., Festa-Bianchet, M., Gaillard, J. M., Jorgenson, J. T. and Jullien, J. M. (1999). Age-specific survival in five populations of ungulates: Evidence of senescence. *Ecology* **80**, 2539-2554.

Lotka, A. J. (1925). 'Elements of Physical Biology.' (Williams and Wilkins: Baltimore MD.)

Lundberg, P. (1988). Functional response of a small mammalian herbivore: the disc equation revisited. *Journal of Animal Ecology* **57**, 999-1006.

Lundberg, P. and Danell, K. (1990). Functional response of browsers: tree exploitation by moose. *Oikos* **58**, 378-384.

Lunney, D., Law, B. and Rummery, C. (1996). Contrast between the visible abundance of the brush-tailed rock-wallaby, *Petrogale penicillata*, and its rarity in fox and dog scats in the gorges east of Armidale, New South Wales. *Wildlife Research* **23**, 373-380.

Lunney, D., Triggs, B., Eby, P. and Ashby, E. (1990). Analysis of the scats of dogs, *Canis familiaris*, and foxes, *Vulpes vulpes*, (Canidae: Carnivora) in coastal forests near Bega, New South Wales. *Australian Wildlife Research* **17**, 61-68.

Maas, S. (1997). 'Population Dynamics and Control of Feral Goats in a Semi-arid Environment.' M. App. Sci. Thesis (University of Canberra: Canberra.)

Maas, S. (1998). Feral goats in Australia: Impacts and costs of control. *In* 'Proceedings of the 18th Vertebrate Pest Conference.' *Eds.* R. O. Baker and A. C. Crabb pp 100-106. (University of California, Davis, USA.)

Macoon, B., Sollenberger, L. E., Moore, J. E., Staples, C. R., Fike, J. H. and Portier, K. M. (2003). Comparison of three techniques for estimating the forage intake of lactating dairy cows on pasture. *Journal of Animal Science* **81**, 2357-2366.

Malthus, T. R. (1803). 'An Essay on the Principle of Population: A View of its Past and Present Effects on Human Happiness; with an Inquiry into Our Prospects Respecting the Future Removal or Mitigation of the Evils which It Occasions .' 2nd Edn. (much revised and expanded from the 1798 edition) (Web Publication: Library of Economics and Liberty http://www.econlib.org/library/Malthus/malPlong.html.)

Manly, B. F. J. (1992). 'The Design and Analysis of Research Studies.' (Cambridge University Press: Cambridge.)

t'Mannetje, L. (2000). Measuring biomass of grassland vegetation. *In* 'Field and Laboratory Methods for Grassland and Animal Production.' *Eds.* L. t'Mannetje and R. M. Jones pp 151-177. (CABI Publishing: London.)

t'Mannetje, L. and Ebersohn, J. P. (1980). Relations between sward characteristics and animal production. *Tropical Grasslands* **14**, 273-280.

t'Mannetje, L. and Jones, R. M. *Eds*. (2000). 'Field and Laboratory Methods for Grassland and Animal Production.' (CABI Publishing: London.)

Marchant, S. and Higgins, P. J. *Eds*. (1993). 'Handbook of Australian, New Zealand and Antarctic birds: Volume 2. Raptors to Lapwings.' (Oxford University Press: Melbourne.)

Marshal, J. P. and Boutin, S. (1999). Power analysis of wolf-moose functional responses. *Journal of Wildlife Management* **63**, 396-402.

Martensz, P. N. (1971). Observations of the food of the fox, *Vulpes vulpes* (L.), in an arid environment. *CSIRO Wildlife Research* **16**, 73-75.

May, R. M. (1973). 'Stability and Complexity in Model Ecosystems.' (Princeton University Press: Princeton, NJ.)

May, R. M. (1981). Models for two interacting populations. *In* 'Theoretical Ecology. Principles and Applications.' 2nd Edn. *Ed.* R. M. May pp 78-104. (Blackwell Science: Oxford.)

Mayes, R. W. and Dove, H. (2000). Measurement of dietary nutrient intake in free-ranging mammalian herbivores. *Nutrition Research Reviews* **13**, 107-138.

Mayes, R. W., Lamb, C. S. and Colgrove, P. M. (1986). The use of dosed and herbage *n*-alkanes as markers for the determination of herbage intake. *Journal of Agricultural Science* **107**, 161-170.

Maynard-Smith, J. and Slatkin, M. (1973). The stability of predator-prey systems. *Ecology* **54**, 384-391.

McCallum, H. I. (1995). Modelling wildlife-parasite interactions to help plan and interpret field studies. *Wildlife Research* **22**, 21-29.

McCallum, H. I. (1999). How to count kangaroos. *Australian Zoologist* **31**, 309-316.

McCallum, H. I. (2000). 'Population Parameters: Estimation for Ecological Models.' (Blackwell Science: London.)

McCarthy, M. A. (1996). Red kangaroo (*Macropus rufus*) dynamics: Effects of rainfall, density dependence, harvesting and environmental stochasticity. *Journal of Applied Ecology* **33**, 45-53.

McCullough, D. R. (1979). 'The George Reserve Deer Herd.' (University of Michigan Press: Ann Arbor.)

McCullough, D. R. (1997). Irruptive behaviour in ungulates. *In* 'The Science of Overabundance: Deer Ecology and Population Management.' *Eds.* W. J. McShea, H. B. Underwood, and J. H. Rappole pp 69-98. (Smithsonian Institution Press: Washington, USA.)

McCullough, D. R. and McCullough, Y. (2000). 'Kangaroos in Outback Australia: Comparative Ecology and Behaviour of Three Coexisting Species.' (Columbia University Press: New York.)

McDonald, C. K., Corfield, J. P., Hargreaves, J. N. G. and O'Toole, J. G. (1996). BOTANAL - a comprehensive sampling and computing procedure for estimating pasture yield and composition. 3. Field recording direct to computer. 'Tropical Agronomy Technical memorandum No. 79.' (Division of Tropical Crops and Pastures, CSIRO: St Lucia, Queensland.)

McDonald, R. C., Isbell, R. F., Speight, J. G., Walker, J. and Hopkins, M. S. (1984). 'Australian Soil and Land Survey: Field Handbook.' (Inkata Press: Melbourne.)

McLeod, S. R. (1996). 'The Foraging Behaviour of the Arid Zone Herbivores the Red Kangaroo (*Macropus rufus*) and the Sheep (*Ovis aries*) and its Role in Their Competitive Interaction, Population Dynamics and Life-history Strategies.' PhD Thesis (University of New South Wales: Sydney.)

McLeod, S. R. (1997). Is the concept of carrying capacity useful in variable environments? *Oikos* **79**, 529-542.

McNamara, J. M. and Houston, A. I. (1987). Starvation and predation as factors limiting population size. *Ecology* **68**, 1515-1519.

Mduma, S. A. R., Sinclair, A. R. E. and Hilborn, R. (1999). Food regulates the Serengeti wildebeest: A 40-year record. *Journal of Animal Ecology* **68**, 1101-1122.

Mech, L. D., Smith, D. W., Murphy, K. M. and MacNulty, D. R. (2001). Winter severity and wolf predation on a formerly wolf-free elk herd. *Journal of Wildlife Management* **65**, 998-1003.

Michell, P. (1982). Value of a rising-plate meter for estimating herbage mass of grazed perennial ryegrass - white clover swards. *Grass and Forage Science* **37**, 81-87.

Miller, G. R. (1979). Quantity and quality of the annual production of shrubs and flowers of *Calluna vulgaris* in northeast Scotland. *Journal of Ecology* **67**, 109-129.

Molsher, R. L., Gifford, E. J. and McIlroy, J. C. (2000). Temporal, spatial and individual variation in the diet of red foxes (*Vulpes vulpes*) in central New South Wales. *Wildlife Research* **27**, 593-601.

Moore, A. D., Donnelly, J. R. and Freer, M. (1997). Grazplan: decision support systems for Australian grazing enterprises. III. Pasture growth and soil moisture submodels, and the GrassGro DSS. *Agricultural Systems* **55**, 535-582.

Moore, B. D., Coulson, G. and Way, S. (2002). Habitat selection by adult female eastern grey kangaroos. *Wildlife Research* **29**, 439-445.

Moore, J. E. (1996). Practical approaches to estimating pasture intake. *In* 'Proceedings, Nutrient Cycling in Forage Systems.' *Eds.* R. E. Joost and C. A. Roberts pp 193-202. (University of Missouri: Columbia, Missouri.)

Morgan, R. A., Brown, J. S. and Thorson, J. M. (1997). The effect of spatial scale on the functional response of fox squirrels. *Ecology* **78**, 1087-1097.

Moss, G. L. and Croft, J. D. (1999). Body condition of the red kangaroo (*Macropus rufus*) in arid Australia: the effect of environmental condition, sex and reproduction. *Australian Journal of Ecology* **24**, 97-109.

Munn, A. J. and Dawson, T. J. (2001). Thermoregulation in juvenile red kangaroos (*Macropus rufus*) after pouch exit: higher metabolism and evaporative water requirements. *Physiological and Biochemical Zoology* **74**, 917-927.

Munn, A. J. and Dawson, T. J. (2003). Energy requirements of the red kangaroo (*Macropus rufus*): Impacts of age, growth and body size in a large desert-dwelling herbivore. *Journal of Comparative Physiology B - Biochemical Systemic and Environmental Physiology* **173**, 575-582.

Muranyi, M. (2000). 'Survey of Eastern Grey Kangroos (*Macropus giganteus*) at Googong Foreshores During Winter 1999.' Internal Report 2000/01 (Environment ACT: Canberra.)

Murdoch, W. (1973). The functional response of predators. *Journal of Applied Ecology* **10**, 335-342.

Murphy, S. R. and Lodge, G. M. (2002). Ground cover in temperate native perennial grass pastures. I. Comparison of four estimation methods. *Rangeland Journal* **24**, 288-300.

Murray, B. G. (1999). Can the population regulation controversy be buried and forgotten? *Oikos* **84**, 148-152.

Murray, D. L., Cary, J. R. and Keith, L. B. (1997). Interactive effects of sublethal nematodes and nutritional status on snowshoe hare vulnerability to predation. *Journal of Animal Ecology* **66**, 250-264.

Murrumbidgee Catchment Management Board (2003). 'Integrated Catchment Management Plan for the Murrumbidgee Catchment 2002.' Also known as '*Murrumbidgee Catchment Blueprint*' (New South Wales Department of Land and Water Conservation: Sydney.)

Nagy, K. A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* **57**, 111-128.

Nagy, K. A., Bradley, A. J. and Morris, K. D. (1987). Field metabolic rates, water fluxes and feeding rates of quokkas, *Setonix brachyurus*, and tammars, *Macropus eugenii*, in Western Australia. *Australian Journal of Zoology* **37**, 553-560.

Nagy, K. A., Girard, I. A. and Brown, T. K. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition* **19**, 247-277.

Nagy, K. A., Sanson, G. D. and Jacobsen, N. K. (1990). Comparative field energetics of two macropod marsupials and a ruminant. *Australian Wildlife Research* **17**, 591-599.

Nave, C. D., Coulson, G., Poiani, A., Shaw, G. and Renfree, M. B. (2002). Fertility control in the eastern grey kangaroo using levonorgestrel implants. *Journal of Wildlife Management* **66**, 470-477.

Neave, H. M. (1991). The ecological impacts of grazing by kangaroos. *National Parks Journal* **35**, 16-18.

Neave, H. M. and Tanton, M. T. (1989). The effects of grazing by kangaroos and rabbits on the vegetation and the habitat of other fauna in the Tidbinbilla Nature Reserve, Australian Capital Territory. *Australian Wildlife Research* **16**, 337-351.

Nelson, L. S. (1996). 'Survey of Eastern Grey Kangaroos (*Macropus giganteus*) on ACT Reserves and Rural Lands During Autumn 1996.' Wildlife Research Unit, ACT Parks and Conservation. Internal Report 96/3 (Wildlife Research Unit, ACT Government: Canberra.)

Newsome, A. E. (1975). An ecological comparison of the two arid zone kangaroos of Australia and their anomalous prospects since the introduction of ruminant stock to their environment. *Quarterly Review of Biology* **50**, 389-424.

Newsome, A. E., Catling, P. C., Cooke, B. D. and Smyth, R. (2001). Two ecological universes separated by the dingo barrier fence in semi-arid Australia: Interactions between landscapes, herbivory and carnivory, with and without dingoes. *Rangeland Journal* **23**, 71-98.

