Modelling the spatial and temporal dynamics of kangaroo populations for harvest management

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Summary

For the past three years, university researchers (University of Queensland and University of New England), kangaroo managers (Queensland, New South Wales, South Australia and the Commonwealth) and Packer Tanning have been collaborating on a research project aimed at improving kangaroo management. The project has three broad aims:

- Predict kangaroo numbers using rainfall or satellite imagery and other environmental data
- Indirectly monitor kangaroo numbers and harvest rate using harvest statistics (e.g. sex ratio, carcass weight, catch-per-unit-effort)
- Optimise survey methods, frequency and design

The work has involved collating over 20 years of data in three states on kangaroo density from aerial surveys, harvest offtake, satellite imagery (greenness index or NDVI) and rainfall. Such a long time series of data covering vast areas has enabled models to be developed that should lead to improved kangaroo management. These models can be used to predict future kangaroo numbers, which should enable the frequency and intensity of expensive aerial surveys to be reduced. Better prediction of kangaroo distribution within management zones should also help quota and tag allocation. Rainfall and pasture conditions obviously influence changes in kangaroo numbers, but the relationships needed to be quantified. The sex ratio and average weight of carcasses vary regionally, for a variety of reasons. Most usefully for managers, these statistics track kangaroo density or harvest rate in some cases. Both harvest statistics and satellite imagery have the advantage of being regularly updated and a high spatial resolution, both shortcomings of broad-scale aerial survey.

Aerials surveys have been conducted annually in the eastern states, which may not be the most efficient survey frequency. The optimal frequency can be identified by considering the risks of the population dropping to low density or rising to high density. These risks can be considered as costs to the kangaroo industry, graziers and to conservation, which must then be balanced. Risk can be reduced by increasing survey frequency or intensity, which is a cost to management, or reducing harvest rate, which is a cost to industry. In more arid, uncertain environments, regular surveys are required. However, in many of these areas, harvests are low and a reduced harvest rate is unlikely to be a cost to industry.

The data also suggest a greater influence of movement on red kangaroo population dynamics than previously thought, with large areas experiencing rates of increase much higher than possible through birth and survival alone. This suggests movement needs to be considered when forecasting kangaroo density even at a regional (>10,000 km^2) scale.

Funding has come from these collaborating groups and the Australian Research Council, which is particularly supportive of research collaboration between industry and universities. The Murray Darling Basin Commission also supported some aspects of this work.

Specific project outcomes

1. Our modelling of the temporal dynamics of kangaroo populations has identified several important determinants of population fluctuations. These include appropriate rainfall and NDVI periods, species and regional variation, harvesting and the strength of density dependence. These results are of both applied and theoretical importance. Managers will be able to make better predictions of population size allowing more sensitive quota setting, using either rainfall or NDVI and population trends in adjoining regions.

2. By using a risk assessment and decision theory frameworks, we have been able to explore optimal monitoring strategies for kangaroo managers. These will be influenced by the harvest strategy, environmental variability and the structure of the model describing population behaviour. A specific application of this was determining appropriate management of kangaroo populations during the recent drought.

3. We have described the fine-scale spatial patterns of kangaroo density in South Australia and their variation over time. Maps of interpolated density and associated local rates of increase suggest a greater influence of movement on red kangaroo dynamics than previously thought.

4. Simple stratification of wallaroo surveys in Queensland using harvest data has substantially improved the accuracy and precision of the wallaroo population estimate. Stratification (regionalisation) of population estimates for all species has improved both the accuracy and precision of the statewide population estimates and allowed more appropriate quota setting.

5. We are currently finalising analyses examining environmental determinants of kangaroo distribution in South Australia, Queensland and New South Wales. We have identified shifts in the distribution of all species and found NDVI to be useful in detecting local shifts in the distribution of kangaroos. We hope to use habitat models to derive small-scale abundance estimates (by integrating under a fitted spatial density surface) and to determine unbiased broad-scale estimates from non-random surveys. A reassessment of the distribution of western grey kangaroos in Queensland has also been possible using ground surveys.

6. We have been able to identify those harvest statistics that appear sensitive to changes in kangaroo density and harvest rate. There is considerable regional variation in both the statistics themselves and the relationships with density and harvest rate. This will provide managers with a clearer picture of how these statistics can be used.

7. As an extension of our initial aims, we have been able to identify the potential effects of harvesting on kangaroo genetics. This work has highlighted the importance of migration in ameliorating any impact.

8. Further extensions include assessment of bias in helicopter surveys of kangaroo populations, design and conduct of surveys in southeastern New South Wales, analysis of the relationship between body size and age at sexual maturity in red kangaroos, effects of drought on the demography of an unharvested red kangaroo population, geographic variation in red kangaroo body size, age structure and harvest

selectivity and determinants of female reproductive success and offspring sex ratio in kangaroos. The latter four pieces of work are yet to be finalised.

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1. General introduction

1.1 Overview

This report details the findings of a research project aimed at improving kangaroo management in the eastern states of Australia. The project has three broad aims:

- Predict kangaroo distribution and abundance using rainfall or satellite imagery and other environmental data
- Indirectly monitor kangaroo density and harvest rate using harvest statistics (e.g. sex ratio, carcass weight, catch-per-unit-effort)
- Optimise survey methods, frequency and design

The need for better information about the distribution and abundance of kangaroos arises partly because kangaroo harvest quotas are currently set annually, each December, on the basis of surveys conducted the preceding winter or earlier, and so the population estimates are somewhat out of date. These surveys, usually aerial surveys, are expensive, large-scale operations and there is an urgent need to develop supplementary techniques, which are both cost effective and able to monitor population changes in a timelier manner. Our study explored two approaches. The first was to combine extensive survey data on population size with rainfall, remotely sensed estimates of pasture condition (available Australia-wide on a monthly basis) and other environmental variables (soil, vegetation and rainfall). The second was to examine the relationship between the aerial survey data (i.e. direct monitoring) with the harvest data, which are collected routinely (available on a monthly basis), as an indication of population density or harvest rate (i.e. to explore indirect monitoring).

These approaches need to be considered in the broader framework of a harvest strategy. This is described in detail in Section 2, providing an introduction to the following sections. Quite clearly, an appropriate monitoring program for kangaroos will depend on the harvest strategy, which in turn will be determined by the management objective. For example, harvesting a constant proportion of animals each year requires annual population estimates. However, an alternative strategy of harvesting only above a threshold density requires only population estimates relative to that threshold. If the population is well above the threshold, then less frequent surveys with lower precision, result in a cost saving to management, may be acceptable. This framework is examined further in Sections 5 and 6.

This report is structured around a series of papers, each a separate section, that are either published or submitted for publication. Other sections are either not destined for publication or are in a less advanced state of preparation. Analyses are nevertheless sufficient to allow a preliminary presentation of results. There is also additional work that was too incomplete for presentation and this has been identified in the final section.

1.2 Collaborators and funding

The project was funded by the Australian Research Council as part of its Strategic Partnerships with Industry (now Linkage) program, which involves cash and in-kind contributions from each of the industry partners. Some aspects of the work were further supported by funding from the Murray Darling Basin Commission (Sections 15 and 16) and New South Wales Department of Conservation (formerly New South Wales National Parks and Wildlife Service) (Sections 5 and 8).

The collaborating organisations and personnel were:

University of Queensland (Tony Pople, Norbert Menke, Hugh Possingham, Gordon Grigg, Stuart Phinn, Clive McAlpine, Cindy Hauser)
Department of Environment and Heritage (Barry Baker, Cindy Steensby, Peter Hemphill, Alex Baumber)
New South Wales Department of Conservation (Joshua Gilroy, Nicole Payne)
Queensland Parks and Wildlife Service (Geoff Lundie-Jenkins, Sally Egan, Murray Evans)
South Australian Department for Environment and Heritage (Lisa Farroway, Peter Alexander)
University of New England (Stuart Cairns)
Packer Tanning (Lindsay Packer)

Other collaborators have been identified in each section as co-authors and assistance from various people has been acknowledged at the end of these sections. In particular, Niclas Jonzen and Brigitte Tenhumberg made major contributions to the overall project.

1.3 Datasets

The aerial survey and harvest data used in this report are summarised in Tables 1.1 and 1.2. Details on the methods of the surveys and correction factors used to make density estimates temporally and in some cases spatially comparable are given in Section 12. Changes to the Queensland survey area and in the calculation of population estimates are given in Section 3. Organisation of the harvest data is described in Sections 9 and 13 along with location of the management regions in New South Wales and South Australia. A large component of the project was collating these datasets, which in some cases included entering data from survey data sheets. The datasets are stored as Microsoft Access or Excel files, copies of which are held by each of the relevant state agencies and by The Ecology Centre at The University of Queensland. Environmental datasets used in the study are described in the relevant sections.

While the datasets are extensive, survey data were not available for spatial analysis at a fine scale in all years (Table 1.1). For example, in New South Wales, raw data prior to 1993 had been lost in a fire. Nevertheless, for these years, data at a broader scale were available for analysis.

Table 1.1. Data on kangaroo density used in this study. Scale refers to the resolution of data available for analysis. HLT, helicopter line transect; WP, western plains; PZ pastoral zone; KMZ, kangaroo management zone; SCB, soil conservation board; Region, areas based approximately on biogeographic boundaries within the core area (see Section 9).

State	Area	Year(s)	Platform	Scale
Qld	Core	1980,1984-1992	Fixed-wing	2 km^2
	Core	2001	Fixed-wing	1 km^2
	Core	1991	HLT	5 blocks
	Core	1992-1994	HLT	9 blocks
	Core	1995-2001	HLT	10 blocks
	>Core	2002-2003	HLT	19 blocks
	Core	1980,1984-2003	Fixed-wing, HLT	Region
NSW	WP	1975-1976	Fixed-wing	1:250,000 map sheets
	WP	1977-1983	Fixed-wing	Monitor blocks
	WP	1984-2003	Fixed-wing	1^o blocks, KMZ
	WP	1993-2000	Fixed-wing	2 km^2
	WP	2001-2003	Fixed-wing	1 km^2
SA	PZ	1978-2003	Fixed-wing	2 km^2, SCB

Harvest data required editing, presumably due to transcription errors during data entry (e.g. implausible weights or nightly harvest). The problem was not with the total harvest for the state, but for the total harvest and associated statistics at finer scales such as a region or property. This unreliability cautions against the use of harvest statistics in management without some scrutiny. For harvest statistics such as carcass weight and catch-per-unit-effort (CPUE), many errors were readily detected as outliers following plots of the data. The problem is likely to be most pronounced at a fine scale (e.g. property). On a broader scale, small errors are likely to be overshadowed by the sheer volume of data. The approach taken in this project was to remove or correct obvious errors, but to generally accept that the harvest data were imperfect. This would introduce some noise in the relationships between harvest statistics and population size, harvest rate and the environment. However, it is unlikely that the quality of the data could be greatly improved. The question was whether these harvest data, in their present form, could be useful to management.

Species have been recorded separately in the harvest for some time, but some adjustment was required for earlier years. In New South Wales, all species were combined in the harvest records for 1975-1981. The two grey kangaroo species were not distinguished in the harvest in New South Wales until 1987. The species composition of the harvest for these early years was therefore based on the composition for 1988-2001. The kangaroo management zone (KMZ) harvest in New South Wales for 1975-1991 was unavailable. These were estimated by apportioning the State harvest based on the fraction in each KMZ in 1992. In Queensland, regional harvests were not available in prior to 1986. Again, these were estimated by apportioning the State harvest based on the fraction in each region in 1986. They were also unavailable for 1987, so the State harvest was apportioned by the average of the fractions in each region in 1986 and 1988. In South Australia, the combined, recorded soil conservation board (SCB) harvest for 1980-1988 underestimated the total reported harvest for the State. The latter was known to be more accurate as it is based on dealer returns, whereas the SCB harvest is based on shooter returns, many of which had either not been received or not entered. The SCB harvest was therefore adjusted by correction factors of 1.1-3.6 for those years, which assumes a constant bias among SCBs. There were only harvest totals for the State in 1978 and 1979 in South Australia. Again, the SCB harvest was estimated assuming a similar proportion of the State harvest taken in SCBs in 1978 and 1979 as was taken in 1980.

Table 1.2. Harvest statistics used in this study. Scale refers to the resolution of data available for analysis. SR, sex ratio; H, harvest; WT weight; SS, skin size; CPUE, catch-per-unit-effort. KMZ, kangaroo management zone; SCB, soil conservation board.

State	Area	Year(s)	Statistics	Spatial scale	Temporal scale
Qld	Harvest zone	1975-2003	H	Harvest zone	Annual
	Harvest zone	1986, 1988-1990	H	Grid square (½° block)	Annual
	Harvest zone	1991-2003	H, SR, WT, SS, CPUE	Grid square (½° block)	Month
NSW	Harvest zone	1975-2003	H	Harvest zone	Annual
	Harvest zone	1992	H	KMZ	Annual
	Harvest zone	1993-2004	H, SR, WT	KMZ	Month
	Harvest zone	1997-2004	CPUE	KMZ	3 months
SA	Harvest zone	1975-2003	H	Harvest zone	Annual
	Harvest zone	1980-2002	H, SR, WT, CPUE	Property, SCB	Month

Section 2

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POPULATION MONITORING FOR KANGAROO MANAGEMENT

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In wildlife management, the program of monitoring will depend on the management objective. If the objective is damage mitigation, then ideally it is damage that should be monitored. Alternatively, population size (*N*) can be used as a surrogate for damage, but the relationship between *N* and damage obviously needs to be known. If the management objective is a sustainable harvest, then the system of monitoring will depend on the harvesting strategy. In general, the harvest strategy in all states has been to offer a quota that is a constant proportion of population size. This strategy has a number of advantages over alternative strategies, including a low risk of over- or underharvest in a stochastic environment, simplicity, robustness to bias in population estimates and allowing harvest policy to be proactive rather than reactive. However, the strategy requires an estimate of absolute population size that needs to be made regularly for a fluctuating population. Trends in population size and in various harvest statistics, while of interest, are secondary. This explains the large research effort in further developing accurate estimation methods for kangaroo populations. Direct monitoring on a large scale is costly. Aerial surveys are conducted annually at best, and precision of population estimates declines with the area over which estimates are made. Management at a fine scale (temporal or spatial) therefore requires other monitoring tools. Indirect monitoring through harvest statistics and habitat models, that include rainfall or a greenness index from satellite imagery, may prove useful.

Key words: Aerial survey, harvesting, *Macropus rufus*, *Macropus giganteus*, *Macropus fuliginosus*, *Macropus robustus*.

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POPULATION monitoring serves two purposes in harvest management. Firstly, it provides necessary information, such as population size or trend, for management to regulate the harvest, such as setting quotas or harvest effort. Secondly, it provides 'research and performance evaluation' (Possingham 2001), by indicating whether a harvest strategy is working and allowing that strategy to be refined. This latter role forms the basis for adaptive management, where management learns about the system and the effects of harvesting through monitoring responses to management actions (Shea *et al.* 1998). Ideally, adaptive management should be structured like an experiment, with controls and a range of treatments, in order to maximise what can be learnt from intervening in the system.

This paper is concerned primarily with the first purpose of monitoring, although much of the discussion will still be relevant to the second purpose. The focus is on evaluating and seeking areas for improvement in the present harvesting system and associated monitoring for kangaroos (*Macropus* spp.). This system has operated for more than two decades across the Australian states (Pople and Grigg 1998). Monitoring should be efficient and the results need to be linked to management actions, otherwise they are only of academic interest (Possingham 2001). The monitoring program used for a managed population will depend on the management objective and, for a harvested population, the harvesting strategy.

MANAGEMENT OBJECTIVES

Broadly, the objectives for kangaroo management in Australia are to:

1. maintain viable populations of all exploited species over their current range;

2. allow for a sustainable and viable kangaroo industry; and

3. allow for reductions in populations where they contribute to overgrazing.

Given that this conference is primarily concerned with areas where kangaroos are abundant enough to be commercially harvested, this discussion will concentrate on **2** and **3**, although **1** is the overriding objective.

Ultimately, the desired management goal is a judgement of value, being neither right nor wrong, and it must be recognised as such. Management undertakes actions to achieve a particular goal, and the choice of actions will be based on factors such as feasibility, cost and the nature and extent of unwanted side-effects. These are technical judgements, which can be right or wrong, and must be challenged at the next step once the objective is identified. Caughley and Sinclair (1994) discuss the process of wildlife management and the importance of distinguishing these two steps, the role of wildlife managers and the role of the community at large.

DAMAGE MITIGATION

If the primary concern was damage mitigation, then ideally damage should be monitored. However, if the relationship between damage and population size (*N*) is known, then one can monitor *N* and use it to indicate damage depending on the form of the relationship (Fig.1). However, the level to which kangaroos need to be reduced so that damage is equivalent to the cost of control is not known (Pople and McLeod 2000).

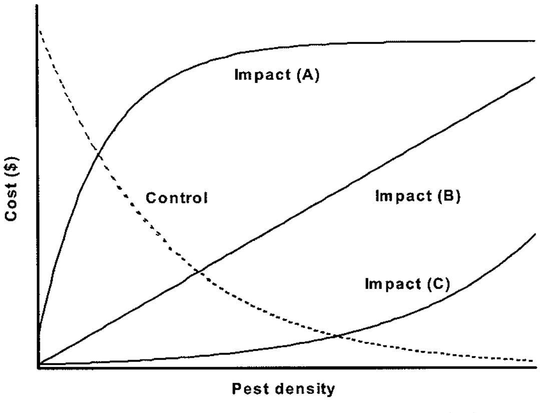

Fig. 1. Relationships between pest density and the *per capita* cost of control (dashed line) and the *per capita* cost of damage or impact (solid lines). A target density could be identified at the point of intersection. After Braysher (1993).

Fig. 1 is an oversimplification, particularly as it assumes that damage (e.g., overgrazing) will be a function of pest density only, and ignores temporal and spatial variation in environmental conditions (e.g., drought vs times of plenty, mulga lands vs Mitchell grass downs) and competitors (e.g., domestic stock). For example, in the rangelands, competition with domestic stock and the potential for land degradation though overgrazing are likely to be heightened during drought. Drought would shift the impact curve from C to A in Fig. 1. The cost of control is also likely to be cheaper during drought as animals are concentrated around persistent feed and water (Newsome 1965).

Even if the cost of damage could be quantified under a range of environmental conditions, it is most unlikely that the kangaroo industry could be responsive enough to remove the necessary numbers of animals at particular times, say during drought. The present strategy of allowing a constant proportion of the population to be harvested each year will lower average population size, producing a lower density than if the population were only harvested at the onset of drought. Shepherd and Caughley (1987) view this suppression of density as a form of insurance against intermittent but inevitable droughts.

SUSTAINABLE HARVESTING

McCallum (1999) contrasted a sustainable harvest with a viable one. The former is an ecological and theoretical concept, while the latter refers to the ability to support a commercial industry. A harvest that is unsustainable will obviously not be viable in the long term, but not all sustainable harvests will be viable for economic reasons. Viability, at least with kangaroos, also requires demonstration of sustainability. So, a monitoring system must not only ensure that the harvest is sustainable, it must ensure that the harvest is seen to be sustainable. In contrast to most fisheries, kangaroo management uses data that are independent of the harvest, providing both a public confidence in the monitoring and a population estimate for setting harvest quotas that is free of the usually untested assumptions associated with indirect monitoring.

It is often remarked that monitoring trends in kangaroo population size, say through an index, is more important than estimating absolute abundance. However, without an absolute population estimate, any harvest policy can only be *reactive*, rather than *pro-active* (McCallum 1999). When populations fluctuate greatly in response to the environment, it is difficult to ascribe a change in an index to harvesting without control areas and a long time series. With estimates of absolute population size, the impact of a certain harvest can at least be predicted. This is not to say that monitoring trends is not important. If an absolute estimate is inaccurate or the impact of harvesting on a population is poorly known, then the ability to detect trends becomes critical.

Harvesting strategies

There are a number of possible strategies, including:
1. Constant yield

2. Constant or variable proportion
3. Constant or variable effort
4. Constant escapement

An ideal strategy is one that returns high (discounted) yields, but has minimal variability in yield among years, and has a low risk of driving the population to extremely low densities. It must also be robust to observation and environmental uncertainty (Milner-Gulland *et al.* 2001).

Since 1984, each of the states has offered quotas that are a constant proportion of estimated population size (i.e., strategy 2). With the exception of Queensland (Qld), these quotas are determined for regions throughout each state. In recent years, there has been some variation on this. South Australia (SA) now adjusts the proportion that can be harvested depending on how close the population is to a target density, which is specific for a region. New South Wales (NSW) and Western Australia have also adjusted the proportion to be harvested, but to a much lesser degree than SA, in response to either an expected increase in the kangaroo population on the back of good rainfall or drought conditions and a high density of kangaroos.

Strategy 1 is considered both inefficient and dangerous for a population that fluctuates (Caughley and Sinclair 1994; McCarthy 1996). Strategy 3 is essentially a tactic used to achieve 2 (Hilborn and Walters 1992). If the relationship between effort and offtake is well known, then regulating effort (e.g., number of shooters) can be effective and efficient. However, if population size is well known, then a quota is likely to be the preferred approach, although there is an element of circularity in this argument.

Harvest strategy 4 involves only harvesting above a threshold (i.e., escapement). Theoretical models suggest that yields will be maximised when all individuals are harvested above a threshold (Lande *et al.* 1995). However, this strategy is prone to overharvesting when there is uncertainty in the population estimates, so adopting a proportional harvesting strategy above the threshold is a better option (Engen *et al.* 1997; Milner-Gulland *et al.* 2001). Under this strategy, population estimates need only to be accurate near the level of escapement. This is relevant to indirect monitoring, where an index (e.g., harvest sex ratio, CPUE) may reach a 'zone of saturation' above a particular density and so no longer reflects changes in N (Caughley 1977).

Simulations of a number of harvesting strategies for red kangaroos (*Macropus rufus*) have shown that, although suboptimal, the current strategy (constant proportional offtake) is only marginally worse than an optimal strategy which involved a threshold density below which there was no harvest (Tables 1, 2; McLeod and Pople 1998). The optimal harvest is an unlikely scenario, as the industry would have to cope with a high variation in yield including long periods of zero offtake (i.e., the strategy is not viable).

For harvest strategy 2, management ideally should have a regular, absolute population estimate for each region where a quota is set. Inaccuracy in the population estimate will lead to over or underharvest, although Milner-Gulland *et al.* (2001) found that harvesting a small proportion of a modelled saiga antelope population each year was robust to biased population estimates. The extent of the problem will be influenced by the size of the bias, the harvest rate, the frequency of population estimates and whether the direction (i.e., negative or positive) of the bias is consistent.

Precision is considered important when monitoring trend (e.g., Caughley and Sinclair 1994), but it is also important when taking a proportional harvest. Increasing precision will reduce the risk of over or underharvest. For a particular sample intensity, decreasing the area for which an estimate of N is being determined leads to poorer precision (Caughley 1979). This is a frustration for management wishing to set quotas over small areas, particularly if these areas are subject to different harvest regimes rather than their quota being a simple carve up of a broader regional or state quota.

Harvesting strategy	Average annual yield	CV of yield (%)	Weeks/year with zero yield
Constant yield	1.7	95	23
Constant proportion	4.1	54	0
Adjusted proportion	3.8	71	0
No quota (shooter FR)	2.5	29	0
Optimal (SDP)	4.5	92	8

Table 1. Average annual yield (red kangaroos/km^2), CV of yield (%), and average number of weeks per year that the season is closed to harvesting from simulations using Caughley's (1987) interactive model. No quota uses the historical functional response of kangaroo shooters. The strategy of an adjusted proportion involves a smaller proportional offtake following a population decline. SDP, Stochastic dynamic programming. After McLeod and Pople (1998).

Harvesting strategy	Average vegetation biomass (kg/ha)	CV of vegetation biomass (%)	Average kangaroo density (kangaroos/km^2)	CV of kangaroo density (%)
No harvest	281	44	49	50
Constant yield	343	35	22	122
Constant proportion	325	36	31	51
Adjusted proportion	314	38	36	49
No quota	304	40	40	55
Optimal	330	35	29	24

Table 2. Population and vegetation dynamics resulting from the alternative harvesting strategies in Table 1.

REVISION OF CORRECTION FACTORS

The importance of an accurate estimate of population size can be gauged from the large research effort over the years in improving estimation methods for kangaroos (Pople and Grigg 1998). The sheer size of the area over which kangaroos are harvested has necessitated the use of aerial survey. However, ground surveys and indirect methods (see below) have been used for species (e.g., wallaroos *Macropus robustus* and whiptail wallabies *Macropus parryi*) and habitats (e.g., forests and ranges) that are not amenable to aerial survey. Initially, most states relied on fixed-wing surveys using strip transect sampling (Pople and Grigg 1998). Not all animals are counted in the strip, usually 200 m, so correction factors are required to bring the raw counts to an estimate of absolute population size. Numerous factors influence the sightability of kangaroos from the air (e.g. speed, height above ground, vegetation cover, temperature, observer and side-of-aircraft) and these need to be standardised, randomised or corrected for if results are to be repeatable (Pople 1999a). In the early 1990s, Qld began using line transect methods from a helicopter. This method has a major advantage over fixed-wing surveys in that survey-specific correction is possible. By comparison with walked line transect counts, the method returned accurate population estimates for *M. rufus* and eastern grey kangaroos (*Macropus giganteus*), but underestimated *M. robustus* population size (Clancy *et al.* 1997). Current work using line transect double counting (Borchers *et al.* 1998) will allow further assessment of this application of line transect sampling. Unfortunately helicopters are about three times the cost of a fixed-wing aircraft with less range. This restricts their use to monitor blocks. However, by direct comparison with fixed-wing surveys, the method has allowed the determination of correction factors for fixed-wing surveys in a range of habitats on a large scale in Qld and NSW.

The historical development of correction factors is shown in Table 3 for 200m strips and Table 4 for 100m strips. The correction factors of 2.3 - 2.4 that were used for many years were based on work on *M. rufus* by Graeme Caughley and co-workers in the 1970s in southern and western NSW. Through the 1980s it became apparent that there were species and possibly regional differences. The work was really only indicative as ground surveys using vehicles are prone to bias and the small scale of many studies

Date	Location	Method	*M. rufus*	*M. giganteus*	*M. fuliginosus*	*M. robustus*
1960s	nw NSW	Vehicle counts	1.8			
1970s	s NSW	Regression	2.3			
	w NSW	Regression	2.4			
1980s	w NSW	Vehicle counts Drive counts	1.8 – 2.8		4.8 – 16.7	11.1
	sw Qld	Walked counts Vehicle counts	1.8 – 4.2	3.5		3.9 – 23.3
1990s	WA rangeland	Fixed-wing line transect	2.3			
	s & cw Qld (7)	Helicopter line transect	1.7 – 3.5	4.0 – 10.2		3.8 – 5.3
2000	NSW rangeland (13)	Helicopter line transect	2.2 – 6.1	3.0 – 13.4		

Table 3. Decade, location (number of sites if more than one) and method of derivation of correction factors for counts of four kangaroo species in 200 m strip transects using fixed-wing aircraft. Most methods involved a comparison with a more accurate technique. The regression method involved extrapolating from counts made at a number of survey heights.