Newsome, A. E. and Coman, B. J. (1989). Canidae. *In* 'Fauna of Australia. Volume 1B. Mammalia.' *Eds.* D. W. Walton and B. J. Richardson pp 993-1005. (Australian Government Publishing Service: Canberra.)

Newsome, A. E., Pech, R. P., Banks, P. B., Dickman, C. R. and Smythe, R. (1997). 'Potential Impacts on Australian Native Fauna of Rabbit Calicivirus Disease.' (Environment Australia: Canberra.)

Nieland, K. A. (1970). Weight of dried marrow as indicator of fat in caribou femurs. *Journal of Wildlife Management* **34**, 904-907.

Nielsen, L. (1999). 'Chemical Immobilization of Wild and Exotic Animals.' (Iowa State University Press: Ames.)

Norbury, G. L., Coulson, G. M. and Walters, B. L. (1988). Aspects of the demography of the western grey kangaroo, *Macropus fuliginosus melanops*, in semiarid northwest Victoria. *Australian Wildlife Research* **1**, 257-266.

Noy-Meir, I. (1975). Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology* **63**, 459-481.

Noy-Meir, I. (1978). Stability in simple grazing models: effects of explicit functions. *Journal of Theoretical Biology* **71**, 347-380.

NRM (Department of Natural Resources and Mines) (1998). 'Enhanced Meteorological Datasets.' Published at http://www.nrm.qld.gov.au/silo Edn. (Department of Natural Resources and Mines: Queensland.)

NSW Department of Environment and Conservation (2003). Trial Commercial Harvest of Kangaroos in South-eastern NSW. http://www3.environment.nsw.gov.au/npws.nsf/Content/southeast_kangaroo_harvesting_trial Accessed May 2004 Edn.

NSW National Parks and Wildlife Service (2002). 'New South Wales Kangaroo Management Program 2002-2006.' (NSW National Parks and Wildlife Service: Sydney.)

O'Gara, B. W. and Harris, R. B. (1988). Age and condition of deer killed by predators and automobiles. *Journal of Wildlife Management* **52**, 316-320.

Oliver, A. J. (1986). 'Social Organisation and Dispersal in the Red Kangaroo.' PhD Thesis (Murdoch University: Perth.)

Owen, M. and Wyborn, D. (1979). 'Geology and Geochemistry of the Tantangara and Brindabella 1:100,000 Sheet Areas, New South Wales and Australian Capital Territory.' Bureau of Mineral Resources Bulletin 204 (Bureau of Mineral Resources: Australia.)

Owen-Smith, N. (1990). Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *Journal of Animal Ecology* **59**, 893-913.

Owen-Smith, N. (2002a). 'Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments.' (Cambridge University Press: Cambridge.)

Owen-Smith, N. (2002b). A metaphysiological modelling approach to stability in herbivore-vegetation systems. *Ecological Modelling* **149**, 153-178.

Patterson, B. R., MacDonald, B. A., Lock, B. A., Anderson, D. G. and Benjamin, L. K. (2002). Proximate factors limiting population growth of white-tailed deer in Nova Scotia. *Journal of Wildlife Management* **66**, 511-521.

Pearse, R. J. (1981). Notes on breeding, growth and longevity of the forester or eastern grey kangaroo, *Macropus giganteus* Shaw, in Tasmania. *Australian Wildlife Research* **8**, 229-235.

Pech, R. P. and Hood, G. M. (1998). Foxes, rabbits, alternative prey and rabbit calicivirus disease: consequences of a new biological control agent for an outbreaking species in Australia. *Journal of Applied Ecology* **35**, 434-453.

Pech, R. P., Hood, G. M., Singleton, G. R., Salmon, E., Forrester, R. I. and Brown, P. R. (1999). Models for predicting plagues of house mice (*Mus domesticus*) in Australia. *In* 'Ecologically-based rodent management.' *Eds.* G. R. Singleton, L. Hinds, H. Leirs, and Z. Zhang pp 81-112. (ACIAR: Canberra.)

Pech, R. P., Sinclair, A. R. E. and Newsome, A. E. (1995). Predation models for primary and secondary prey species. *Wildlife Research* **22**, 55-64.

Pech, R. P., Sinclair, A. R. E., Newsome, A. E. and Catling, P. C. (1992). Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. *Oecologia* **89**, 102-112.

Pharo, E. J. and Kirkpatrick, J. B. (1994). Vegetation of the alpine sand dunes at Lake Augusta, Tasmania. *Australian Journal of Ecology* **19**, 319-327.

Pierce, B. L., Baccus, J. T. and Pettengill, S. C. (2001). Estimating deer density from non-linear transects (abstract). *at* International Conference on Distance Sampling (http://dolphin.mcs.st-and.ac.uk/icods/: accessed June 2003.)

Poole, W. E. (1973). A study of breeding in grey kangaroos *Macropus giganteus* Shaw, and *M. fuliginosus* (Desmarest), in central New South Wales. *Australian Journal of Zoology* **21**, 183-212.

Poole, W. E. (1975). Reproduction in the two species of grey kangaroo, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest) II. Gestation, parturition and pouch life. *Australian Journal of Zoology* **23**, 333-353.

Poole, W. E. (1983). Breeding in the grey kangaroo, *Macropus giganteus*, from widespread locations in eastern Australia. *Australian Wildlife Research* **10** , 453-466.

Poole, W. E. (1995). Eastern grey kangaroo *Macropus giganteus*. *In* 'The Mammals of Australia.' *Ed.* R. Strahan pp 335-338. (Reed Books: New South Wales.)

Poole, W. E., Carpenter, S. M. and Wood, J. T. (1982). Growth of grey kangaroos and the reliability of age determination from body measurements. I. The eastern grey kangaroo, *Macropus giganteus*. *Australian Wildlife Research* **9**, 9-20.

Poole, W. E. and Catling, P. C. (1974). Reproduction in the two species of grey kangaroo, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest). I. Sexual maturity and oestrus. *Australian Journal of Zoology* **22**, 277-302.

Pople, A. R. (1996). 'Effect of Harvesting upon the Demography of Red Kangaroos in Western Queensland.' PhD Thesis (University of Queensland: Brisbane.)

Pople, A. R. (1999). Repeatability of aerial surveys. *Australian Zoologist* **31**, 280-284.

Pople, A. R., Cairns, S. C., Clancy, T. F., Grigg, G. C., Beard, L. A. and Southwell, C. J. (1998). An assessment of the accuracy of kangaroo surveys using fixed-wing aircraft. *Wildlife Research* **25**, 315-326.

Pople, A. R., Cairns, S. C. and Mencke, N. (2003). Monitoring kangaroo populations in southeastern New South Wales. Report prepared for the New South Wales National Parks and Wildlife Service

Pople, A. R., Grigg, G. C., Cairns, S. C., Beard, L. A. and Alexander, P. (2000). Trends in the number of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation? *Wildlife Research* **27**, 269-276.

Pople, T. and Grigg, G. (1999). Commercial Harvesting of Kangaroos in Australia. (Environment Australia: Web Publication http://www.deh.gov.au/biodiversity/trade-use/wild-harvest/kangaroo/harvesting/ Accessed 2005.)

Preisser, E. L., Bolnick, D. I. and Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* **86**, 501-509.

Priddel, D. (1987). The mobility and habitat utilisation of kangaroos. 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.' *Eds.* G. Caughley, N. Shepherd, and J. Short pp 100-118. (Cambridge University Press: Cambridge.)

Quin, D. E. (1989). Age structures, reproduction and mortality of the eastern grey kangaroos (*Macropus giganteus* Shaw) from Yan Yean, Victoria. *In* 'Kangaroos , Wallabies and Rat-Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. Hume pp 787-794. (Surrey Beatty: Sydney.)

Real, L. A. (1977). The kinetics of functional response. *The American Naturalist* **111**, 289-300.

Richardson, B. J. (1975). *r* and K selection in kangaroos. *Nature* **255**, 323-324.

Ricklefs, R. E. (1973). 'Ecology.' 3rd Edn. (W. H. Freeman: New York.)

Riney, T. (1955). Evaluating condition of free-ranging red deer (*Cervus elaphus*) with special reference to New Zealand. *New Zealand Journal of Science and Technology, B* **36**, 429-463.

Risbey, D. A., Calver, M. C., Short, J., Bradley, J. S. and Wright, I. W. (2000). The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research* **27**, 223-235.

Risbey, D. A., Calver, M. C. and Short, J. (1999). The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. I. Exploring potential impact using diet analysis. *Wildlife Research* **26**, 621-630.

Robertshaw, J. D. and Harden, R. H. (1986). The ecology of the dingo in north-eastern New South Wales. IV. Prey selection by dingoes and its effects on the major prey species the swamp wallaby, *Wallabia bicolor* (Desmarest). *Australian Wildlife Research* **13**, 141-163.

Robertshaw, J. D. and Harden, R. H. (1989). Predation in Macropodidae: a review. *In* 'Kangaroos, Wallabies and Rat-Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. Hume pp 735-753. (Surrey Beatty: Sydney.)

Robertson, G. G. (1986). The mortality of kangaroos in drought. *Australian Wildlife Research* **13**, 349-354.

Robertson, G. G. (1987a). Plant dynamics. *In* 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.' *Eds.* G. Caughley, N. Shepherd, and J. Short pp 50-68. (Cambridge University Press: Cambridge.)

Robertson, G. G. (1987b). Effect of drought and high summer rainfall on biomass and composition of grazed pastures in western New South Wales. *Australian Rangeland Journal* **9**, 79-85.

Robertson, G. G. (1988). Effect of rainfall on biomass growth and dieback of pastures in an arid grazing system. *Australian Journal of Ecology* **13**, 519-528.

Robertson, G. G., Short, J. and Wellard, G. (1987). The environment of the Australian sheep rangelands. *In* 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.' *Eds.* G. Caughley, N. Shepherd, and J. Short pp 14-34. (Cambridge University Press: Cambridge.)

Rosenzweig, M. L. and Macarthur, R. H. (1963). Graphical representation and stability conditions of predator-prey interactions. *American Naturalist* **97**, 209-223.

Roughgarden, J. (1997). Production functions for ecological populations: a survey with emphasis on spatially explicit models. *In* 'Spatial Ecology.' *Eds.* D. Tilman and P. Kareiva pp 296-317. (Princeton University Press: Princeton, NJ.)

Ruette, S., Stahl, P. and Albaret, M. (2003). Applying distance-sampling methods to spotlight counts of red foxes. *Journal of Applied Ecology* **40**, 32-43.

Russell, E. M. (1982). Patterns of parental care and parental investment in marsupials. *Biological Reviews* **57**, 423-486.

Sabelis, M. W. (1992). Predatory arthropods. *In* 'Natural Enemies: the Population Biology of Predators, Parasites and Diseases.' *Ed.* M. J. Crawley pp 225-264. (Blackwell Scientific Publications: Oxford.)

Saether, B.-E., Engen, S., Filli, F., Aanes, R., Schroder, W. and Andersen, R. (2002). Stochastic population dynamics of an introduced Swiss population of the ibex. *Ecology* **83**, 3457-3465.

Saunders, G., Coman, B., Kinnear, J. and Braysher, M. (1995). 'Managing Vertebrate Pests: Foxes.' (Bureau of Resource Sciences and Australian Nature Conservation Agency: Australian Government Publishing Service: Canberra.)

Savolainen, P., Leitner, T., Wilton, A. N., Matisoo-Smith, E. and Lundeberg, J. (2004). A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Science* **101**, 12387-12390.

Schumack, S. (1977). 'An Autobiography, or Tales and Legends of Canberra Pioneers.' *Eds.* J. E. Schumack and S. Schumack (ANU Press: Canberra.)

Seber, G. A. F. (1992). A review of estimating animal abundance II. *International Statistical Review* **60**, 129-166.

Sharp, A., Gibson, L., Norton, M., Ryan, B., Marks, A. and Semeraro, L. (2002). The breeding season diet of wedge-tailed eagles (*Aquila audax*) in western New South Wales and the influence of rabbit calicivirus disease. *Wildlife Research* **29**, 165-184.

Sharrow, S. H. and Motazedian, I. (1983). A comparison of three methods for estimating forage disappearance. *Journal of Range Management* **36**, 469-471.

Shepherd, N. C. (1981). Capture myopathy in the red kangaroo (*Macropus rufus*). *In* 'Wildlife Diseases of the Pacific Basin and Other Countries.' *Ed.* M. E. Fowler

Shepherd, N. C. (1981). Predation of red kangaroos, *Macropus rufus* by the dingo, *Canis familiaris dingo*, in north-western New South Wales. *Australian Wildlife Research* **8**, 255-262.