Date	Location	Method	*M. rufus*	*M. giganteus*	*M. fuliginosus*	*M. robustus*
1970s	s NSW	Regression	1.8			
1980s	w NSW	Vehicle counts IMI Regression	1.0 – 1.8		2.3 – 2.9	
1990s	s & cw Qld (3)	Helicopter line transect	1.8 – 2.1	2.1 – 3.8		2.0 – 2.1
2000	NSW rangeland (13)	Helicopter line transect	1.7 – 3.0	3.0 – 5.8		
	nw Qld (3)	Helicopter line transect	1.8 – 2.1	3.5 – 3.8		6.5 – 16.0

Table 4. Decade, location (number of sites if more than one) and method of derivation of correction factors for counts of four kangaroo species in 100 m strip transects using fixed-wing aircraft. Most methods involved a comparison with a more accurate technique. The regression method involved extrapolating from counts made at a number of survey heights. IMI refers to index-manipulation-index using drought mortality.

meant the results did not necessarily translate to the broader scale of a statewide survey. Recent work, using helicopters as a benchmark, has largely circumvented these problems and has been applied across many regions (Pople *et al.* 1998; Cairns and Gilroy 2001). However, the population densities determined by helicopter surveys are not true densities, but are estimates with an associated error. This will increase the variation in the resultant correction factors. The population estimates from helicopter surveys are also likely to be underestimates on average, because walked line transect estimates are known to be negatively biased (Southwell 1994). See Southwell (1989), Pople and Grigg (1998) and Pople (1999b) for further details on survey methods and references for correction factors. Recently determined correction factors for 100m strips in the Mitchell grass downs in northwest Qld are unpublished.

The original correction factors were applied at the level of a survey unit (e.g., 200 m × 5 km), with higher factors applied in more heavily timbered country. While this has intuitive appeal there are obviously differences across regions beyond the level of vegetation cover in a survey unit. Furthermore, vegetation cover varies within a unit and kangaroos may not be counted in the dominant cover type. Ideally, a correction factor should be applied at the level of the animal, accounting for the surrounding habitat and the animal's behaviour. This requires more complex data collection and it would be no small task to determine appropriate correction factors at this scale. The recent work using helicopters generates regional correction factors for each species. These values are obviously insensitive to shifts in habitat use within regions that may lead to a change in sightability. However, the relatively wide variation in regional correction factors (Table 3) suggests that regional factors have a greater effect on bias. It is worth noting that the recent NSW work (Cairns and Gilroy 2001) recorded correction factors very close to those of Caughley and co-workers in the locations where they worked. In other words, Caughley and co-workers were not wrong, rather their results were inappropriately extrapolated to other areas and other species.

Table 3 shows that correction factors for 100 m strips are lower than those for 200 m strips. This is a clear advantage because of smaller random errors. In some cases, sightability in a 100 m strip is close to twice that in a 200 m strip. This suggests that sampling in a 200 m strip, advantageous because of the greater area sampled, has not resulted in many additional animals being counted, reducing this advantage. There is also some suggestion that the 100 m strip counts are more repeatable which is important for any assessment of a population's dynamics. On the strength of this, NSW have narrowed their survey strip width to 100 m and recent fixed-wing surveys in the Qld pastoral zone used a 100 m strip width. Importantly, historical data can be reworked to be compatible with these changes.

These recent studies may also provide an estimate of the error associated with correction factors. In the past, error in the estimate of population size has comprised only sampling error and so it is obviously an underestimate. Using the delta method (Seber 1982), an approximation of the variance of N is (Lancia *et al.* 1996):

$$\mathrm{var}(N) = N^2\left\{\frac{\mathrm{var}(x)}{x^2}(1-\alpha)+\frac{\mathrm{var}(\beta)}{\beta^2}\right\}$$

where x is the raw count of kangaroos, α is the proportion of the study area sampled (i.e., $1-\alpha$ is the finite population correction), and β is the proportion of animals counted in the strip or the reciprocal of the correction factor (i.e., $N = x/(\alpha\beta)$).

Estimates of N are also likely to be biased unless survey-specific correction factors are applied. McCallum (1999) advocated double sampling as a means of achieving this. Briefly, helicopters (using line transect sampling) and fixed-wing aircraft are flown over the same, relatively small areas to derive season, observer and habitat-specific correction factors for the fixed-wing team. Broader-scale surveys are then conducted by the fixed-wing team. Large regional differences in correction factors suggest that the comparison would similarly need to be conducted across many regions, making this approach costly. Nevertheless, the year-to-year variation in correction factors in some regions of NSW reported by Cairns and Gilroy (2001) suggests this approach should not be dismissed and could be used for some areas.

STRATIFICATION

Despite its potential for substantial gains in precision being well known, stratification has been used at only a basic level in broad-scale kangaroo surveys. For example, in SA, densities and standard errors are determined in regions, which are the strata, across the pastoral zone and a pastoral zone estimate and error calculated from these. This is an example of post-sampling stratification with sample intensity not varying among strata. As a rule of thumb, precision will be optimal when sampling effort is proportional to N (or more formally, the variance) within strata (McCallum 2000). There are at least three difficulties in moving to stratified sampling. Firstly, there would be a reluctance to alter fixed sampling units, which are generally best for monitoring trends. Secondly, reducing sampling effort in regions with smaller N will improve the precision at a state level, but not regionally. Thirdly, uneven sampling across the landscape would be less suited to habitat modelling. Nevertheless, there is potential for stratification within regions that would obviously not compromise monitoring population trends at a regional or state level. Indeed, these would be enhanced.

An alternative to conventional stratification is to fit spatial models to count data. Hedley *et al.* (1999) reported improved precision for estimates of minke whale population size using spatial models fitted to line transect data. Other potential advantages include deriving small-scale abundance estimates by integrating under the fitted spatial density surface, determining unbiased estimates from non-random surveys and identifying habitat associations with density (Thomas *et al.* 2002).

INDIRECT MONITORING

Broad-scale aerial surveys have three important limitations: estimates are only available annually at best, precision declines with area and cost restricts the area that can be surveyed. For relatively small areas such as a property, an imprecise regional population estimate provides an even rougher guide to population size on the property. In some areas, such as outside monitor blocks in Qld, there may be no broad-scale population estimate. Other information must be used if the population is to be adequately monitored between surveys, at small scales and outside areas that are surveyed directly. Two types of information may be useful here. The first is using harvest statistics to indirectly monitor population size or harvest rate. The second is to use rainfall and other environmental data to predict population size.

There are now long-term data, over 20 years in some cases, on numbers, harvest offtake and composition for each of the commercially harvested species in regions throughout Australia. These data have been used in the past to develop numerical response models for *M. rufus* and western grey kangaroos (*Macropus fuliginosus*) in western NSW and in SA (e.g., Bayliss 1987; Cairns and Grigg 1993; Cairns *et al.* 2000). These models describe the relationship between rate of increase and food supply or rainfall, and can be used for both prediction and explanation. Such simple models are often inadequate for accurate prediction (Cairns and Grigg 1993; Cairns *et al.* 2000), for which greater complexity will usually be needed (McCallum 2000). At least with more data, regional variation, species differences and the effects of harvesting can be examined.

One new and promising approach is to use spatial analytical techniques (Isaaks and Srivastava 1989) to integrate kangaroo abundance and distribution data from aerial surveys with maps of vegetation, pasture greenness (from satellite imagery, providing an index of pasture condition) and other biophysical variables, to develop models which describe and predict likely herbivore responses to environmental conditions at local scales. This approach is similar to that described in the previous section, but the modelling here is spatiotemporal, with the goal of predicting future population size and distribution.

Harvest data such as sex ratio, carcass weight and catch-per-unit-effort are collected routinely by state agencies and provide more detailed spatial and temporal coverage than direct methods such as aerial survey. By analogy with fisheries, this information could be very useful, especially as it is available continuously, but previous analyses have not attempted to build models predicting abundance and have either lacked abundance data (e.g., Prince 1984), or been restricted to short time series and considered only correlations between harvest statistics and harvest rate (Pople 1996).

CONCLUSION

Methods for counting kangaroos and surveys for estimating their population size over large areas have been successfully developed and implemented over the past 25 years. Further improvement is likely through the use of line transect methods, stratification, spatiotemporal modelling and indirect monitoring. This is optimising monitoring given the present harvest strategy for a given cost. However, two related issues remain unresolved.

Firstly and more generally, the most appropriate harvest strategy for kangaroos is not clearcut. The goals of damage mitigation and sustainable harvesting may require different target population densities and harvest strategies; a conflict with which kangaroo managers continue to grapple. Decision theory (Shea *et al.* 1998) may help resolve this conflict although data are still lacking on the relationship between kangaroo density and damage. There are likely to be tradeoffs between maximising harvest revenue and minimising damage. There are also a number of constraints such as where kangaroos can be harvested and the rate at which they can be taken, and conservation constraints such as threshold densities that populations should not drop below. These tradeoffs and constraints, along with the system's properties, can be modelled, allowing alternative harvest strategies or management options to be compared. Monitoring would then be tailored to the 'best' harvest strategy.

The second issue that needs to be addressed is how much monitoring should be done. Should more or less resources be invested in estimating kangaroo numbers? Little use is made of standard errors in broadscale population estimates of kangaroos beyond assessing whether there has been a significant year-to-year change in population size. Standard errors can also be used to determine the risk of an undesirable management outcome. This may be harvesting at too high a rate, leading to reduced future yields and possibly density dropping below an unacceptable threshold, or harvesting at too low a rate, leading to less effective damage mitigation. The uncertainty in future population size due to environmental stochasticity would also need to be incorporated into this risk assessment (McCarthy 1996). This framework could then be used to determine the adequacy of present monitoring. Surveys could obviously be increased in frequency or intensity to reduce risk. Similarly, there would be an argument for a reduction in monitoring if the resulting increased risks were acceptable.

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3. Regional management in Queensland

3.1 Harvest management 1975-2002

In Queensland, commercial harvest quotas for kangaroos have been set for a single, large zone (Fig 3.1). This has allowed some areas to be harvested at much higher rates than others (Pople 1996). This is despite the claims of Kirkpatrick and Amos (1985) that licensing of shooters and restrictions on the numbers of dealer sites in regions ensures an even spread of the harvest. The problem is exacerbated by the method of estimating population size in the commercial harvest zone. Aerial surveys have been conducted regularly in a core area of ~500,000 km^2 within this region (Fig. 3.2; see Section 1, Table 1.1; Caughley and Grigg 1982). However, outside this area within the commercial harvest zone (~400,000 km^2), surveys have been infrequent. Some areas were surveyed by air in 1980-1982 and 1984, and ground surveys were conducted in eastern areas over 1988-1992 (Southwell *et al*. 1997). Density has therefore at best been extrapolated from these surveys in line with fluctuations in the core area and at worst determined from a guess at the kangaroo density outside the core area relative to that inside the core area.

The concentration of the statewide harvest in the core area is shown Figure 3.2. When compared with estimates of population size, this translates into areas of harvest rates well in excess of the 15% (eastern grey kangaroos) or 20% (red kangaroos) set by the quota throughout the core area (Fig. 3.3). There will invariably be spatial variation in harvest rate, but the overharvest in Figure 3.3 is in large areas. Furthermore, Figure 3.3 shows average harvest rates, which hides the fact that there can be a considerable overharvest in years when the quota is met. This has been seen even at a regional level (see Section 12, Fig. 12.x) where harvests have exceeded 15% for eastern grey kangaroos and 20% for red kangaroos over a number of years. In defence of the management agency, quotas are not the only regulatory mechanism used in the harvest. Shires can be closed to harvesting and harvest statistics have been used to monitor the status of the population (Anon. 1984; Queensland National Parks and Wildlife Service 1989; Queensland Parks and Wildlife Service 2003).

3.2 Harvest management since 2003

The obvious solution to the problem of regional overharvest is to apply regional quotas, which were implemented in Queensland in 2003. Three regions were identified using a combination of the previous core area and administrative (shire) boundaries (Fig. 3.4). As a result, the core area was enlarged. It is likely that this will be extended to five regions (Fig. 3.5). Ideally, the quotas should reflect the level of uncertainty in the population estimates and more generally the risk associated with harvesting for each region. These concerns are examined in Section 5. Queensland Parks and Wildlife Service (QPWS) have addressed this by surveying more regularly in the new western and eastern zones and harvesting at a lower rate in these zones than in the central zone. Furthermore, in the southwestern area of the central zone, where there is no surveying, a density estimate of zero is assumed for all species.

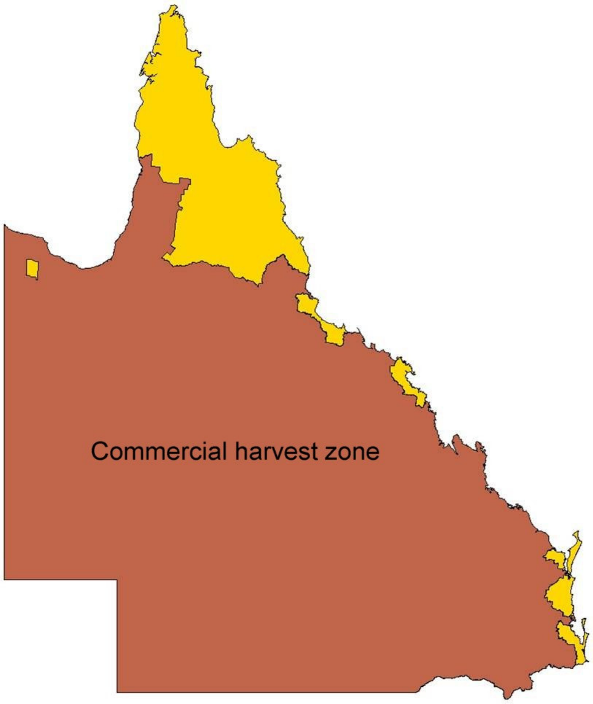

Fig. 3.1. Zone (brown) in which commercial harvesting of kangaroos has been allowed in Queensland. Harvesting is excluded in other areas within this zone such as National Parks and State Forests.

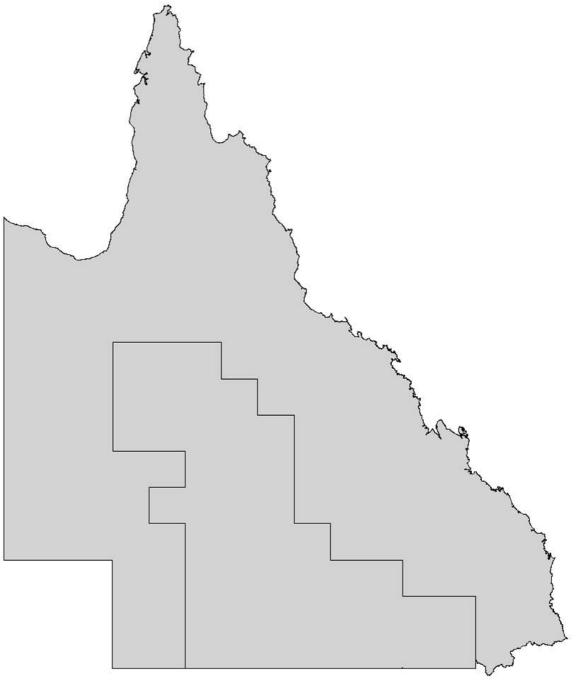

Fig. 3.2. Core area where aerial surveys have been conducted in Queensland in 1980, 1984-present. Outside this area, densities have been interpolated from infrequent surveys or guessed.

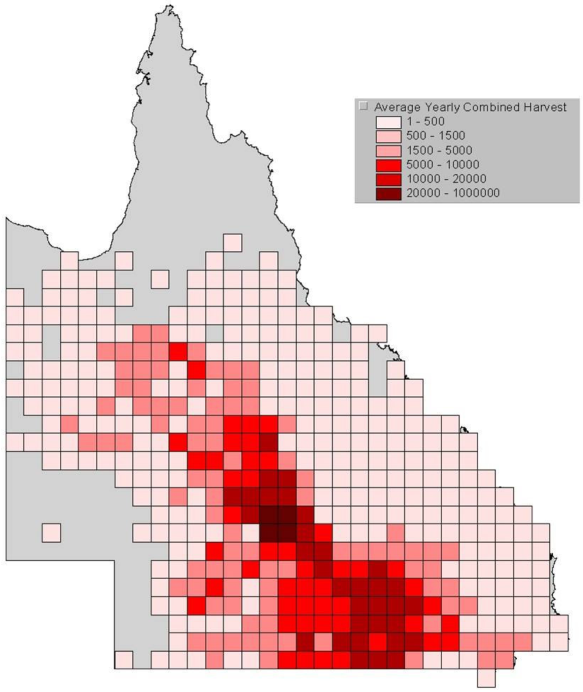

Fig. 3.3. Average annual harvest of all species in grid squares (½° blocks) Queensland 1986-2001.

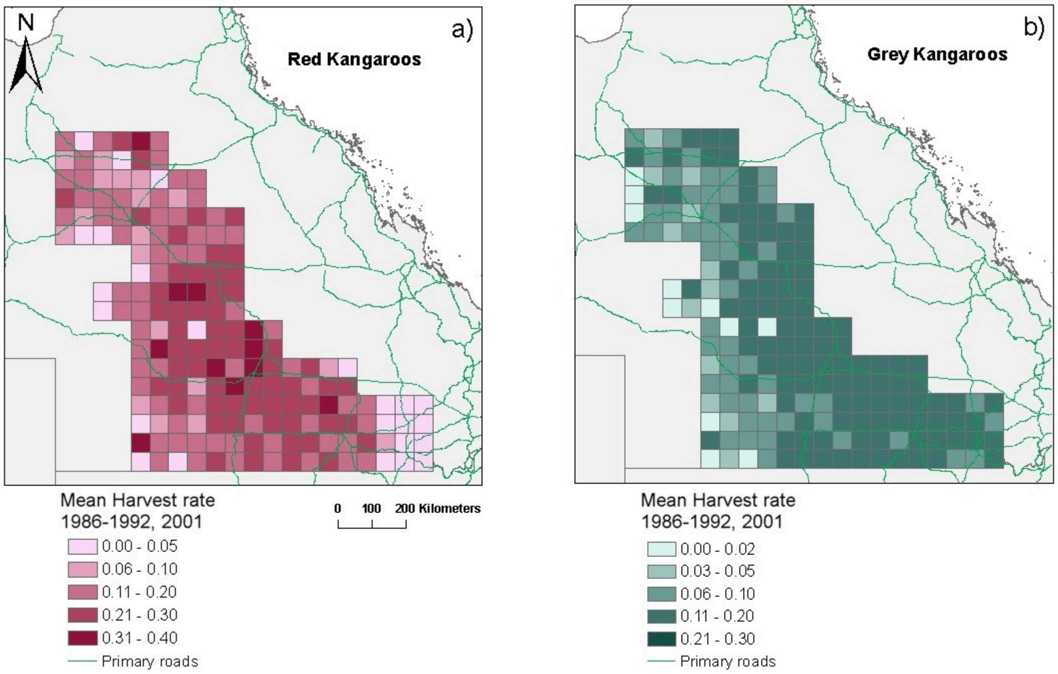

Fig. 3.4. Average harvest rate of (a) red and (b) eastern grey kangaroos in grid squares in the core area (Fig. 3.2) of Queensland for 1986-1992, 2001.

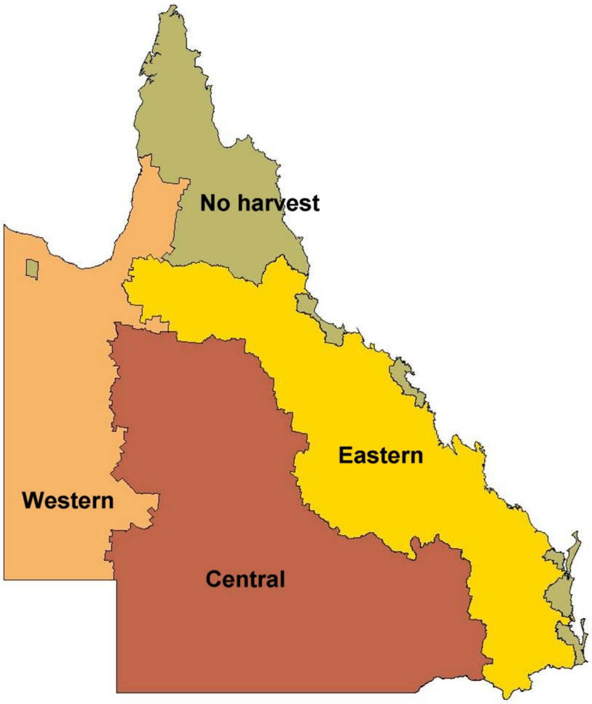

Fig. 3.5. Three commercial harvest zones used in Queensland since 2003. Harvesting is not permitted in the green zone along the coast and on Cape York Peninsula.

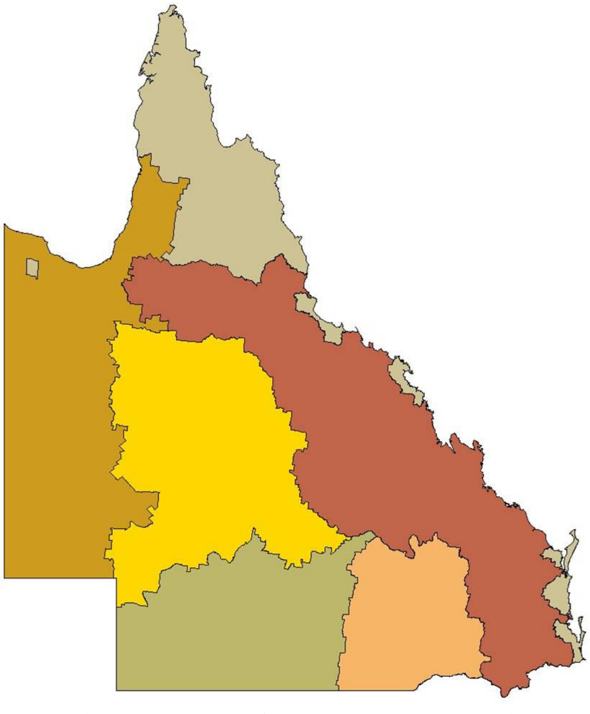

Fig. 3.6. Proposed five commercial harvest zones for Queensland. Harvesting would not be permitted in the light green zone along the coast and on Cape York Peninsula.

3.3 Acknowledgements

Norbert Menke provided the maps in this section.

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4. Estimating wallaroo numbers in Queensland

4.1 Simple estimates of population size

It is well known that wallaroo density is often markedly underestimated by fixed-wing surveys (see Section 2) and so quotas are not set on these data. This has been particularly problematic in Queensland where there is a substantial wallaroo harvest relative to the other states. The use of helicopter surveys has enabled wallaroo numbers to be estimated, although this is still recognised as an underestimate (Clancy *et al*. 1997). The pattern of distribution of wallaroos in Queensland is strongly clumped, with moderate densities only found in an area between Charleville and Winton, with particularly high densities in the Blackall district. It is not surprising then, that population estimates calculated as an average of 10 survey blocks (Fig. 4.1) has poor precision (Table 4.1). An additional 6 survey blocks were flown in an enlarged core area in 2002 (Fig. 4.2; see Section 3, Fig. 3.5), which improved precision (i.e. reduced the 95% confidence interval) and reduced the point estimate of density for wallaroos (Table 4.1). However, the confidence intervals are still broad because of the high variation amongst blocks and the relatively small sample size.

Table 4.1. Density estimates and 95% C.I. for wallaroos in the core area (Fig. 4.1) of Queensland in 2002. Estimates were calculated from 10 or 16 survey blocks or stratifying the 16 survey blocks by harvest density (Fig. 4.3).

Stratification	Survey blocks	Density (km^{-2})	95% C.I.
None	10	11.4	0-23
None	16	8.8	3-14
By harvest	16	3.1	2-4

4.2 Stratified estimates of population size

An alternative estimate of wallaroo density can be obtained by using the historical wallaroo harvest to stratify the core area. Six strata, including a zero harvest, were identified (Fig. 4.3). Stratification should almost improve precision with the main requirement that the area of each stratum is known (McCallum 2000). The resulting estimate is shown in Table 4.1 and, as expected, has a much tighter confidence interval. What is particularly noteworthy is the much lower population estimate. The conclusion is that the survey blocks represent a biased sample for estimating wallaroo density. The implications for management are shown in Table 4.2 with a greatly reduced quota. A quota based on the original 10 survey blocks with no stratification would have represented over half of the revised population estimate.

Despite these previous problems in estimating wallaroo numbers, a number of factors have ensured the sustainability of the harvest and the population. Firstly, wallaroo numbers in Queensland are likely to be underestimated by a factor of 2-3 (Clancy *et al*. 1997). However, comparisons of ground and helicopter counts in the more open habitat of the Barrier Ranges of New South Wales suggests slightly less bias (S. C. Cairns and J. Gilroy unpublished data). Line transect double counting from helicopters will hopefully provide a better quantification of the bias in estimating wallaroo density (see Sections 2 and 7). The second factor is that the wallaroo harvest is >98% male in Queensland because females are generally below the minimum weight set by dealers (see Section 13). Finally, there are large areas which are harvest refuges for wallaroos, including hilly areas and areas of dense vegetation which shooters cannot access, and areas remote from dealer sites where it is uneconomic to harvest (Hacker *et al*. 2003).

Table 4.2. Estimates of wallaroo population size in 2002 in the core area (Fig. 4.1) of Queensland. Estimates were calculated from 10 survey blocks or stratifying the 16 survey blocks by harvest density (Fig. 4.3).

Stratification	Population size	Quota (15%)
None	5.7 million	860,000
By harvest	1.6 million	235,000

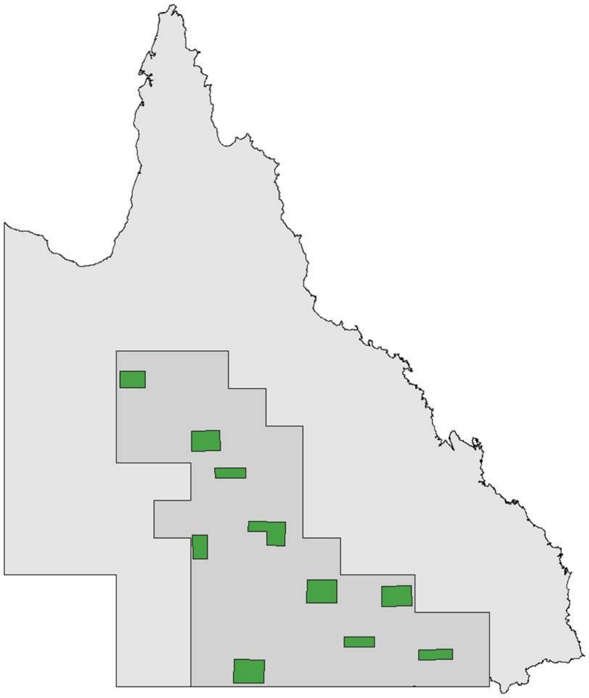

Fig. 4.1. Blocks (dark green) surveyed by helicopters in Queensland since 1992 to estimate kangaroo numbers in the core area (dark grey).