Shepherd, N. C. (1987). Condition and recruitment of kangaroos. *In* 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.' *Eds.* G. Caughley, N. C. Shepherd, and J. Short pp 135-158. (Cambridge University Press: Cambridge.)

Shepherd, N. C. and Caughley, G. (1987). Options for management of kangaroos. *In* 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.' *Eds.* G. Caughley, N. Shepherd, and J. Short pp 188-219. (Cambridge University Press: Cambridge.)

Shipley, L. A., Blomquist, S. and Danell, K. (1998). Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry, and morphology. *Canadian Journal of Zoology* **76**, 1722-1733.

Shipley, L. A. and Spalinger, D. E. (1992). Mechanics of browsing in dense food patches: effects of plant and animal morphology on intake rate. *Canadian Journal of Zoology* **70**, 1743-1752.

Short, J. (1985). The functional response of kangaroos, sheep and rabbits in an arid grazing system. *Journal of Applied Ecology* **22**, 435-447.

Short, J. (1986). The effect of pasture availability on food intake, species selection and grazing behaviour of kangaroos. *Journal of Applied Ecology* **23**, 559-571.

Short, J. (1987). Factors affecting food intake of rangelands herbivores. *In* 'Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia.' *Eds.* G. Caughley, N. Shepherd, and J. Short pp 84-98. (Cambridge University Press: Cambridge.)

Short, J. and Bayliss, P. (1985). Bias in aerial survey estimates of kangaroo density. *Journal of Applied Ecology* **22**, 415-422.

Short, J. and Hone, J. (1988). Calibrating aerial surveys of kangaroos by comparison with drive counts. *Australian Wildlife Research* **15**, 277-284.

Sibly, R. M. and Hone, J. (2003). Population growth rate and its determinants: an overview. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 11-40. (Cambridge University Press: Cambridge.)

Sibly, R. M., Hone, J. and Clutton-Brock, T. H. (2003). Introduction to wildlife population growth rates. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 1-10. (Cambridge University Press: Cambridge.)

Sibly, R. M., Newton, I. and Walker, C. H. (2000). Effects of dieldrin on population growth rates of sparrowhawks. *Journal of Applied Ecology* **37**, 540-546.

Sibly, R. M. and Smith, R. H. (1998). Identifying key factors using lambda-contribution analysis. *Journal of Animal Ecology* **67**, 17-24.

Sinclair, A. R. E. (1977). 'The African Buffalo: A Study of the Resource Limitation of Populations.' (University of Chicago Press: Chicago.)

Sinclair, A. R. E. (1989). Population regulation in animals. *in* 'Ecological Concepts.' *Ed.* J. M. Cherrett pp 197-241. (Blackwell Scientific: Oxford.)

Sinclair, A. R. E. (1996). Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. *In* 'Frontiers of Population Ecology.' *Eds.* R. B. Floyd, A. W. Sheppard, and P. J. De Barro pp 127-154. (CSIRO: Melbourne.)

Sinclair, A. R. E. and Arcese, P. (1995). Population consequences of predation-sensitive foraging - the Serengeti wildebeest. *Ecology* **76**, 882-891.

Sinclair, A. R. E., Dublin, H. and Borner, M. (1985). Population regulation of Serengeti wildebeest: a test of the food hypothesis. *Oecologia* **65**, 266-268.

Sinclair, A. R. E. and Krebs, C. J. (2003). Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 127-147. (Cambridge University Press: Cambridge.)

Sinclair, A. R. E., Mduma, S. and Brashares, J. S. (2003). Patterns of predation in a diverse predator-prey system. *Nature* **425**, 288-290.

Sinclair, A. R. E., Olsen, P. D. and Redhead, T. D. (1990). Can predators regulate small mammal populations? Evidence from house mouse outbreaks in Australia. *Oikos* **59**, 382-392.

Sinclair, A. R. E. and Pech, R. P. (1996). Density dependence, stochasticity, compensation and predator regulation. *Oikos* **75**, 164-173.

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D., Mahon, P. and Newsome, A. E. (1998). Predicting effects of predation on conservation of endangered prey. *Conservation Biology* **12**, 564-575.

Smith, R. L. (1974). 'Ecology and Field Biology.' (Harper and Row: New York.)

Snedecor, G. W. (1962). 'Statistical Methods.' (Iowa State University Press: Ames.)

Solomon, M. E. (1949). The natural control of animal populations. *Journal of Animal Ecology* **18**, 1-35.

Southwell, C. J. (1984a). Variability in grouping in the eastern grey kangaroo, *Macropus giganteus*. I. Group density and group size. *Australian Wildlife Research* **11**, 423-435.

Southwell, C. J. (1984b). Variability in grouping in the eastern grey kangaroo, *Macropus giganteus*. II. Dynamics of group formation. *Australian Wildlife Research* **11**, 437-449.

Southwell, C. J. (1987a). Activity pattern of the eastern gray-kangaroo *Macropus-giganteus*. *Mammalia* **51**, 211-224.

Southwell, C. J. (1987b). Macropod studies at Wallaby Creek. II. Density and distribution of macropod species in relation to environmental variables. *Australian Wildlife Research* **14**, 15-33.

Southwell, C. J. (1989). Techniques for monitoring the abundance of kangaroo and wallaby populations. *In* 'Kangaroos, Wallabies and Rat-Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. Hume pp 659-693. (Surrey Beatty: Sydney.)

Southwell, C. J. (1994). Evaluation of walked line transect counts for estimating macropod density. *Journal of Wildlife Management* **58**, 348-356.

Southwell, C. J., Cairns, S. C., Palmer, R., Delaney, R. and Broers, R. (1997). Abundance of large macropods in the eastern highlands of Australia. *Wildlife Society Bulletin* **25**, 125-132.

Southwell, C. J., Fletcher, M., McRae, P., Porter, B. and Broers, R. (1995a). Abundance and harvest rate of the Whiptail Wallaby in southeastern Queensland, Australia. *Wildlife Society Bulletin* **23**, 726-732.

Southwell, C. J. and Fletcher, M. (1990). The use of roads and tracks as transect routes for surveying the abundance of whiptail wallabies, *Macropus parryi* (Marsupialia: Macropodidae). *Australian Mammalogy* **13**, 223-226.

Southwell, C. J. and Sheppard, N. (2000). Assessing harvested populations of the euro (*Macropus robustus erebescens*) in the Barrier Ranges of western New South Wales. *Australian Mammalogy* **21**, 165-171.

Southwell, C. J., Weaver, K. E., Cairns, S. C., Pople, A. R., Gordon, A. N., Sheppard, N. W. and Broers, R. (1995b). Abundance of macropods in north-eastern New South Wales, and the logistics of broad-scale ground surveys. *Wildlife Research* **22**, 757-766.

Southwell, C. J. and Weaver, K. (1993). Evaluation of analytical procedures for density estimation from line-transect data: Data grouping, data truncation and the unit of analysis. *Australian Wildlife Research* **20**, 433-44.

Spalinger, D. E., Hanley, T. A. and Robbins, C. T. (1988). Analysis of the functional response in foraging in the sitka black-tailed deer. *Ecology* **69**, 1166-1175.

Spalinger, D. E. and Hobbs, N. T. (1992). Mechanisms of foraging in mammalian herbviores: new models of functional response. *The American Naturalist* **140**, 325-348.

Speare, R., Donovan, J. A., Thomas, A. D. and Speare, P. J. (1989). Diseases of free-ranging Macropodidae. *In* 'Kangaroos, Wallabies and Rat Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. D. Hume pp 705-734. (Surrey Beatty: Sydney.)

StatSoft Inc. (1995). 'Statistica for Windows Vol. 1-5.' (StatSoft Inc.: Tulsa, OK.)

StatSoft Inc. (2004). STATISTICA (data analysis software system), version 6. (StatSoft Inc.: www.statsoft.com.)

Stein, A., Irvine, R. J., Ropstad, E., Halvorsen, O., Langvatn, R. and Albon, S. D. (2002). The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. *Journal of Animal Ecology* **71**, 937-945.

Stenseth, N. C. and Mysterud, A. (2003). A different approach to modeling: book review. *Science* **299**, 518.

Stewart, K. M., Bowyer, R. T., Dick, B. L., Johnson, B. K. and Kie, J. G. (2005). Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia* **143**, 85-93.

Stillman, R. A., Goss-Custard, J. D., West, A. D., Durell, S., Caldow, R. W. G., McGrorty, S. and Clarke, R. T. (2000). Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *Journal of Applied Ecology* **37**, 564-588.

Stillman, R. A., Goss-Custard, J. D., West, A. D., Durell, S., McGrorty, S., Caldow, R. W. G., Norris, K. J., Johnstone, I. G., Ens, B. J., Van der Meer, J. and Triplet, P. (2001). Predicting shorebird mortality and population size under different regimes of shellfishery management. *Journal of Applied Ecology* **38**, 857-868.

Stillman, R. A., West, A. D., Goss-Custard, J. D., Caldow, R. W. G., McGrorty, S., Durell, S., Yates, M. G., Atkinson, P. W., Clark, N. A., Bell, M. C., Dare, P. J. and Mander, M. (2003). An individual behaviour-based model can predict shorebird mortality using routinely collected shellfishery data. *Journal of Applied Ecology* **40**, 1090-1101.

Stuart-Dick, R. I. (1987). 'Parental Investment and Rearing Schedules in the Eastern Grey Kangaroo.' PhD. Thesis (University of New England: Armidale.)

Stuart-Dick, R. I. and Higginbottom, K. B. (1989). Strategies of parental investment in Macropodoids. *In* 'Kangaroos, Wallabies and Rat Kangaroos.' *Eds.* G. C. Grigg, P. J. Jarman, and I. D. Hume pp 571-592. (Surrey Beatty: Sydney.)

Sutherland, W. J. and Norris, K. (2003). Behavioural models of population growth rates: implications for conservation and prediction. *In* 'Wildlife Population Growth Rates.' *Eds.* R. M. Sibly, J. Hone, and T. H. Clutton-Brock pp 225-248. (Cambridge University Press: Cambridge.)

Suttie, J. M. (1983). The relationship between kidney fat index and marrow fat percentage as indicators of condition in red deer stags (*Cervus elaphus*). *Journal of Zoology* **201**, 563-565.

Tanner, Z. and Hocking, G. (2001). 'Status and Management of the Forester Kangaroo in Tasmania, 2000.' (Department of Primary Industries, Tasmania: Hobart.)

Taylor, I. (1994). 'Barn Owls. Predator-Prey Relationships and Conservation.' (Cambridge University Press: Cambridge.)

Taylor, R. J. (1980). Distribution of feeding activity of the eastern grey kangaroo, *Macropus giganteus*, in coastal lowland of south-east Queensland. *Australian Wildlife Research* **7**, 317-325.

Taylor, R. J. (1983). The diet of the eastern grey kangaroo and wallaroo in areas of improved and native pasture in the New England Tablelands. *Australian Wildlife Research* **10** , 203-212.

Thomas, L., Laake, J. L., Derry, J. F., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Strindberg, S., Hedley, S. L., Burt, M. L., Marques, F. F. C., Pollard, J. H. and Fewster, R. M. (1998). 'Distance 3.5.' (Research Unit for Wildlife Population Assessment, University of St Andrews: UK.)

Thomson, P. C. (1992). The behavioral ecology of dingoes in north-western Australia. 3. Hunting and feeding behavior, and diet. *Wildlife Research* **19**, 531-541.

Thornley, J. H. M. and Johnson, I. R. (1990). 'Plant and Crop Modelling: a Mathematical Approach to Plant and Crop Physiology.' (Clarendon Press: Oxford.)

Torbit, S. C., Carpenter, L. H., Bartmann, R. M., Alldredge, A. W. and White, G. C. (1988). Calibration of carcass fat indices in wintering mule deer. *Journal of Wildlife Management* **52**, 582-588.

Tothill, J. C., Hargreaves, J. N. G., Jones, R. M. and McDonald, C. K. (1992). BOTANAL - a comprehensive sampling and computing procedure for estimating pasture yield and composition. 1. Field sampling. Tropical Agronomy Technical Memorandum No. 78 (Division of Tropical Crops and Pastures, CSIRO: St Lucia, Queensland.)

Trexler, J. C., McCulloch, C. E. and Travis, J. (1988). How can the functional response best be determined? *Oecologia* **76**, 206-214.