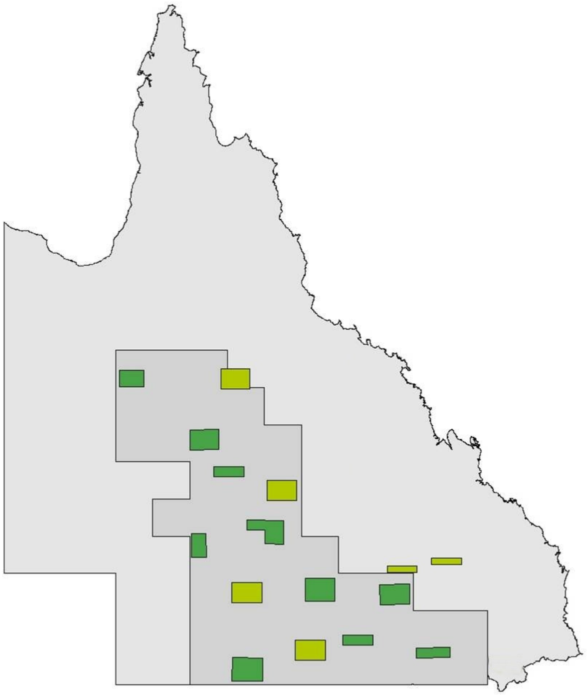

Fig. 4.2. Blocks (dark green) surveyed by helicopters in Queensland since 1992 to estimate kangaroo numbers in the core area (dark grey) and additional blocks (light green) surveyed since 2002.

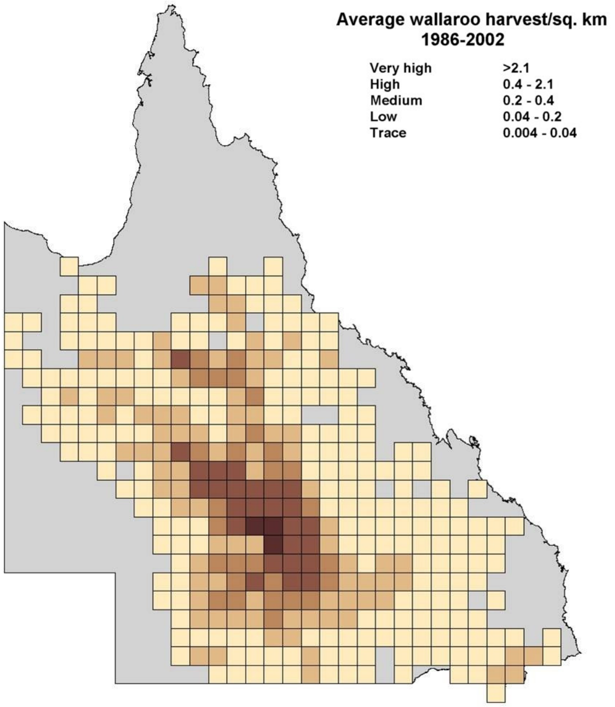

Fig. 4.3. Average wallaroo harvest in Queensland, 1986-2002.

4.3 Other species and spatial modelling

A similar approach could be taken in estimating red kangaroo and eastern grey kangaroo abundance. Indeed, QPWS are using historical harvest data to stratify the new western and eastern zones for these species (see Section 3, Fig. 3.5). Within the central zone, the advantages of stratification for these species are likely to be less spectacular than for wallaroos because their density is far more uniform yielding a lower variation between survey blocks and the survey blocks return similar density estimates to those from fixed-wing surveys (see Section 11; A. R. Pople unpublished data). Using kangaroo densities from the fixed-wing surveys averaged over 1980-1992 in grid squares (i.e. $\frac{1}{2}^{o}$ blocks), the additional survey blocks (Fig. 4.2) were located to minimise the overall bias between the average block density and the density from all grid squares (A. R. Pople unpublished data). There should nevertheless be concern with using a small sample size of blocks which were not randomly located. Spatial modelling is one way of accounting for this problem and is discussed briefly in Section 2. Some analyses have been done for estimating kangaroo density in Queensland and South Australia and preliminary results are summarised in Section 17.

4.4 Acknowledgements

Norbert Menke provided the maps in this section.

4.5 References

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5. Survey frequency and precision

5.1 Introduction

This section draws heavily on two reports produced for New South Wales Department of Conservation on harvest management of kangaroos during drought (Pople 2003) and monitoring kangaroo populations in southeastern New South Wales (Pople *et al.* 2003).

In wildlife management, the appropriate survey frequency and precision has generally been considered with the aim of detecting trends (Caughley 1979; Harris 1986; Gerrodette 1987). In kangaroo management, harvest regulation is primarily through quotas that are set as proportions of absolute estimates of population size (see Section 2). Trends are of secondary importance. This strategy has been well studied and is considered relatively safe and efficient for a fluctuating population (Caughley 1987; Engen *et al.* 1997; McLeod and Pople 1998). However, the strategy requires a regular estimate of abundance on which to set a quota. Imprecision in population estimates and infrequent estimates will risk applying a quota that is either too high or too low (Pople 2003). By not harvesting at the desired rate (e.g. 15%), costs are incurred to the kangaroo industry through reduced and more variable yield, to graziers through increased competition with sheep and damage to crops and there is a social cost if kangaroos are reduced below some arbitrarily low density (i.e. quasiextinction). These costs must be balanced against the cost of more intensive and frequent surveys (i.e. there is a trade-off). Alternative harvest strategies can also be considered in order to reduce the risk of over- or underharvest. These include harvesting at a different, and even variable, rate, regulating effort or incorporating spatial reserves.

Kangaroo managers set annual quotas for a calendar year that represent a percentage (e.g. 15%) of the population estimated annually (in most areas) by aerial survey in the winter of the previous year. Even if the quotas are taken, the actual rates of harvest will differ from 15%, because populations will rarely remain stable. There is therefore some risk of over- or underharvest. If the population halves over 12 months, the *actual* harvest rate over the year becomes roughly 21% instead of the *desired* (set by quota) rate of 15%. If the decline is 80% (see below), the annual harvest rate is likely to be around 34%. A doubling of the population will result in a harvest rate of roughly 11%. These actual rates are approximate because they assume constant geometric growth and decline in the population.

Overharvesting may result in reduced long-term yields if harvest rates are much greater than the maximum sustainable yield (MSY). Underharvesting results in higher average population densities that may result in unacceptable grazing impacts. It may also result in reduced long-term yields if harvest rates are well below the MSY.

In most years, this risk of over- or underharvest is likely to be small, because year-to-year fluctuations are relatively small. On a broad scale, *increase* in the population will be constrained physiologically by the reproductive capacity of females, and modified by sex ratio and age structure. The maximum rate of increase, even in a male-biased population with few juveniles, will fall short of doubling. However, the rate of *decline* can be more pronounced as it is unconstrained by an animal's physiology. In the drought of 1982-83, kangaroos declined by approximately 40% over 12 months in the sheep rangelands of eastern Australia (Caughley *et al.* 1985). However, most of this decline occurred over a shorter period of perhaps 4 months (Robertson 1986), when possibly the more vulnerable individuals died. Had this period of decline been maintained, the decline over 12 months would have been 80%.

These risks will be exacerbated by uncertainty in population size, which is measured by the standard error or confidence interval of the population estimate. For example, population size may be overestimated through chance (sampling error) alone, resulting in an effective harvest rate higher than the desired 15%. This potential overharvest will be compounded if the population then declines.

Changes in population size (i.e. rate of increase) of kangaroos are closely linked to pasture biomass that is driven largely by rainfall in arid areas. Because there is an upper limit to a population's rate of increase, the difference between desired and actual harvest rate is potentially greater during drought than during times of plenty. Moreover, quotas are more likely to be taken during drought because animals are more accessible, graziers are more active in having animals culled and the kangaroo industry will have a relatively greater capacity to take animals as a result of previous higher population densities.

The discussion above ignores how harvesting affects a population depending on whether it is increasing or decreasing. Harvest mortality can be *additional* to natural mortality or *compensatory* (Anderson and Burnham 1976). The latter results from some animals being harvested that would have died anyway. For a fluctuating population of herbivores, mortality will tend to be additive during population increases when pasture is abundant, but tend to be compensatory during declines in drought (Pople 1996). Harvesting will therefore have a greater effect on a population's rate of increase when it is increasing than during drought. Harvesting is unlikely to be completely compensatory or completely additive as there will be potential survivors of drought that may be harvested and there is invariably natural mortality even when food is abundant. The relevance of compensatory mortality to this discussion is that, while the disparity between desired and actual harvest rates is greatest during declines, the overall impact of harvesting is less during declines.

Using a risk assessment framework, this section attempts to identify the appropriate survey frequency and precision for kangaroo harvest management in two locations spanning a broad range of annual rainfall.

5.2 Methods

There is considerable uncertainty in the future dynamics of kangaroo populations. There is uncertainty in the environment (process uncertainty), in the response of kangaroos to the environment and harvesting (model uncertainty) and also in the density of kangaroos estimated from aerial survey (observation uncertainty). Therefore, simulation modelling was used to assess risk (Burgman *et al.* 1993) in harvest management of kangaroo populations and included all three forms of uncertainty. Scenarios covering the following factors were examined:

1. Two alternative population models
2. An arid and more mesic environment
3. Harvest rates ranging from 0-20%
4. Threshold and proportional harvest strategies

5. Survey frequency varying from 1-5 years
6. Precision of population estimates, which determine harvest offtake, varying over coefficients of variation (CV=SE/mean × 100) of 0-200%.

The additional risk posed to the population through harvesting can be couched in terms of probability of quasiextinction (i.e. population falling below an unacceptably low density), minimum, average and variation in population density, time spent below particular threshold densities, average and variation in harvest offtake, or average pasture biomass.

Two models describing the dynamics of kangaroo populations in arid areas were considered: an interactive model described by Caughley (1987) and a ratio dependent model developed by McCarthy (1996). In the interactive model, rainfall drives pasture biomass, which in turn determines the rate of increase of the kangaroo population. There are two negative feedback loops. The first is pasture biomass reducing pasture growth. The second is kangaroo density reducing kangaroo rate of increase by reducing the available biomass by eating it. The ratio dependent model is much simpler, with kangaroo rate of increase a function of the ratio of rainfall to population size.

Both models are based on data for red kangaroos, so extrapolation of the results to the two species of grey kangaroos and common wallaroos needs to be made cautiously. In particular, the two grey kangaroo species have lower maximum rates of increase than red kangaroos and perhaps higher rates of decline in drought in arid regions (Robertson 1986; Bayliss 1987). However, the qualitative differences between the species' dynamics are slight, suggesting the qualitative results from the modelling should apply to all four species in an arid environment. Management agencies accommodate species' differences in lower quotas for grey kangaroos as a percentage of the population.

Contrasting the results of the two models addresses just one form of model uncertainty. A range of parameters for each model can also be considered. This was not done here for two reasons. Firstly, overall model structure was considered a greater influence. Secondly, for the interactive model, the maximum rate of decline was parameterised from a four-month period observed in the 1982-3 drought (Caughley 1987). Whether this rate of decline could be maintained over a longer period is presently unknown, but a model allowing this should provide conservative estimates of risk (i.e. tend to overestimate risk).

Both the interactive and ratio dependent models require rainfall as the main input variable, which was introduced into the model seasonally (i.e. three monthly). Rainfall was taken from Menindee Post Office in western New South Wales (annual mean = 244 mm, SD = 106 mm) where Caughley's (1987) interactive model was parameterised. McCarthy's (1996) model was based on the South Australian Pastoral Zone, so Menindee rainfall needed to be rescaled.

Although the interactive model was developed for an arid-zone population of red kangaroos, it can yield results relevant to eastern grey kangaroos in a more mesic environment. Firstly, predictions of such entities as harvest rates for maximised yield, average population size and harvest yield were not sought; rather the objective of the modelling was to *compare* management scenarios. It is the qualitative rather than the quantitative results of the modelling that are of relevance. Nevertheless, the modelled population needed to show similar dynamics and a similar response to harvesting to an eastern grey kangaroo population in the east of the sheep rangelands. The population fluctuations in Caughley's (1987) interactive model therefore required dampening by reducing the standard deviation in seasonal rainfall by 37% so that it was equivalent to that around Yass (annual mean rainfall = 652 mm) in southeastern New South Wales. Altering the standard deviation in rainfall and not the mean avoided the 'paradox of enrichment', which would have increased the mean kangaroo density and amplitude of fluctuations in kangaroo density (Crawley 1983).

For the interactive model, the kangaroo population was harvested and pasture grew and was grazed down in weekly time steps. Sheep competed with the kangaroo population, consuming 1.5 times the pasture that the kangaroos ate. For the ratio dependent model, the time step was three months. In both models, instantaneous harvest rates were converted to isolated rates of harvesting (Caughley 1977), appropriate to the time step, to simulate harvesting spread evenly throughout each year. Harvest offtake for each three months was determined from a population estimate in the previous year. Harvest offtake was therefore the same for each three months of the year, despite population size changing at each three monthly time step. Population estimates were drawn from a lognormal distribution with a standard deviation dependent upon the survey precision (standard deviation/mean). Survey precision varied from 0 to 2 (i.e. 0-200%), but was set at 0.2 unless otherwise stated.

The initial population size was 10 kangaroos km^{-2} (0.1 kangaroos ha^{-1}). For each scenario (i.e. combinations of factors in 1-6 above), the average of 1,000 simulations is reported. Population models were run in Excel with the add-in POPTOOLS (Greg Hood CSIRO 2002, http://www.dwe.csiro.au/vbc/poptools/index.htm).

5.3 Results

5.3.1 Differences between population models

The two models of population dynamics displayed quite different population behaviour despite fitting data from the South Australian Pastoral Zone reasonably well (McCarthy 1996, Pople *et al.* unpublished). The interactive model generated greater amplitude in population size over time than the ratio dependent model, resulting from weaker density dependence. In the ratio dependent model, the population would recover relatively rapidly from declines in drought and population eruptions were similarly tempered.

Furthermore, the ratio dependent model predicted smaller declines during drought (Pople 2003). This disparity is the result of different rainfall periods ultimately driving population rate of change of kangaroos in the two models. For the interactive model, kangaroos essentially respond to rainfall without any lag. In the ratio dependent model, there is a 12-month lag in the response. A 12-month lag may be appropriate where enhanced juvenile survival is not detected immediately by aerial survey, but it is implausible during drought where there is substantial adult mortality that would be (and has been) detected immediately by aerial survey (see Section 9). A final difference between the two models is that the ratio dependent model generates little effect of harvesting over the range of 0-20% on population decline (Pople 2003), again resulting from its stronger density dependence. The differences between the models are clearly seen in the yield curves (Fig. 5.1), with the ratio dependent model indicating much higher sustainable harvests than the interactive model and a highly implausible MSY of >30%.

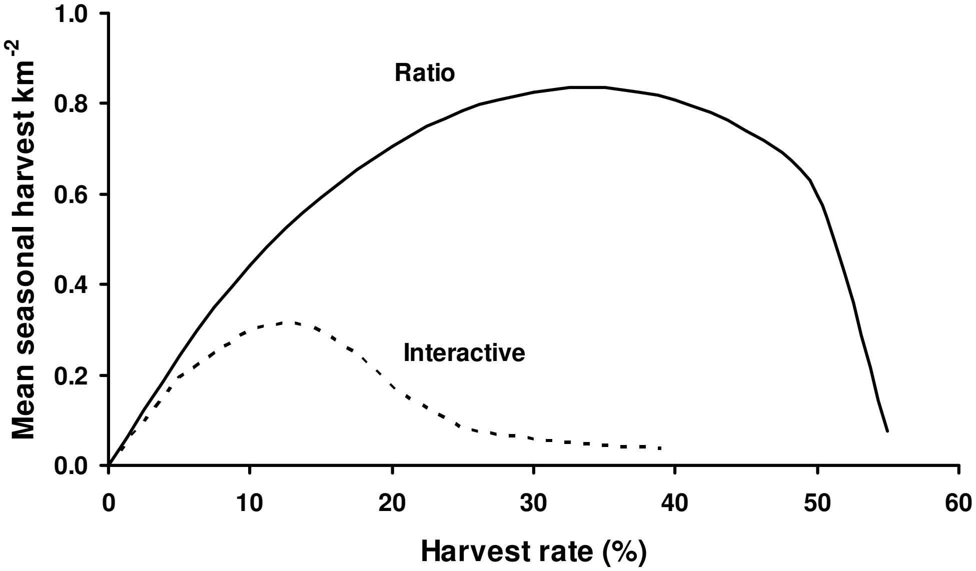

Fig. 5.1. Yield curves based on the ratio dependent model (solid line) and the interactive model (dotted line) of red kangaroo dynamics where the population is harvested annually at constant rates ranging 0-25% over 100 years. Lines represent the average of 1,000 simulations.

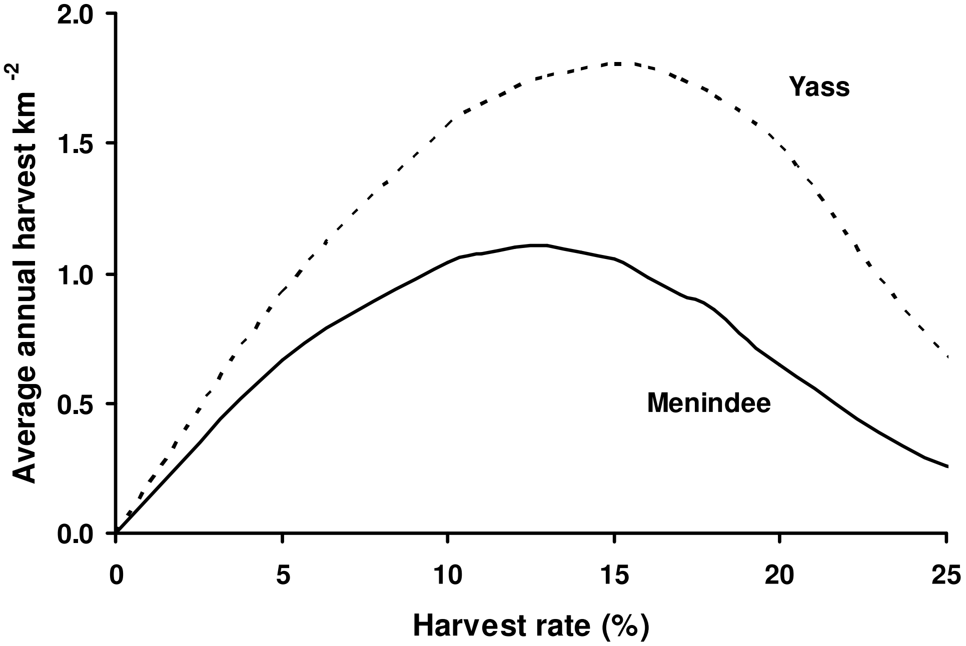

Fig. 5.2. Yield curves for Menindee (solid line) and Yass (dashed line) based on simulations over 100 years of a red kangaroo population harvested annually at constant rates ranging 0-25%. Lines represent the average of 1,000 simulations.

Overall these differences result in a lower risk of overharvest in the ratio dependent model, particularly during drought. Therefore a more conservative risk assessment was undertaken solely with the more realistic interactive model.

5.3.2 Contrasting environments

Not surprisingly, average yield at Yass was higher than at Menindee and the maximum sustained yield is pushed slightly to the right (~13% for Menindee and ~15% for Yass, Fig. 5.2). These yield curves and the associated population dynamics appear plausible for both environments, although the fluctuations in kangaroo numbers in more mesic environments have been poorly described. Modelled average density over 100 years is higher at Yass and declines non-linearly with harvest rate (Fig. 5.3). It obviously follows that the probability of the population falling below some low density increases with increasing harvest rate (Pople 2003). Though not shown, risk does not increase linearly with harvest rate, with risk accelerating from 10-15% and decelerating from 15-20%, which coincides with the MSY for these models of 10-15% (Fig. 5.2). The effect of varying survey frequency, precision and harvest strategy was compared across these two environments, which are roughly at either end of a continuum in aridity across the area where kangaroos are commercially harvested in Australia (Pople and Grigg 1998).

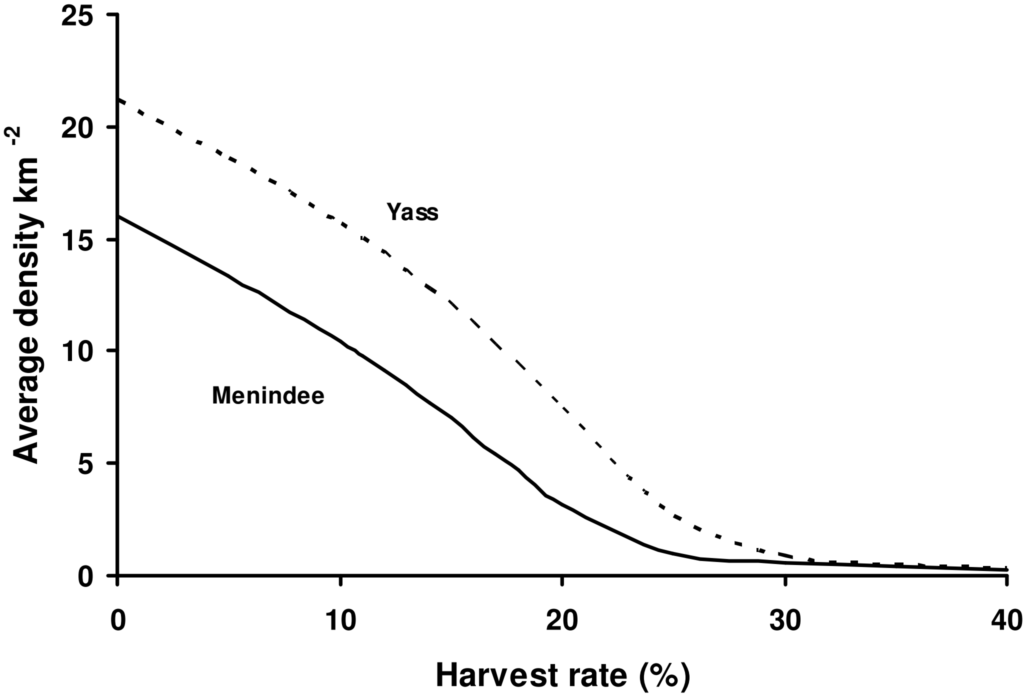

Fig. 5.3. Average kangaroo densities for Menindee (solid line) and Yass (dashed line) based on simulations over 100 years of a red kangaroo population harvested annually at constant rates ranging 0-40%. Lines represent the average of 1,000 simulations.

5.3.3 Survey frequency and harvest strategy

As expected, the risk of quasiextinction is lower at Yass (Fig. 5.4) than at Menindee (Fig. 5.5). Reducing survey frequency not surprisingly increases the probability of quasiextinction. Although the increase does not appear dramatic, a five-year survey frequency at Yass returns a risk of ~10% of the population falling below 2 kangaroos km^{-2} and ~20% for a threshold of 5 kangaroos km^{-2}. The equivalent risks for an annual survey frequency are <1% and 10%, respectively.

An alternative to the probability of quasiextinction shown in Figures 4 and 5 is the time (e.g. number of months) spent below particular thresholds. The pattern is similar (Pople 2003), but allows an acceptable threshold to be identified in different terms. For example, it may not be cost-effective for harvesters to operate at densities below ~3 kangaroos km^{-2}. The risk curve can then be used to identify the likely period of time when harvesting will not be possible. Alternatively, harvesters may simply want to avoid densities below a particular threshold and there may be some socio-political cost of dropping below some density, in which case Figures 4 and 5 are appropriate.

If the harvest rate is reduced to 10%, then the risk of quasiextinction is greatly reduced (Figs 6 and 7). It is only at the lower threshold of ~3 kangaroos km^{-2} that reducing survey frequency with a 10% harvest becomes riskier than a 15% harvest with annual surveys. Even then, it is only when surveys are as infrequent as every five years. On average, reducing the harvest rate from 15% to 10% results in an increase in average population density of 30-50% and a reduction in average harvest offtake of 1-13% (Figs 2 and 3).

Reducing survey frequency results in only a slight increase in population and harvest variability and has little effect on average harvest offtake and population density. At Menindee, harvest coefficient of variation (i.e. SD/mean) increases in a sigmoidal fashion from 0.41 to 0.55 as survey frequency is increased from 1 to 5 years. Quasiextinction is likely to be of principal concern to the kangaroo industry as well as landholders and conservationists, because harvesting is unlikely to be commercially viable below some threshold density. Hacker *et al*. (2003) suggest that this is around 5 kangaroos km^{-2}. However, in practice there are regions where harvesting occurs at densities as low as 2-3 kangaroos km^{-2}, such as in the northwest of the South Australian Pastoral zone (Cairns and Grigg 1993). Incorporating a threshold density in the model below which no harvesting occurs will increase harvest variability. The latter increases exponentially as the threshold is raised (Pople 2003).

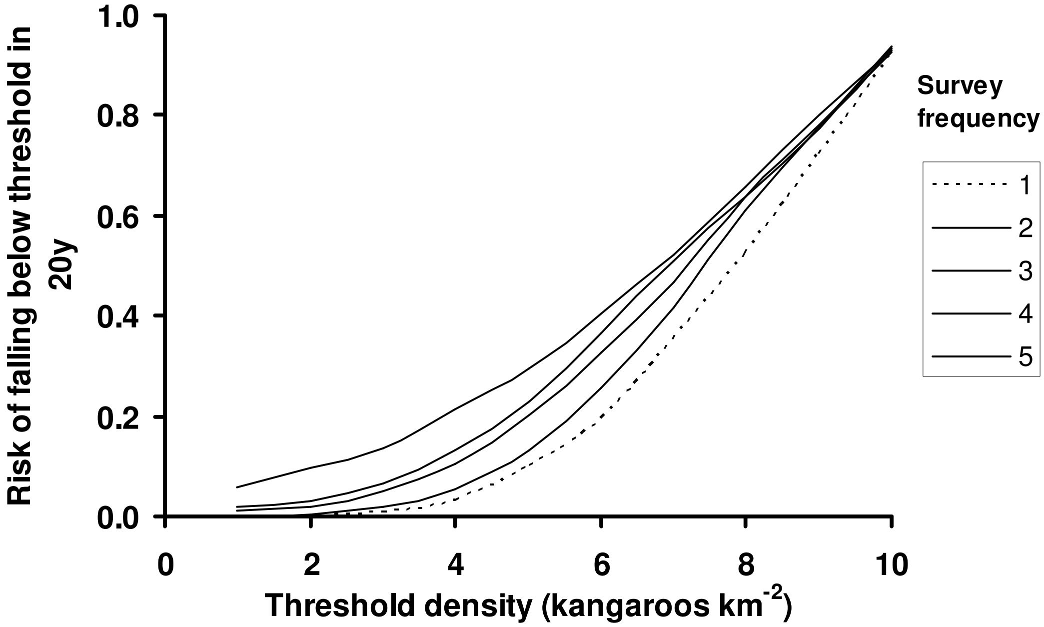

Fig. 5.4. Probability of quasiextinction over 20 years from a harvest rate of 15% with a survey frequency of 1-5 years for Yass.