Tribe, A. and Spielman, D. (1996). Restraint and handling of captive wildlife. *ANZCCART News* **9**, 1-8.

Turchin, P. (1999). Population regulation: a synthetic view. *Oikos* **84**, 153-159.

Turchin, P. and Hanski, I. (1997). An empirically based model for latitudinal gradient in vole population dynamics. *American Naturalist* **149**, 842-874.

Tyndale-Biscoe, C. H. and Janssens, P. A. (1988). 'The Developing Marsupial: Models for Biomedical Research.' (Springer Verlag: Berlin.)

Ungar, E. D. and Noy-Meir, I. (1988). Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. *Journal of Applied Ecology* **25**, 1045-1062.

Van Ballenberghe V. and Ballard W. B. (1994). Limitation and regulation of moose populations: the role of predation. *Canadian Journal of Zoology* **72**, 2071-2077.

van Lenteren, J. D. and Bakker, K. (1976). Functional responses in invertebrates. *Netherlands Journal of Zoology* **26**, 567-572.

Vere, D. T., Jones, R. E. and Campbell, M. H. (2001). The economics of temperate pasture systems on the central and southern tablelands of New South Wales. *Rangeland Journal* **23**, 159-172.

Verme, L. J. and Holland, J. C. (1973). Reagent-dry assay of marrow fat in white-tailed deer. *Journal of Wildlife Management* **37**, 103-105.

Viggers, K. L. and Hearn, J. P. (2005). The kangaroo conundrum: home range studies and implications for land management. *Journal of Applied Ecology* **42**, 99-107.

Vivas, H. J. and Saether, B. E. (1987). Interactions between a generalist herbivore, the moose *Alces alces*, and its food resources - an experimental study of winter foraging behavior in relation to browse availability. *Journal of Animal Ecology* **56**, 509-520.

Volterra, V. (1926). 'Variations and fluctuations of the number of individuals in animal species living together.' *Reprinted in* R. N. Chapman (1931) *Animal Ecology* (McGraw Hill: New York.)

Vucetich, J. A. and Waite, T. A. (2003). Spatial patterns of demography and genetic processes across the species range: Null hypotheses for landscape conservation genetics. *Conservation Genetics* **4**, 639-645.

Waddington, J. and Cooke, D. A. (1971). The influence of sample size and number on the precision of estimates of herbage production and consumption in grazing experiments. *Journal of the British Grassland Society* **26**, 95-101.

Wagener, R. E., Hein, M. A., Shepherd, J. B. and Ely, R. E. (1950). A comparison of cage and mower strip methods with grazing results in determining production of dairy pastures. *Agronomy Journal* **42**, 487-491.

Waite, R. B. (1994). The application of visual estimation procedures for monitoring pasture yield and composition in exclosures and small plots. *Tropical Grasslands* **28**, 38-42.

Waite, R. B. and Kerr, J. D. (1996). Measuring yields of green leaf blade in pastures by visual estimation techniques. *Tropical Grasslands* **30**, 314-318.

Wallis, I. R. and Foley, W. J. (2003). Validation of near-infrared reflectance spectroscopy to estimate the potential intake of *Eucalyptus* foliage by folivorous marsupials. *Australian Journal of Zoology* **51**, 95-98.

Walter, M. (2002). 'The Population Ecology of Wild Horses in the Australian Alps.' PhD Thesis (University of Canberra: Canberra.)

Webb, C. L. (2001). 'Macropod Browsing Damage: Impacts in Namadgi National Park and Techniques for its Control.' Hons. Thesis (Australian National University: Canberra.)

Werner, E. E., Gilliam, J. F., Hall, D. J. and Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**, 1540-1548.

White, P. J. and Garrott R. A. (1999). Population dynamics of kit foxes. *Canadian Journal of Zoology* **77**, 486-493.

Wilby, A., Shachak, M. and Boeken, B. (2001). Integration of ecosystem engineering and trophic effects of herbivores. *Oikos* **92**, 436-444.

Williams, B. K., Nichols, J. D. and Conroy, M. J. (2001). 'Analysis and Management of Animal Populations: Modeling, Estimation and Decision Making.' (Elsevier: San Diego.)

Williams, K., Parer, I., Coman, B., Burley, J. and Braysher, M. (1995). 'Managing Vertebrate Pests: Rabbits.' (Australian Government Publishing Service: Canberra.)

Wilman, D., Mtengeti, E. J. and Moseley, G. (1996). Physical structure of twelve forage species in relation to rate of intake by sheep. *Journal of Agricultural Science* **126**, 277-285.

Wilson, B. A. and Woldridge, J. (2000). Assessment of the diet of the fox (*Vulpes vulpes)* in habitats of the eastern Otway Ranges, Victoria. *Australian Mammalogy* **21**, 201-211.

Wilson, G. R. (1975). Age structures of populations of kangaroos (Macropodidae) taken by professional shooters in New South Wales. *Australian Wildlife Research* **2**, 1-9.

Wilson, H., Sinclair, A. G., Hovell, F. D., Mayes, R. W. and Edwards, S. A. (1999). Validation of the *n*-alkane techniques for measuring herbage intake in sows. *Proceedings of the British Society of Animal Science* **171**.

Wilson, J. R. and Kennedy, P. M. (1996). Plant and animal constraints to voluntary feed intake associated with fibre characteristics and particle breakdown and passage in ruminants. *Australian Journal of Agricultural Research* **47**, 199-225.

Wilson, K., Grenfell, B. T., Pilkington, J. G., Boyd, H. E. G. and Gulland, F. M. D. (2004). Parasites and their impact. *In* 'Soay Sheep: Dynamics and Selection in an Island Population.' *Eds.* T. Clutton-Brock and J. Pemberton (Cambridge University Press: Cambridge.)

Witte, I. (2005). Kangaroos - misunderstood and maligned reproductive miracle workers. *In* 'Kangaroos: Myths and Realities.' 3rd Edn. *Eds.* M. Wilson and D. B. Croft pp 188-207. (Australian Wildlife Protection Council Inc.: Sydney.)

Woodland, C. (1988). Wedge-tailed eagles co-operatively hunting a kangaroo. *Canberra Bird Notes* **13** , 127.

Woolnough, A. P. and Johnson, C. N. (2000). Assessment of the potential for competition between two sympatric herbivores--the northern hairy-nosed wombat, *Lasiorhinus krefftii*, and the eastern grey kangaroo, *Macropus giganteus*. *Wildlife Research* **27**, 301-308.

APPENDIX 1: Names of people who assisted with the project

First	Surname
Tony	Agostino
John	Alcock
Stephen	Alegria
Kate	Alexander
Will	Andrew
Dean	Ansell
Odile	Arman
Frank	Armstrong
Karen	Aus
Rupen	Avakian
Kathryn	Barker
Sean	Barker
Julian	Barnard
James	Barritt
Lance	Bates
Jo	Bauer
Emma	Beatty
Matt	Beitzel
Tony	Bell
Alan	Bendell
Emma	Bendetti
Neil	Bensley
Nina	Bishop
Graham	Blinksell
Richard	Bomford
John	Bray
Tom	Breen
Andrew	Britt
Melinda	Brouwer
Adrian	Brown
Joe	Brown
Luke	Bulkley
John	Bunn
Dominic	Burton
Les	Caldrmoski
Peter	Caley
Peter	Callan
Amanda	Carey
Matt	Carey
Nathan	Caroll
Rachael	Carter
Emma	Clunas
Andrew	Cottrell
Michelle	Cozadinos
Liam	Curtis
Annie	Davies
Luke	Davis
Adrian	Dickson
Sean	Doody
Mark	Dunford
Alan	Duus
Nadene	Edwards
Clare	Ellis
Lindsay	Emmett
Murray	Evans
Carmen	Evans
Sharon	Farley
Anna	Farnham
Scott	Farquhar
Ian	Faulkner
Justin	Ferris
Amy	Fletcher
Bryden	Fletcher
Esteban	Fuentes
Peter	Galvin
Anne	Gibson
Maree	Gilbert
Madeleine	Gisz
Simon	Godschalx
Edmund	Golabek
Tara	Goodsell
Janine	Goodwin
Kristy	Gould
Dennis	Gray
Jeff	Green
Bernd	Gruber
Andrew	Halley
Joe	Halloran
Peter	Hann
Michael	Hanski
Lee	Harris
Graham	Heanes
Aminya	Hepp
Paul	Higginbotham
Tony	Corrigan
Lyn	Hinds
Graeme	Hirth
Marion	Hoehn
Jim	Hone
?	Hone
Fraser	Howard
Carmen	Huckle
Daniel	Iglesias
Mark	Jekabensens
Edgar	Jimenz
Peter	Kallio
Margaret	Kalms
Lenne	Kate
Fiona	Keen
Ian	Kenny
Anitra	Kenny
Robert	Kwiatkowski
Singh	Kylie
Finnian	Lattimore
John	Lawler
Brendan	Linton
Isobel	Logan
Michael	Maconachie
Andrew	Maconagie
Lyn	Macoustra
Anton	Maher
Bill	Martin
Nicki	Mazur
Megan	McCann
Tessa	McDonald
Trish	McDonald
Lisa	McIntosh
Peter	McKay
Luke	McLachlan
Brett	McNamara
Angelina	McRae
Dave	McRae
Ali	Merghani
Mark	Mickleborough
Kerry	Moir
Bernard	Morris

Appendix 1 (cont): Names of people who assisted with the project

First	Surname	First	Surname
Monica	Muranyi	Daniel	Todd
Robert	Norton	Graham	Todkill
Bernadette	O'Leary	Simon	Tozer
Toni	Oliver	Michael	Traynor
Ollie	Orgill	Peter	Turner
Peter	Ormay	Chrisafina	Valakas
Lois	Padgham	Nikki	Van beurden
Ashe	Pepper	Karen	Viggers
Teagan	Perry	Cristian	Villalon
Lisa	Petheram	Stephen	Virtue
Geoff	Price	Michelle	Walter
Elysha	Pritchard	Jeremy	Watson
Michelle	Pryke	Karen	Watson
Baden	Ranger	Nick	Webb
David	Rhind	Geoff	Webb
Greg	Ritchie	Steve	Welch
Mark	Rodden	Mel	White
Renge	Roser	Bob	White
Darren	Roso	Dave	Whitfield
Ian	Ross	Belinda	Wicks
Raylea	Rudov	Daniel	Williams
Andy	Russell	David	Wong
Katie	Ryan	Grant	Woodbridge
John	Savy	Bill	Woodruff
David	Scott	Kara	Woodward
Angela	Seymour	Lana	Woolard
Margot	Sharp	Damien	Woolcombe
Mark	Simon	Lara	Woolcombe
Graham	Simpson	Debbie	Worner
Gemma	Skelly	Alex	Wotzko
Keith	Smith	Geoff	Young
Tlaylock	Strickland	Phil	Zammit
Darren	Summerrell	Oscar	Zamora
David	Swan	Christy	##
Peter	Synnott	David	##
Steve	Taylor	Heather	##
Jason	Thiem	Megan	##

= CIT or UC student assisting on drive count; no surname given.

APPENDIX 2: Pasture sampling design

App 2 – 2.1 Number of pasture samples required

To determine an appropriate sampling effort for each visit to each study site, I used 570 herbage mass estimates from Googong, supplied by Dr Karen Viggers (RSBS, ANU). Based on the relationship in her data between sample size and CV (Figure A2.1), I established 150 sampling locations at each site because the decline in CV per 50 additional cages becomes marginal above this number.

I also used the formula given by Cayley and Bird (1996, p. 6) to estimate the number of samples required to achieve given allowable errors, which is derived from Snedecor (1962, 501), based on the relationship shown in Equation A2.1, for the 95% confidence level;

$$L = 1.96 * s / \sqrt{n} \qquad \text{Eqn A2.1}$$

Where L = allowable error; s = standard deviation; and n = number of samples.

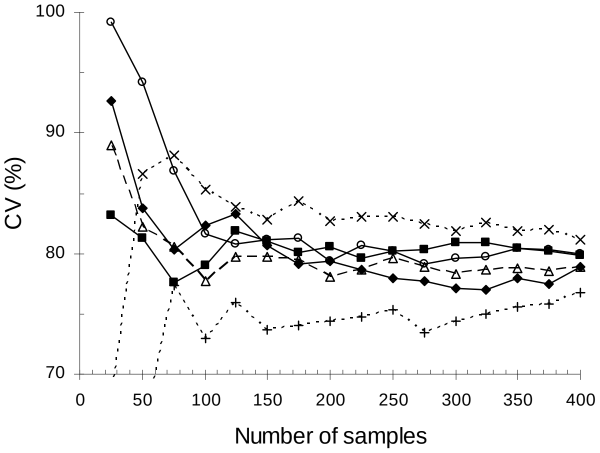


Figure A2.1: Effect of sample size on CV of estimates of herbage mass, illustrating six different series of random draws from 570 measurements. My Ref: 7.3.5 Pilot survey & Setting Up/GF_KVbms_01_3_7.xls

For this pasture whose herbage mass was 2100 kg ha^{-1}, 150 samples would generate an error (L) of plus or minus 270 kg ha^{-1}. To reduce the error to 100 kg ha^{-1} would require an impossible 1,112 samples per site-visit. To reduce it to 200 kg ha^{-1} would require 278 samples, which could have been achieved only by reducing the number of study sites. Cayley and Bird (1996) indicate that the CV of yield of grazed pasture is greater at higher yield which they attribute to greater selectivity by the grazing animals. The herbage mass in this case was relatively high so the error associated with 150 samples was considered likely to be acceptable also for eaten down winter pastures, if the experience of Cayley and Bird (1996) is applicable to these sites.

App 2 – 2.2 Measurement frequency

Quarterly assessment has been widely practiced in comparable studies (Caughley *et al*. 1987; Maas 1997, 1998; Choquenot 1998). However I conducted more frequent pasture assessment due to the more seasonal environment of my study areas. Bimonthly intervals were selected to align the simultaneous estimates of nocturnal kangaroo density with periods of no moon. I constructed a crude model of pasture biomass based on the growth index of Fitzpatrick and Nix (1970) using Canberra monthly weather values from 1991 to 1999. The model indicated a possibility of a short-lived peak of biomass in summer and rapid change in early winter. Quarterly sampling frequency might miss the summer peak but bimonthly sampling would record it in at least one sample on every occasion, so that frequency was chosen. Bimonthly sampling was carried out mainly in the odd-numbered months, from September 2001 to July 2003, but the work overflowed into the months either side.

App 2 – 2.3 Stratified-random survey design

The sites were classified on the basis of vegetation structure, as either ‘woody’ (woodland, open forest, shrubland, or closed shrubland) or ‘open’ (open woodland, sparse shrubland, and isolated trees or shrubs) categories, as defined by McDonald *et al*. (1984). The open areas were further categorised by (a) slope (steep, ≥ 6º; gentle, 3º - 6º; flat ≤ 3º); and (b) aspect (northerly or southerly). In mapping each category, a minimum unit of 3 ha was recognised (i.e. any category could contain patches of a different category providing each patch was smaller than 3 ha).

Maps of the vegetation, slope and aspect were combined using a Geographical Information System (GIS) program (ArcView 3.2, ESRI 1999) resulting in six possible strata (woody, flat, steep northerly, gentle northerly, steep southerly, gentle southerly) which is the maximum recommended (Krebs 1999). However (a) the woody stratum was excluded from sampling, and (b) not all strata were present at every site. The woody stratum was mainly a feature of the Tidbinbilla site. It was used by eastern grey kangaroos for shelter, (although only the outer margin of closed shrubland was used much) but preliminary results indicated no sign of feeding activity, and the grasses there were mostly mature tussocks producing little growth. Also the deep leaf litter in some woodland and forest areas made assessment of ‘pasture’ growth impractical, and the dense nature of the closed shrubland made the work in this stratum more time consuming. For these reasons, pasture sampling was restricted to the other five strata.

At each site, two or three examples of each stratum (‘polygons’) were selected for sampling. These were ones judged likely to remain accessible in all weather and unlikely to be interfered with by people. A pilot survey was carried out in these polygons (100 quadrats each) in the winter of 2001 to estimate the standard deviation of pasture yield in each stratum. This was to enable the total sampling effort to be apportioned between strata so as to minimise the standard error of the mean, using the method given by Manly (1992, pp 30 – 31).

App 2 – 2.4 Positioning the pasture sampling locations

The number of pasture sampling locations for each stratum at each site, was divided between the selected polygons representative of the stratum, in proportion to the polygon areas. The GIS program was used to map that number of sampling locations onto randomly chosen grid references within each polygon. The map coordinates of these were downloaded from the GIS program to a global positioning system receiver (GPS), that was used to navigate to each location in the field, which was then marked with a labelled steel post. Figure A2.3 illustrates the arrangement of sampling points resulting from this procedure for part of one site.

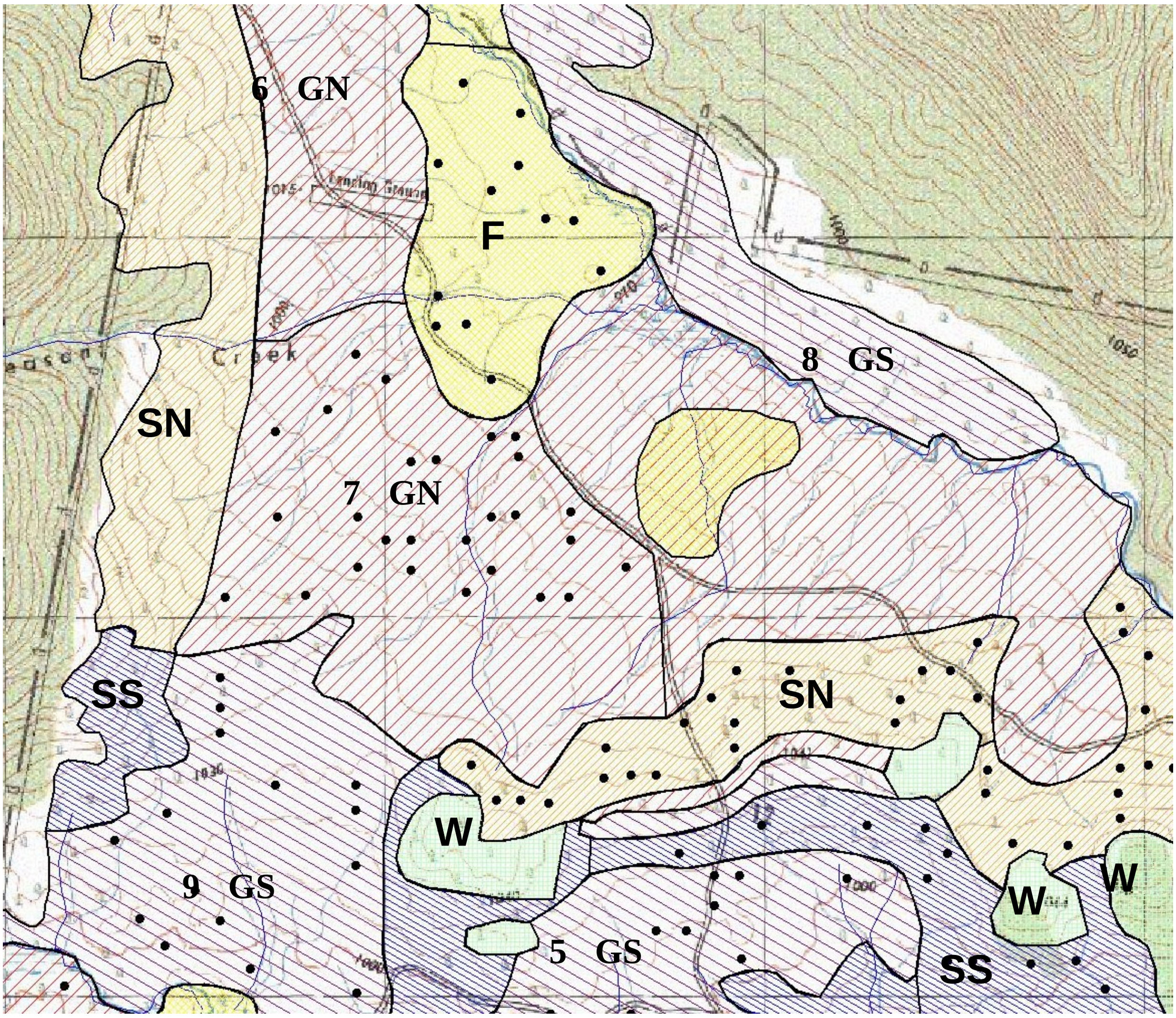


Figure A2.3: Part of the Gudgenby study site illustrating the result of the stratified random sampling design process. The gridlines are at 1 km spacing. Hatching and shading distinguish six strata, which are also labeled (W = woody, F = flat, SS = steep southerly, GS = gentle southerly, SN = steep northerly, GN = gentle northerly). Dots mark pasture sampling locations. The steep, forested valley sides outside the study area are also evident to the west (left) and north east (upper right).

APPENDIX 3: Operational Plan for Gudgenby drive count

INSTRUCTIONS FOR COUNTERS - KANGAROO DRIVE COUNT 10 April 2002

IMPORTANT

Counting

- Count only kangaroos that **CROSS** the imaginary line between you and the person to your **LEFT**. Fold this page into a small pad as indicated on the back. Record where marked (a) your name and the other details; (b)kangaroos crossing the line to pass behind you out of the area being counted; and (c) kangaroos passing in the opposite direction, ie back into the counted area. ***Please complete all three portions including any zero counts and hand your completed form to your team leader.***
- Clarify with your team leader which direction your team is 'facing', ie which person is to your left. (In some cases this is tricky.) Start a new form at anytime you perceive a significant change, eg if you change teams or locations. Team Leaders have spare forms.
- We are counting eastern grey kangaroos (EGK). The few red-necked wallabies (RNW) should be recorded separately. Also note foxes and dingoes if you see any.
- Start counting as soon as you are in position and can see the next counter to your left.

Stationary teams

The marked and numbered positions for each person are sometimes far apart. Ensure you will be visible to the person on the right as well as being able to see the person to your left. Stop counting when you are passed by the line of mobile counters (see separate note and diagram). When departing please take the marker tapes and labels from your position.

Mobile teams- Distance between you and your neighbours and how fast to walk.

The area is generally open with a few small patches of woodland. Stay close enough to your neighbours to see them down to their knees, but minimise the extent to which kangaroos are driven ahead of the line by maintaining sufficient space to let kangaroos pass, ie in open areas, at least 50m, preferably 200m. When the gap is closing, double up with the person next to you (see over) to allow kangaroos through. After doubling up, remember, only one of you should continue recording. Don't both count!! Some teams will start with people doubled up to allow for the less open terrain ahead, or a wider counting area. Your line will be told to stop, slow or speed up as your team leader coordinates with others by radio. Those on the ends of the line have to interact with the stationary teams as described in the note 'How and why people in stationary teams stop counting when passed by the mobile team'.

Operational Structure And Summary Of Action

There are four SECTORS. Sectors comprise multiple TEAMS. Sector Bosses and Team Leaders wear the tops of yellow bushfire overalls. Know who your team leader is. There are separate action plans and maps for each sector and team.

Mesh Cages

There are 150 white mesh exclosure cages in the area. It is best to leave them as they are.