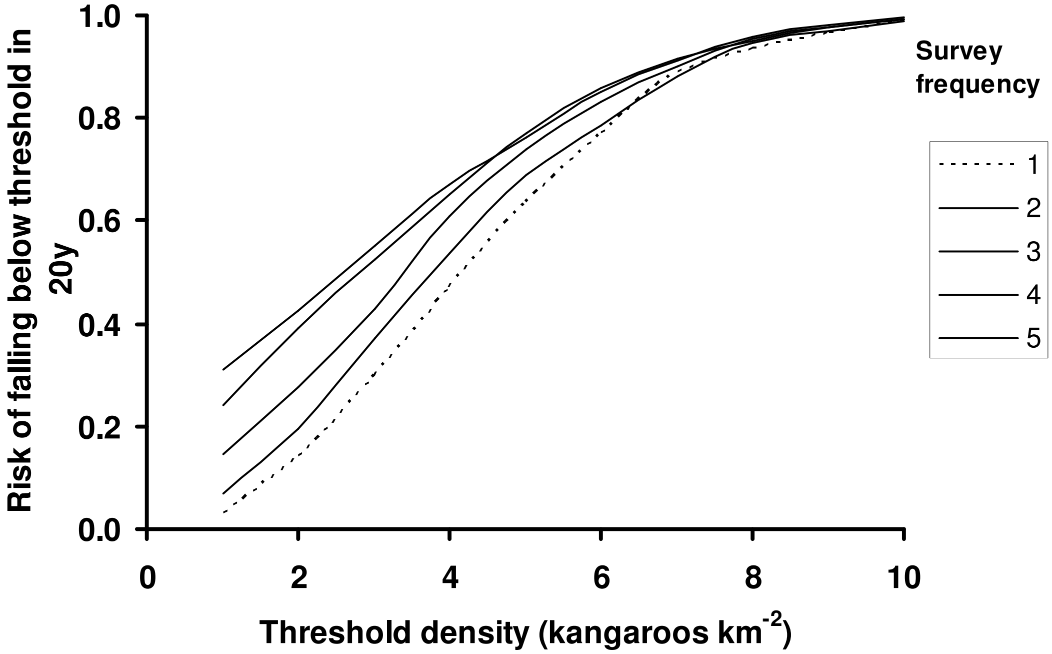

Fig. 5.5. Probability of quasiextinction over 20 years from a harvest rate of 15% with a survey frequency of 1-5 years for Menindee.

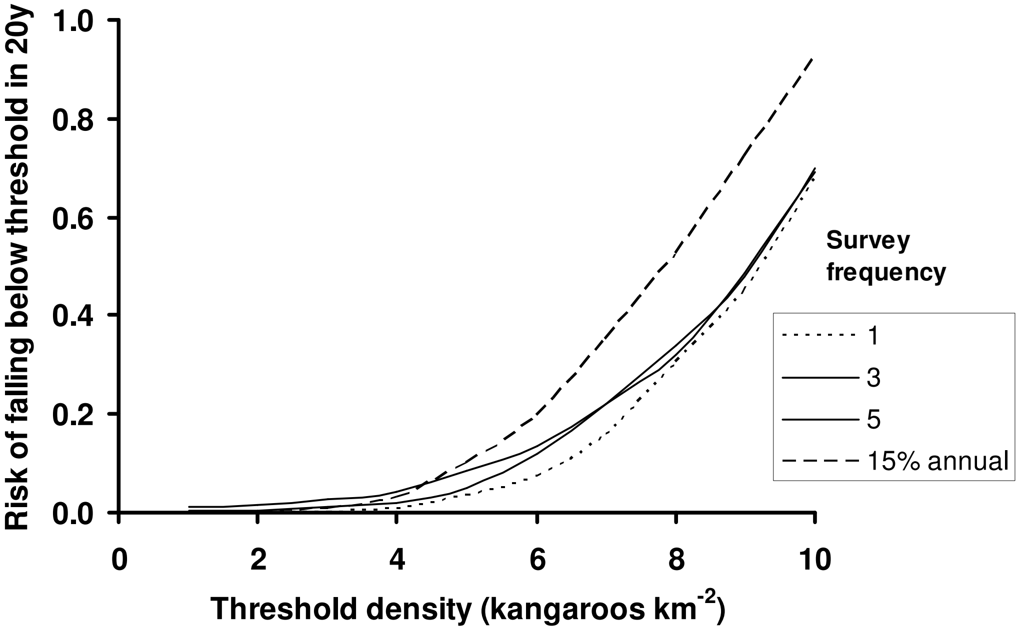

Fig. 5.6. Probability of quasiextinction over 20 years from a harvest rate of 10% with a survey frequency of 1-5 years for Yass. The risk for a 15% harvest with an annual survey frequency (Fig. 5.4) is shown as a dashed line.

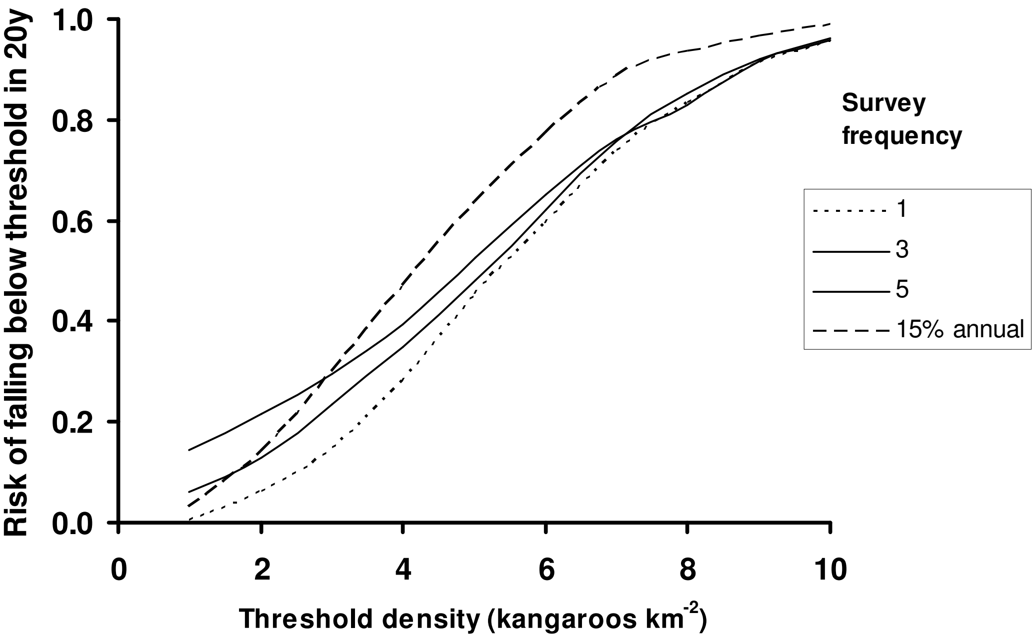

Fig. 5.7. Probability of quasiextinction over 20 years from a harvest rate of 10% with a survey frequency of 1-5 years for Menindee. The risk for a 15% harvest with an annual survey frequency (Fig. 5.5) is shown as a dashed line.

These simulations assume that quotas remain constant between surveys. There are a number of examples from kangaroo management where quotas have been adjusted between infrequent (> 1 year interval) surveys. In the northern tablelands of New South Wales, quotas have been adjusted for changes in kangaroo numbers in adjoining management zones and for recent rainfall (Gilroy 1999). Quotas have been similarly adjusted in Western Australia where the harvest area was surveyed triennially, but now there are three survey areas with a different area surveyed each year (Pople and Grigg 1998). The risks of overharvest described by these simulations are therefore worst-case scenarios. A simple rule was incorporated into the simulations whereby a survey was undertaken at set frequency (three or five years) unless rainfall in the previous year had been ≥ 50% below average, in which case the population was surveyed. This made little difference to quasiextinction risk compared to annual surveys at Yass, but there was some reduction in risk for the 5-year survey program at Menindee (Figs 8 and 9). This presumably reflects the greater likelihood of rainfall ≥ 50% below average.

5.3.4 Survey precision

Pople (2003) found that precision of ≤ 50% had little effect on the probability of quasiextinction under harvesting. Here, a broader range of possible precisions and drawing population size from a lognormal rather than a normal distribution identifies when there is a substantial risk (Figs 10 and 11). Above 50%, precision increases the probability of quasiextinction dramatically. Interestingly, there is an interaction between survey precision and frequency (Figs 12 and 13). Reducing survey frequency from every one to every five years when precision is 50% has a much greater impact on quasiextinction risk than if precision is only 20%.

With poorer precision population size becomes more variable, but not greatly (Fig. 5.14). Harvest variation increases much more markedly with worsening precision (Fig. 5.14). Interestingly, the lines for the two locations converge at extremely poor precision (i.e. high CV=SE/mean), as the latter becomes an increasingly greater influence on harvest and population variation than rainfall variation.

5.3.5 Trade-off between survey frequency and cost

The appropriate survey frequency will depend on the costs of the surveys and the costs of compromising the harvest strategy through not always knowing population size. Imprecision can also incur costs, but this only seems a problem in this case when precision is > 50% (Figs 10 and 11). To make costs comparable, the potential gains and losses incurred by the kangaroo industry, graziers, conservationists and any other stakeholders from adopting various monitoring programs need to be put onto the same scale. This would require detailed exploration and so is not determined here. Instead, a simple estimate of survey cost is contrasted with quasiextinction risk for increasing survey frequency. This should provide a first approximation of the appropriate survey frequency and the nature of the trade-off.

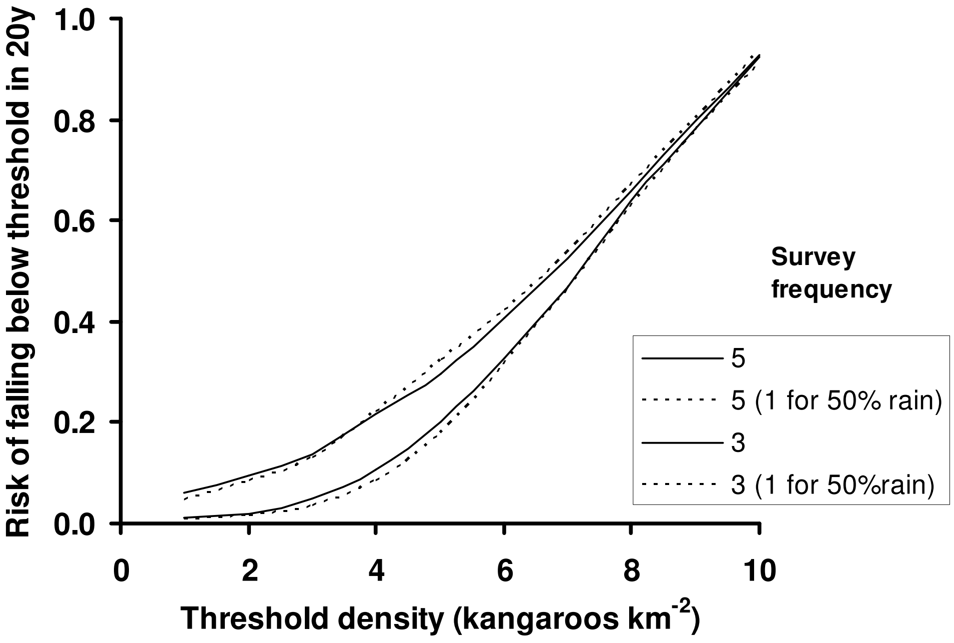

Fig. 5.8. Probability of quasiextinction over 20 years from a harvest rate of 15% with a survey frequency of 3 or 5 years (solid lines) and annual if rainfall is <50% of the long-term mean (dotted lines) for Yass.

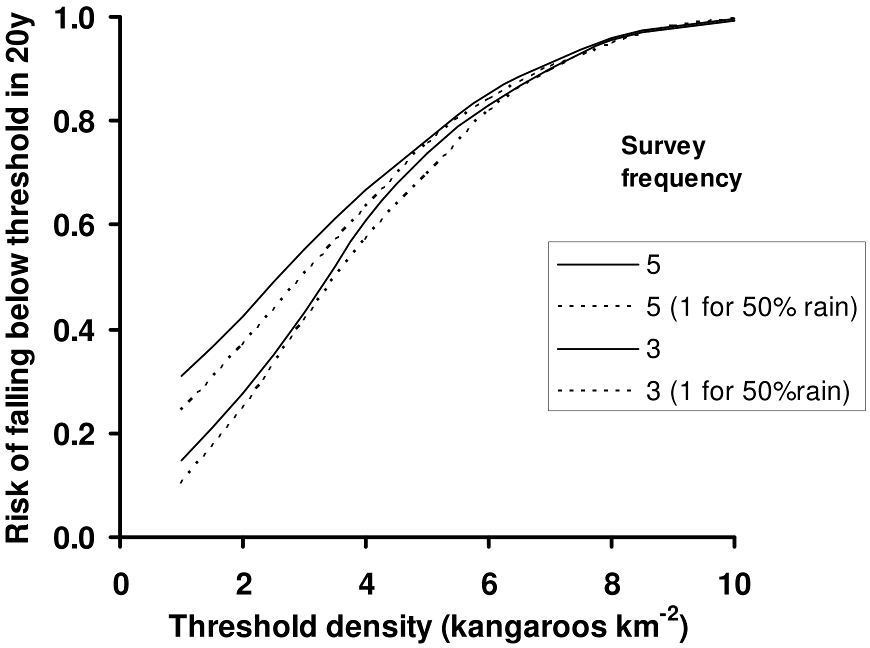

Fig. 5.9. Probability of quasiextinction over 20 years from a harvest rate of 15% with a survey frequency of 3 or 5 years (solid lines) and annual if rainfall is <50% of the long-term mean (dotted lines) for Menindee.