NAME: ____________

Team: ____________

Pos'n No. (if stationary) : ____

Count Tally:

YOUR TOTAL: ____________

- - - - - - - - - - - - - - SECOND FOLD IN HALF AGAIN - - - - -

- - - - - - - THIRD FOLD IN HALF AGAIN -

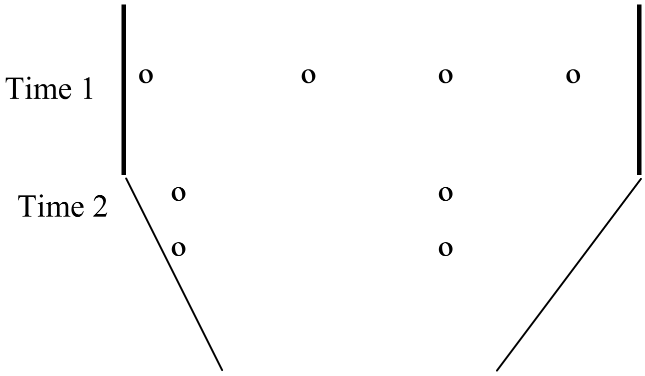
REVERSE COUNT

(ie animals travelling back into the area being counted)

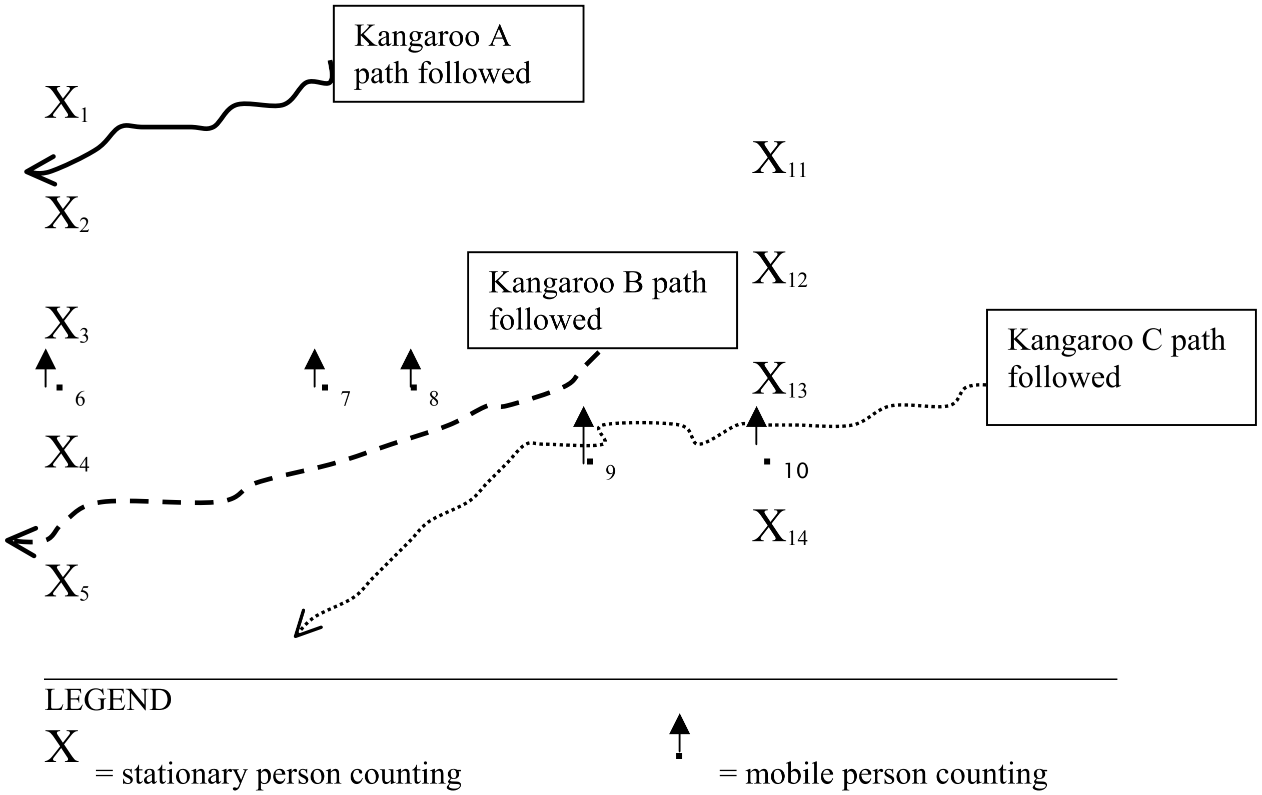
TOTAL: ____________

- - - - - - - FIRST FOLD IN HALF -

'Doubling-up' to let animals pass where counted area narrows. Circles = people



WHY PEOPLE IN STATIONARY TEAMS STOP COUNTING WHEN PASSED BY THE MOBILE TEAM?

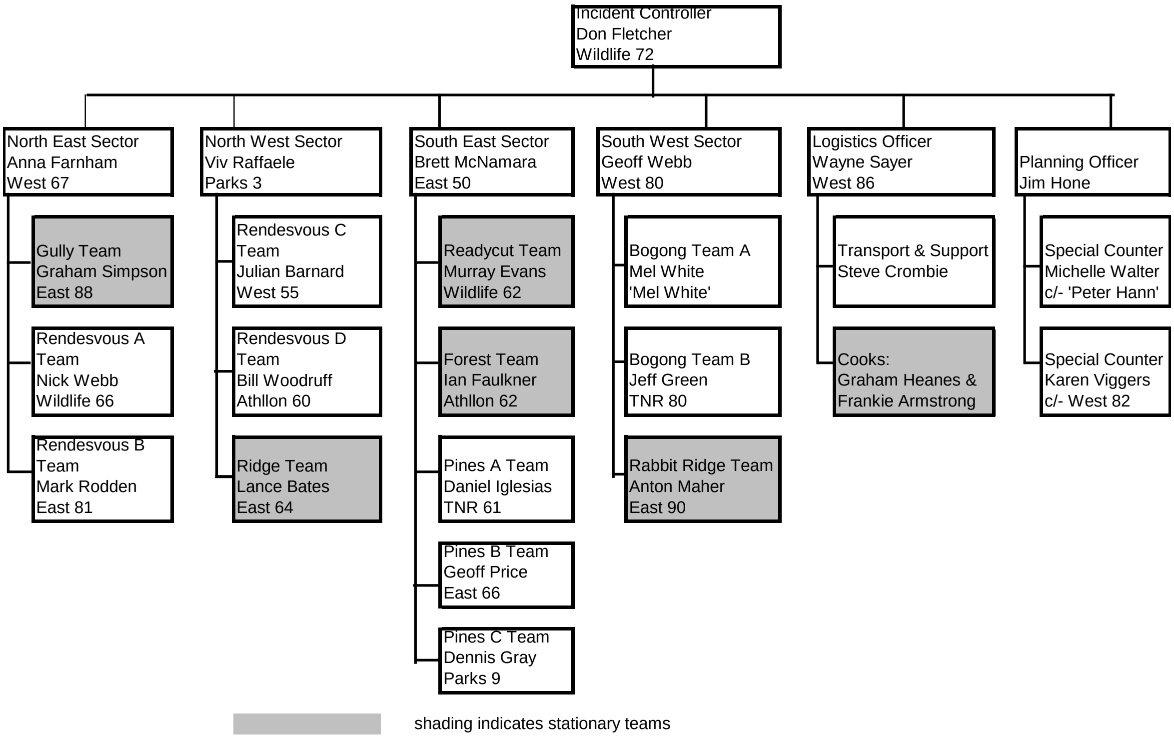


The people at the ends of the line of mobile counters (positions 6 and 10) must walk along the line of stationary counters from person to person, and remind them to stop counting now they have been reached by the mobile line. In the diagram, Kangaroo A is counted by the person at position 2. Kangaroo B is counted by the person at position 9 but the person at position 5 has stopped recording otherwise Kangaroo B would be counted twice. (In some cases team leaders will move the people who have been passed into other locations, eg into the mobile line.)

On the left end the mobile person counts only the gap between themselves and the next person ahead of them. On the right, people in the stationary positions count to the person at the end of the mobile line once it has passed their neighbour to the left (eg position13 counts the gap to position 10) but they stop counting once they are passed, eg position 14 has stopped counting.

Kangaroo C is recorded as a reverse count by the person at position 10 and a normal count by the person at position 9.

ORGANISATION CHART FOR KANGAROO COUNT AT GUDGENBY ON 10 APRIL 2002



REQUIREMENTS OF SECTOR BOSSES AND TEAM LEADERS

Team Leaders direct counters (span of command ≤6 mobile or 10 stationary) and are responsible for their comfort and safety and for the data collected. They operate on foot or from a vehicle and are responsible for seeing the whole team gets on and off the counting area. Assistance with transport will be available.

Sector Bosses have to oversight progress by teams on their sector, (span of command ≤ 5) to maintain steady progress and prevent counting gaps between teams, and solve problems that arise. They should be vehicle based.

Preparation beforehand

1. Wear the top portion of bushfire overalls (or more). (Also have a hat, rain parka etc.)
2. Bring a portable radio with a fresh battery and a spare battery as well. Bring additional portables and batteries where possible. Team leaders from other agencies will borrow P&C radios.
3. Know the role of your team or sector (below), the roles of team leaders and sector bosses (this page), and the names and callsigns of the other team leaders and sector bosses (below).
4. Please wash the underside of 4WD vehicles the day before travelling to Gudgenby (which lacks some of the weeds otherwise widespread in the ACT) and wash it again afterward, eg using the excellent facility at Glendale, as Gudgenby has very nasty weeds, currently in seed, which are not found further north at present.

On site before and after the count

5. Before teams go out to the counting site, Team Leaders record the names of your team on the form provided.
6. As soon as counting stops in your area, and preferably before travelling back to base, complete your own form(s), **collect a completed form from each member of your team, including zero counts, and bag them.** Hand the bag to the Planning Officer (Jim Hone) after you have confirmed that all your team members have arrived back at base.
7. The additional blank forms are in case any of your team may be reallocated to another location, or in the event they have to continue counting somewhere after they hand you their first form.

In action

8. In mobile sectors, the main role of team leaders is to maintain optimum spacing and pace within your team, as per ‘Instructions for Counters’. This is paramount. In mobile sectors, team leaders should be ahead of the line or moving up and down it, and should not count. Focus on your team, the terrain they are about to encounter, and the linkage to neighbouring teams. Halt the line, speed it up, or slow it down by communicating directly to your team and by radio to other team leaders and your sector boss.
9. Team leaders in stationary sectors are needed mainly to get the team in and out of their correct positions. A minimum set of positions is marked and numbered on site. Note that some require a scramble to the top of a boulder. In some stationary teams, the leader can take a place as a counter (see sector plans). Some stationary counters can be transferred into the mobile team, or elsewhere, after they have been passed by the mobile team.

TEAM LEADER TO COMPLETE – PERSONNEL SUMMARY AND ACCOUNTING

Name of Sector: ___________________________

Name of Team: ____________________________

Name of Team Leader: _____________________

TEAM MEMBERS

Name of Counter	Position No. (stationary teams only)	Count form received at end of count?	Returned safe to base? (If moved to other team, name it)

ROLES AND RADIO CALLSIGNS OF KEY PERSONNEL

POSITION	NAME	CALL-SIGN
Incident Controller	Don Fletcher	Wildlife 72
Planning Officer	Jim Hone	Jim Hone
Logistics Officer	Wayne Sayer	West 86
Special counter	Karen Viggers (w Don Moore)	West 82
Special counter	Michelle Walter (w Peter Hann)	Peter Hann
Sector Boss – North East	Anna Farnham	West 67
Team Leader – Gully (stationary 8pns)	Graham Simpson	East 88
Team Leader – Rendesvous A (mobile)	Nick Webb	Wildlife 66
Team Leader – Rendesvous B (mobile)	Mark Rodden	East 81
Sector Boss – North West	Viv Raffaele	Parks 3 ????
Team Leader – Rendesvous C (mobile)	Julian Barnard	West 55??
Team Leader – Rendesvous D (mobile)	Bill Woodruff	Athllon 60
Team Leader - Ridge (stationary 6 pns)	Lance Bates	East 84
Sector Boss - South East	Brett McNamara	East 50
Team Leader – Readycut (stationary 4 pns)	Murray Evans	Wildlife 62
Team Leader - Forest (stationary 5 pns)	Ian Faulkner	Athllon 62
Team Leader – Pines A (mobile)	Daniel Iglesias	TNR 61
Team Leader – Pines B (mobile)	Geoff Price	East 66
Team Leader – Pines C (mobile)	Dennis Gray	Parks 9
Sector Boss – South West	Geoff Webb	West 80
Team Leader - Bogong Creek A (mobile)	Mel White	Mel White
Team Leader - Bogong Creek B (mobile)	Jeff Green	TNR 80
Team Leader – Rabbit Ridge (stationary 5 pns)	Anton Maher	East 90

LOGISTICS SECTION PLAN

Objectives:

Assist with transporting and guiding crews to and from count locations. Provide lunch. Oversee portable toilets and supply of 240 V power (for urns, battery chargers etc). Deliver either a first aid kit or rifle where necessary. Solve unexpected difficulties that arise.

Personnel

Name	Callsign	Location	Duties
Wayne Sayer	West	Gud HS / As req'd	As required
Steve Crombie	West	Gud HS / As req'd	Truck, Rifle, Other duties as required
Graham Heanes	East	Gudgenby HS	Cooking
Frank Armstrong	East	Gudgenby HS	Cooking

Resources to be serviced, supplied or installed

Resource type	Location	Timing Requirement
Portaloos (2)*	Gudgenby HS, adjacent to flat rock near footbridge	all of 10/4/2002 (deliver previously and collect later)
240V generator, leads etc**	HS vicinity	most of 10/4/2002
trestle tables (3)*??	shed @ HS	most of 10/4/2002
Gas BBQ (1)**	shed @ HS	most of 10/4/2002
Gas BBQ (1)*	shed @ HS	most of 10/4/2002
Urns**	shed @ HS	most of 10/4/2002
Town water in containers* and **	shed @ HS	most of 10/4/2002
Lunch*	shed @ HS	1230 to 1430 on 10/4/2002
Plates, cups*	shed @ HS	1230 to 1430 on 10/4/2002
battery chargers for portable radios** and *	shed @ HS	1230 to 1430 on 10/4/2002
First Aid Kit**	In vehicle @ HS	all of 10/4/2002
Stretcher**	In vehicle @ HS	all of 10/4/2002
0.22" cal Rifle & ammunition**	In vehicle @ HS	all of 10/4/2002
Truck**	near Gudgenby HS	10/4/2002
Roo Road Signs	Boboyan Rd either side of site	most of 10/4/2002

** = materials delivered by Jason Meredith's NNP staff * = delivery by others.

PLANNING SECTION PLAN

Objectives: 1. Provide a view of the events that is independent of that of the Incident Controller, with particular reference to sources of bias in the count (eg animals flushed from the area before counting commences). 2. Advise and support the Incident Controller eg re coordination and timing. 3. Collect a bag of data sheets from each team at the end of the morning and afternoon sessions.

Personnel

Name	**Callsign**	**Duties**	**Location**
Jim Hone	'Jim Hone'	Planning Officer: Make observations, Maintain independent overview. Decision support as required. Collect data sheets. **initially:** assess disturbance effect in south eastern area	with Don Fletcher
Michelle Walter	'Peter Hann'	**Special counter** Assess disturbance effect of teams getting into position in south eastern area. Assess other sources of error.	with Peter Hann
Karen Viggers	West 82	**Special counter** Assess disturbance effect of teams getting into position in northern area. Assess other sources of error.	with Don Moore
Peter Hann	'Peter Hann'	**Guide** **initially:** guide for southern area, and driver for Michelle Walter **subsequently**: Critic, Help assess sources of error.	**initially:** perimeter of counted area – south eastern area **later**: roaming independently
Don Moore	West 82	**Guide** guide for northern area, and driver for Karen Viggers	**initially:** perimeter of counted area – northern area **later**: roaming independently

SECTOR PLAN for **North East Sector** Wed 10 April 2002

Objective:

Count EGKs in the eastern portion of an area between Rendesvous Ck and Middle Ck. Maintain partnership with North West sector.

North East Sector comprises 3 teams.

Gully Team (8 positions) forms the eastern boundary of the counted area. The five positions at its northern end are under a powerline that eventually reaches Gudgenby HS. People in positions 3 and 6 should wear safety vests or other bright colours to be sufficiently visible. The first one or two people reached by the mobile Rendesvous A team should be transferred into Rendesvous A team to assist with counting the patch of woodland they will encounter on top of the ridge. Positions 1 and 2 in Gully Team are readily accessible from the Homestead entrance track. The other positions are reached most easily from the Rendesvous Ck track. Note carefully the separate instruction for what is to happen where the mobile line of counters, ie Rendesvous A team, meets the stationary line, ie Gully Team ('How and why people in stationary teams stop counting when passed by the mobile team'). Gully team is to be one of the first teams to be put in place in the Northern area, along with Rendesvous A team.

Rendesvous A Team (approx 6 people). Note carefully the separate instruction for what is to happen where the mobile line of counters meets the stationary line, ie Gully Team ('Why people in stationary teams stop counting when passed by the mobile team'). See above re transfer of Gully Team members into Rendesvous A Team before entering the patch of woodland. If sufficient people are available, also consider starting with two people 'doubled up', later to spread out when the woodland is reached.

Rendesvous B Team (approx 6 people). Intermediate between Rendesvous A and Rendesvous C.

All Teams

When proceeding onto the site, fill the count positions from nearest first, to furthest last, gradually extending the line of counters in position. Follow the guide vehicle into position, or obtain clearance to proceed without it. The Guide vehicle assesses the effect on the total count of the disturbance caused by getting the teams into place. Counters start recording as soon as they are in place.

Mobile teams stop at least 100m before any part of the line reaches Middle Ck.

SECTOR PLAN for **North West Sector** Wed 10 April 2002

Objective:

Count EGKs in the western portion of an area between Rendesvous Ck and Middle Ck. Maintain partnership with North East sector.

North West Sector comprises 3 teams.

Rendesvous C Team (approx 6 people). Intermediate between Rendesvous B and Rendesvous D. See below re transfer of Ridge Team members into this team and/or others.

Rendesvous D Team (approx 6 people). Note carefully the separate instruction for what is to happen where the mobile line of counters meets the stationary line, ie Ridge Team ('Why people in stationary teams stop counting when passed by the mobile team'). Be aware of the patch of woodland (marked on map) and adjoining scrubby area to its west, just before Middle Ck. May need to add an extra person or two to the line here.

Ridge Team (6 positions) forms the western boundary of the counted area. The person in position 2 should not be wearing obscure colours. The people passed by the mobile Rendesvous D team could be transferred into Rendesvous D or other teams as required. to assist with counting the patch of woodland they will encounter on top of the ridge. Access to all positions is from the north. Note carefully the separate instruction for what is to happen where the mobile line of counters, ie Rendesvous D team, meets the stationary line, ie Ridge Team ('Why people in stationary teams stop counting when passed by the mobile team'). Ridge team is to be one of the last teams to be put in place in the Northern area.

All Teams

When proceeding onto the site, fill the count positions from nearest first, to furthest last, gradually extending the line of counters in position. Follow the guide vehicle into position, or obtain clearance to proceed without it. The Guide vehicle assesses the effect on the total count of the disturbance caused by getting the teams into place. Counters start recording as soon as they are in place.

Mobile teams stop at least 100m before any part of the line reaches Middle Ck.

SECTOR PLAN for **South East Sector** Wed 10 April 2002

Objective:

Count EGKs in the eastern portion of an area between Boboyan Pine Plantation and Middle Ck. Maintain partnership with South West sector.

South East Sector comprises 5 teams. CHANGE FRM HERE DOWN

Rendesvous C Team (approx 6 people). Intermediate between Rendesvous B and Rendesvous D. See below re transfer of Ridge Team members into this team and/or others.

Rendesvous D Team (approx 6 people). Note carefully the separate instruction for what is to happen where the mobile line of counters meets the stationary line, ie Ridge Team ('Why people in stationary teams stop counting when passed by the mobile team'). Be aware of the patch of woodland (marked on map) and adjoining scrubby area to its west, just before Middle Ck. May need to add an extra person or two to the line here.

Ridge Team (6 positions) forms the western boundary of the counted area. The person in position 2 should not be wearing obscure colours. The people passed by the mobile Rendesvous D team could be transferred into Rendesvous D or other teams as required. to assist with counting the patch of woodland they will encounter on top of the ridge. Access to all positions is from the north. Note carefully the separate instruction for what is to happen where the mobile line of counters, ie Rendesvous D team, meets the stationary line, ie Ridge Team ('Why people in stationary teams stop counting when passed by the mobile team'). Ridge team is to be one of the last teams to be put in place in the Northern area.

All Teams

When proceeding onto the site, fill the count positions from nearest first, to furthest last, gradually extending the line of counters in position. Follow the guide vehicle into position, or obtain clearance to proceed without it. The Guide vehicle assesses the effect on the total count of the disturbance caused by getting the teams into place. Counters start recording as soon as they are in place.

Mobile teams stop at least 100m before any part of the line reaches Middle Ck.

APPENDIX 4: STATISTICS FOR EACH LINE TRANSECT SURVEY, SURVEYS GROUPED BY SITE

Summary statistics for the line transect data from 38 surveys of eastern grey kangaroos at the Googong, Gudgenby and Tidbinbilla study sites. Following Burnham and Anderson (2002, p 257) Density D_i (number ha^{-1}) is used to clarify that D_i is conditional on model g_i. log (£(q)) = log likelihood of the model; AIC = Akaike's Information Criterion; w_i = model weight. See Methods for details. The model - averaged values of D and SE are those presented in Results.

GOOGONG

Date	Key function	Series expansion (selected for each key function based on lowest AIC)	K	log (£(q))	AIC	ΔAIC	exp(-D_i/2)	w_i	D_i	SE	var (D_i/g_i)
Jun-01	Half normal	nil	2	-594.60759	1191.215	0.141	0.932	0.437	5.35	0.954	2.339
	Hazard rate	nil	2	-595.14702	1194.294	3.220	0.200	0.094	5.90	1.390	0.553
	Uniform	simple polynomial 2nd order	3	-594.53724	1191.075	0.000	1.000	0.469	5.08	0.853	2.385
	AVERAGED								5.28	1.629	
Jul-01	Half normal	nil	2	-384.44753	770.895	0.507	0.776	0.318	4.82	1.064	1.533
walked	Hazard rate	nil	2	-383.60019	771.200	0.812	0.666	0.273	4.98	1.036	1.358
	Uniform	simple polynomial 2nd order	3	-384.19419	770.388	0.000	1.000	0.409	4.92	1.029	2.015
	AVERAGED								4.91	1.478	
Jul-01	Half normal	nil	2	-600.28781	1202.576	0.604	0.739	0.338	5.42	0.932	1.830
	Hazard rate	nil	2	-599.78268	1203.565	1.593	0.451	0.206	4.79	0.756	0.987
	Uniform	simple polynomial 2nd order	3	-599.98605	1201.972	0.000	1.000	0.457	5.35	0.870	2.442
	AVERAGED								5.26	1.204	
Sep-01	Half normal	nil	2	-582.41826	1166.837	1.115	0.573	0.320	4.93	0.979	1.575
	Hazard rate	nil	2	-582.38152	1168.763	3.041	0.219	0.122	5.16	1.160	0.629
	Uniform	nil	1	-582.8609	1165.722	0.000	1.000	0.558	4.90	0.868	2.734
	AVERAGED								4.94	1.474	
Nov-01	Half normal	nil	2	-939.5946	1881.189	0.162	0.922	0.428	5.03	0.920	2.152
	Hazard rate	nil	2	-939.96643	1883.933	2.906	0.234	0.108	5.02	1.056	0.545
	Uniform	simple polynomial 2nd order	2	-939.51345	1881.027	0.000	1.000	0.464	4.99	0.887	2.314
	AVERAGED								5.01	1.381	

Appendix 4 cont. GOOGONG

Date	Key function	Series expansion (selected for each key function based on lowest AIC)	K	log (£(q))	AIC	ΔAIC	exp(-D_i/2)	w_i	D_i	SE	var (D_i/g_i)
Jan-02	Half normal	nil	2	-601.83914	1205.678	1.941	0.379	0.250	4.84	0.822	1.211
	Hazard rate	nil	2	-601.86866	1207.737	4.000	0.135	0.089	4.70	0.693	0.420
	Uniform	nil	1	-601.86866	1203.737	0.000	1.000	0.660	4.70	0.693	3.106
	AVERAGED								4.74	1.056	
Mar-02	Half normal	nil	2	-825.66622	1653.332	0.172	0.917	0.427	5.58	0.946	2.383
	Hazard rate	simple polynomial 4th order	6	-825.0528	1656.106	2.946	0.229	0.107	5.63	1.066	0.602
	Uniform	nil	1	-825.58003	1653.160	0.000	1.000	0.466	5.75	0.966	2.681
	AVERAGED								5.67	1.426	
May-02	Half normal	nil	2	-502.95935	1007.919	0.085	0.958	0.390	3.54	0.826	1.380
	Hazard rate	nil	2	-502.61243	1009.225	1.391	0.499	0.203	3.54	0.800	0.719
	Uniform	nil	1	-502.91693	1007.834	0.000	1.000	0.407	3.55	0.810	1.445
	AVERAGED								3.54	1.151	
Jul-02	Half normal	nil	2	-377.16211	756.324	0.356	0.837	0.378	2.72	0.610	1.028
	Hazard rate	nil	2	-376.95306	757.906	1.938	0.379	0.171	2.54	0.559	0.436
	Uniform	nil	1	-377.98401	755.968	0.000	1.000	0.451	2.07	0.393	0.936
	AVERAGED								2.40	0.764	
Sep-02	Half normal	nil	2	-306.49924	614.998	1.913	0.384	0.216	2.22	0.689	0.481
	Hazard rate	nil	2	-305.47909	614.958	1.872	0.392	0.221	2.07	0.585	0.457
	Uniform	nil	1	-306.54294	613.086	0.000	1.000	0.563	2.11	0.597	1.187
	AVERAGED								2.13	0.895	
Nov-02	Half normal	cosine 2nd order	4	-783.80135	1571.603	0.014	0.993	0.393	8.84	1.669	3.475
	Hazard rate	nil	2	-784.42225	1572.845	1.255	0.534	0.211	8.40	1.731	1.774
	Uniform	cosine 1st order	2	-784.79453	1571.589	0.000	1.000	0.396	7.94	1.304	3.141
	AVERAGED								8.39	2.256	

Appendix 4 cont. GOOGONG

Date	Key function	Series expansion (selected for each key function based on lowest AIC)	K	log (£(q))	AIC	□AIC	exp(-D_i/2)	w_i	D_i	SE	var (D_i/g_i)
Jan-03	Half normal	nil	2	-450.21321	902.426	1.745	0.418	0.265	3.74	0.832	0.994
	Hazard rate	nil	2	-450.1957	904.391	3.710	0.156	0.099	3.83	0.928	0.380
	Uniform	nil	1	-450.34049	900.681	0.000	1.000	0.635	3.63	0.713	2.306
	AVERAGED								3.68	1.215	
Mar-03	Half normal	nil	2	-678.79209	1359.584	0.460	0.794	0.296	5.11	0.996	1.511
	Hazard rate	nil	2	-677.56201	1359.124	0.000	1.000	0.372	5.29	0.962	1.970
	Uniform	simple polynomial 2nd order	3	-678.67711	1359.354	0.230	0.891	0.332	5.17	0.986	1.717
	AVERAGED								5.20	1.392	
May-03	Half normal	nil	2	-383.33816	768.676	1.920	0.383	0.252	5.59	1.305	1.410
	Hazard rate	nil	2	-383.37825	770.757	4.000	0.135	0.089	4.99	1.030	0.445
	Uniform	nil	1	-383.37825	766.757	0.000	1.000	0.659	4.99	1.030	3.287
	AVERAGED								5.14	1.617	
Jul-03	Half normal	nil	2	-700.74246	1403.485	1.236	0.539	0.277	5.45	1.065	1.509
	Hazard rate	nil	2	-700.02156	1404.043	1.795	0.408	0.209	5.77	1.055	1.207
	Uniform	nil	1	-701.12426	1402.249	0.000	1.000	0.514	5.43	0.945	2.789
	AVERAGED								5.51	1.466	

GUDGENBY

Date	Key function	Series expansion (selected for each key function based on lowest AIC)	K	log (£(q))	AIC	□AIC	exp(-D_i/2)	w_i	D_i	SE	var (D_i/g_i)
Sep-01	Half normal	nil	2	-700.34324	1402.687	0.482	0.786	0.373	5.82	1.186	2.168
	Hazard rate	nil	2	-700.23168	1404.463	2.259	0.323	0.153	5.84	1.805	0.895
	Uniform	cosine 1st order	2	-700.10224	1402.205	0.000	1.000	0.474	5.92	1.299	2.807
	AVERAGED								5.87	2.130	
Nov-01	Half normal	nil	2	-1014.5964	2031.193	0.098	0.952	0.440	4.64	0.943	2.043
	Hazard rate	nil	2	-1013.5474	2031.095	0.000	1.000	0.462	4.70	1.064	2.174
	Uniform	simple polynomial 2nd order	3	-1016.1019	2034.204	3.109	0.211	0.098	4.35	0.803	0.424
	AVERAGED								4.64	1.303	

Appendix 4 cont. GUDGENBY

Date	Key function	Series expansion (selected for each key function based on lowest AIC)	K	log (£(q))	AIC	ΔAIC	exp($-D_i/2$)	w_i	D_i	SE	var (D_i/g_i)
Jan-02	Half normal	nil	2	-916.59368	1835.187	2.000	0.368	0.158	4.34	0.892	0.686
	Hazard rate	nil	2	-914.63397	1833.268	0.081	0.961	0.413	4.39	0.829	1.809
	Uniform	nil	1	-916.59368	1833.187	0.000	1.000	0.429	4.34	0.821	1.865
	AVERAGED								4.36	1.211	
Mar-02	Half normal	nil	2	-2517.1166	5036.233	0.000	1.000	0.431	5.85	0.676	2.526
	Hazard rate	nil	2	-2517.2563	5038.513	2.280	0.320	0.138	5.90	0.775	0.814
	Uniform	simple polynomial 2nd order	3	-2517.1187	5036.237	0.004	0.998	0.431	5.85	0.660	2.516
	AVERAGED								5.86	1.015	
May-02	Half normal	nil	2	-870.68502	1743.370	0.324	0.851	0.394	3.61	0.617	1.423
	Hazard rate	nil	2	-870.69725	1745.395	2.348	0.309	0.143	3.68	0.704	0.527
	Uniform	cosine 1st order	2	-870.52319	1743.046	0.000	1.000	0.463	3.64	0.641	1.687
	AVERAGED								3.64	0.939	
Jul-02	Half normal	nil	2	-1688.6416	3379.283	2.454	0.293	0.197	5.31	0.897	1.047
	Hazard rate	nil	2	-1688.0505	3380.101	3.272	0.195	0.131	5.63	1.074	0.736
	Uniform	cosine 1st order	2	-1687.4145	3376.829	0.000	1.000	0.672	5.47	0.920	3.675
	AVERAGED								5.46	1.390	
Sep-02	Half normal	nil	2	-614.00228	1230.005	0.458	0.795	0.307	4.20	0.975	1.288
	Hazard rate	nil	2	-613.77085	1230.005	0.458	0.795	0.307	3.98	0.899	1.221
	Uniform	nil	1	-614.77338	1229.547	0.000	1.000	0.386	3.82	0.804	1.473
	AVERAGED								3.98	1.274	
Nov-02	Half normal	nil	2	-1348.0351	2698.070	0.268	0.874	0.334	4.24	0.724	1.414
	Hazard rate	nil	2	-1347.1929	2698.386	0.584	0.747	0.285	4.08	0.674	1.162
	Uniform	simple polynomial 2nd order	3	-1347.901	2697.802	0.000	1.000	0.381	4.25	0.715	1.619
	AVERAGED								4.20	1.000	

Appendix 4 cont. GUDGENBY

Date	Key function	Series expansion (selected for each key function based on lowest AIC)	K	log (£(q))	AIC	ΔAIC	exp(-D_i/2)	w_i	D_i	SE	var (D_i/g_i)
Jan-03	Half normal	nil	2	-701.9389	1405.878	2.000	0.368	0.245	4.48	0.980	1.095
	Hazard rate	nil	2	-701.9389	1407.878	4.000	0.135	0.090	4.48	0.904	0.403
	Uniform	nil	1	-701.9389	1403.878	0.000	1.000	0.665	4.48	0.904	2.978
	AVERAGED								4.48	1.323	
Mar-03	Half normal	nil	2	-1215.7638	2433.528	1.998	0.368	0.243	4.22	0.800	1.024
	Hazard rate	nil	2	-1215.6665	2435.333	3.803	0.149	0.098	4.35	0.802	0.428
	Uniform	nil	1	-1215.7649	2431.530	0.000	1.000	0.659	4.10	0.735	2.703
	AVERAGED								4.15	1.121	
May-03	Half normal	nil	2	-1492.0754	2986.151	2.001	0.368	0.232	5.22	0.763	1.208
	Hazard rate	nil	2	-1491.5853	2987.171	3.020	0.221	0.139	5.31	0.708	0.739
	Uniform	nil	2	-1492.0751	2984.150	0.000	1.000	0.629	5.22	0.683	3.284
	AVERAGED								5.23	1.030	
Jul-03	Half normal	nil	2	-1129.849	2261.699	2.003	0.367	0.226	3.55	0.682	0.80
	Hazard rate	nil	2	-1129.188	2262.377	2.680	0.262	0.161	3.46	0.596	0.56
	Uniform	nil	2	-1129.848	2259.696	0.000	1.000	0.614	3.55	0.625	2.18
	AVERAGED								3.54	0.903	

TIDBINBILLA

Jan-02	Half normal	Hermite polynomial 4th order	6	-827.22228	1658.445	1.488	0.475	0.265	5.80	1.194	1.537
	Hazard rate	nil	2	-826.47803	1656.956	0.000	1.000	0.557	5.67	0.996	3.163
	Uniform	Cosine 3rd order	4	-826.62107	1659.242	2.286	0.319	0.178	6.03	1.048	1.072
	AVERAGED								5.77	1.548	
Mar-02	Half normal	nil	2	-912.23531	1826.471	0.000	1.000	0.445	8.21	1.305	3.655
	Hazard rate	nil	2	-912.36449	1828.729	2.258	0.323	0.144	8.41	1.629	1.211
	Uniform	Cosine 1st order	2	-912.31636	1826.633	0.162	0.922	0.411	8.44	1.356	3.468
	AVERAGED								8.33	2.075	

Appendix 4 cont TIDBINBILLA

Date	Key function	Series expansion (selected for each key function based on lowest AIC)	K	log (£(q))	AIC	ΔAIC	exp($-D_i/2$)	w_i	D_i	SE	var (D_i/g_i)
May-02	Half normal	nil	2	-442.94073	887.881	0.349	0.840	0.359	3.53	0.625	1.269
	Hazard rate	nil	2	-442.46323	888.926	1.393	0.498	0.213	3.44	0.631	0.733
	Uniform	Simple polynomial 2nd order	3	-442.76648	887.533	0.000	1.000	0.428	3.48	0.565	1.488
	AVERAGED								3.49	0.870	
Sep-02	Half normal	nil	2	-603.1205	1208.241	1.030	0.597	0.264	5.26	1.008	1.388
	Hazard rate	nil	2	-601.60548	1207.211	0.000	1.000	0.441	5.10	0.881	2.252
	Uniform	Simple polynomial 2nd order	3	-603.0089	1208.018	0.807	0.668	0.295	5.31	0.990	1.565
	AVERAGED								5.21	1.372	
Nov-02	Half normal	nil	2	-634.07671	1270.153	1.140	0.566	0.278	5.21	0.977	1.447
	Hazard rate	nil	2	-633.2629	1270.526	1.512	0.470	0.231	4.77	0.792	1.100
	Uniform	nil	1	-634.50686	1269.014	0.000	1.000	0.491	4.62	0.765	2.272
	AVERAGED								4.82	1.216	
Jan-03	Half normal	nil	2	-701.1639	1404.328	0.000	1.000	0.435	5.03	0.763	2.191
	Hazard rate	nil	2	-701.13207	1406.264	1.936	0.380	0.165	5.08	0.960	0.840
	Uniform	Cosine 1st order	2	-701.25087	1404.502	0.174	0.917	0.399	4.98	0.727	1.987
	AVERAGED								5.02	1.194	
Feb-03	Half normal	nil	2	-529.34761	1060.695	0.174	0.917	0.403	3.01	0.615	1.212
	Hazard rate	nil	2	-529.28132	1062.563	2.041	0.360	0.158	3.04	0.728	0.481
	Uniform	Cosine 1st order	2	-529.26079	1060.522	0.000	1.000	0.439	3.04	0.636	1.336
	AVERAGED								3.03	0.953	
Mar-03	Half normal	nil	2	-614.40347	1230.807	0.000	1.000	0.401	2.31	0.506	0.925
	Hazard rate	nil	2	-613.70711	1231.414	0.607	0.738	0.296	2.50	0.681	0.740
	Uniform	Simple polynomial 4th order	5	-613.68627	1231.373	0.566	0.754	0.302	2.42	0.534	0.732
	AVERAGED								2.40	0.830	

Appendix 4 cont TIDBINBILLA

Date	Key function	Series expansion (selected for each key function based on lowest AIC)	K	log (£(q))	AIC	ΔAIC	exp($-D_i/2$)	w_i	D_i	SE	var (D_i/g_i)
May-03	Half normal	nil	2	-373.81153	749.623	1.888	0.389	0.253	2.68	0.697	0.678
	Hazard rate	nil	2	-373.77073	751.541	3.806	0.149	0.097	2.70	0.670	0.262
	Uniform	nil	1	-373.86758	747.735	0.000	1.000	0.650	2.60	0.610	1.692
	AVERAGED								2.63	0.953	
Jul-03	Half normal	nil	2	-195.81671	393.633	2.000	0.368	0.242	1.18	0.427	0.285
	Hazard rate	nil	2	-195.69345	395.387	3.753	0.153	0.101	1.22	0.382	0.122
	Uniform	nil	1	-195.81671	391.633	0.000	1.000	0.657	1.18	0.367	0.776
	AVERAGED								1.18	0.570	