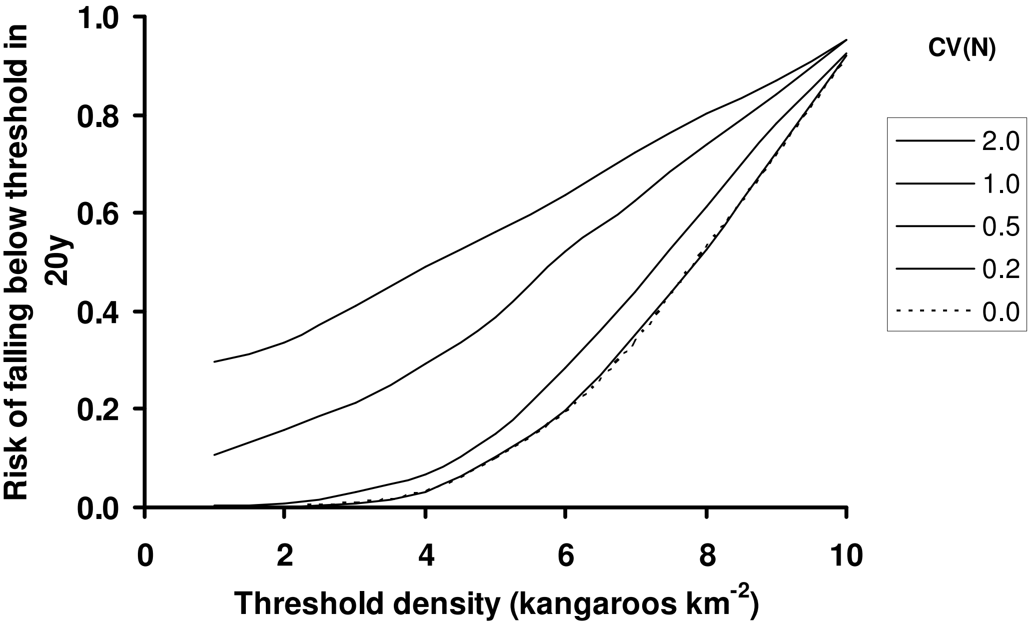

Fig. 5.10. Probability of quasiextinction over 20 years from a harvest rate of 15% with a precision (CV=SE/mean) of 0-2 for Yass.

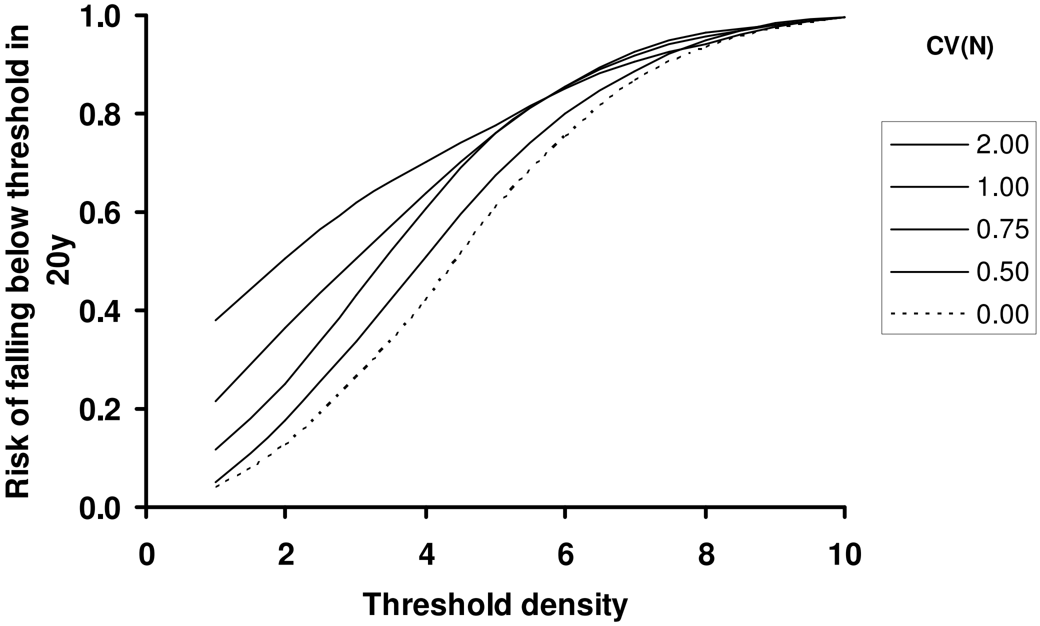

Fig. 5.11. Probability of quasiextinction over 20 years from a harvest rate of 15% with a precision (CV=SE/mean) of 0-2 for Menindee.

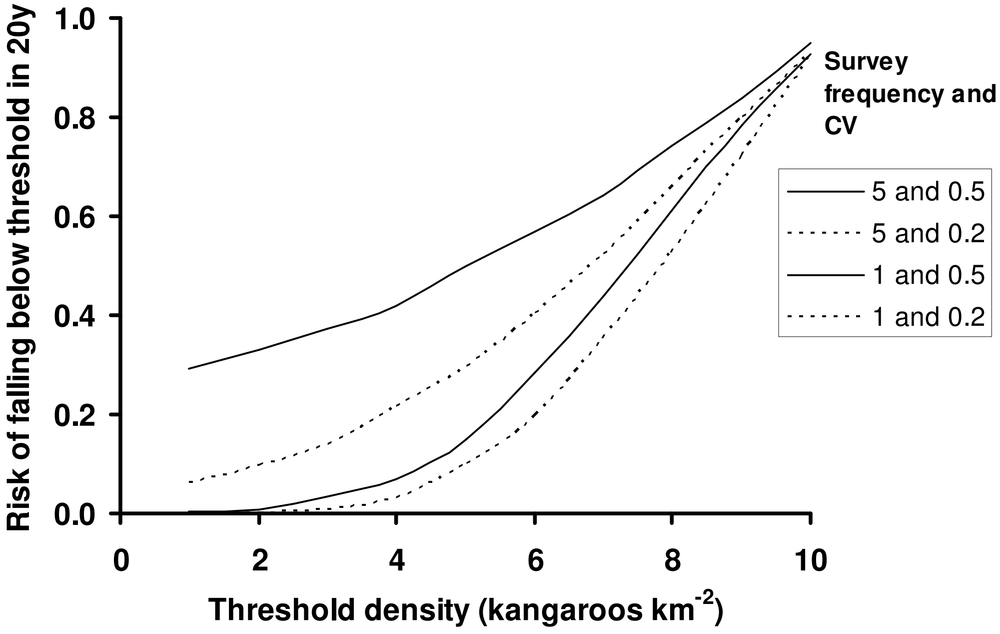

Fig. 5.12. Probability of quasiextinction over 20 years from a harvest rate of 15% with a precision (CV=SE/mean) of 0-2 for Yass.

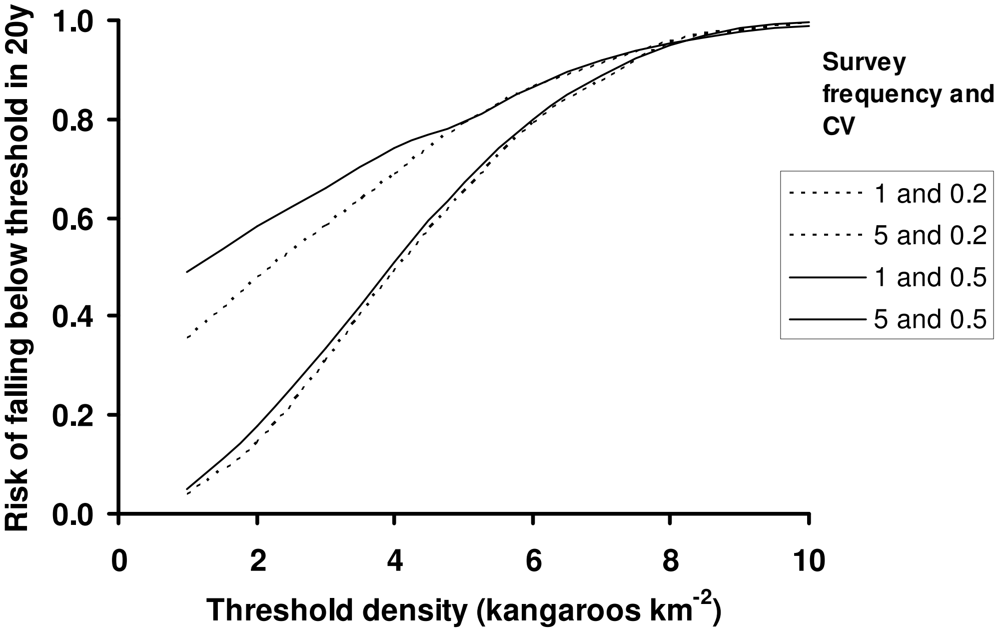

Fig. 5.13. Probability of quasiextinction over 20 years from a harvest rate of 15% with a precision (CV=SE/mean) of 0-2 for Menindee.

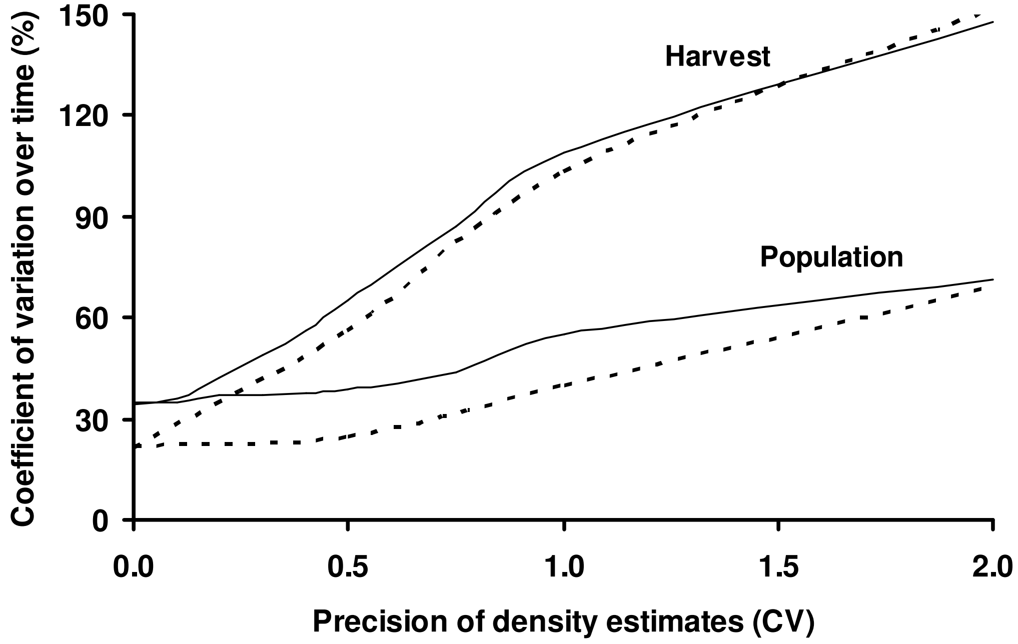

Fig. 5.14. Coefficient of variation (SD/mean) of population density and harvest offtake over 20 years for Yass (dashed line) and Menindee (solid line) for precisions (CV=SE/mean) varying between 0 and 2.

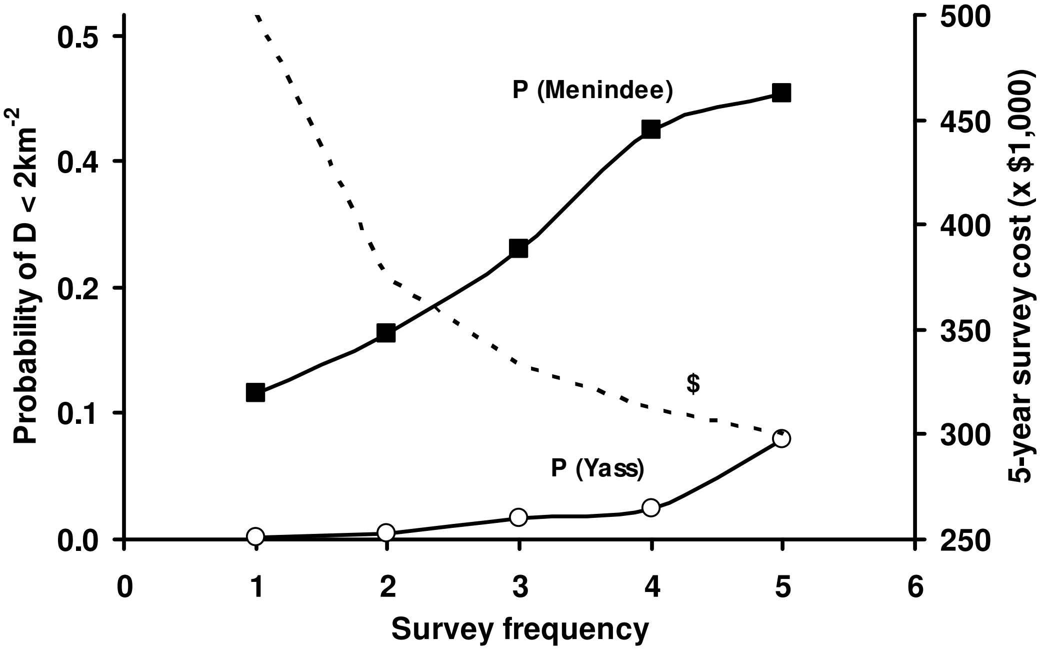

Fig. 5.15. Probability of quasiextinction (solid line) and survey cost over five years (dotted line) for survey frequencies of 1-5 years for Yass (open circles) and Menindee (solid squares).

There are fixed costs associated with conducting aerial surveys that do not change if surveys are conducted less frequently. These include labour costs and can be assumed to be $50,000 per annum. The variable costs primarily comprise aircraft running costs and are assumed to be $50,000 per survey. The total five-year survey cost (fixed + variable × no. of surveys) is shown in Figure 5.15. This shows the ever-diminishing savings from reducing survey frequency. Quasiextinction risk from Figures 4 and 5 is also shown in Figure 5.14, but only for a threshold density of 2 kangaroos km^{-2}. Risk of quasiextinction increases dramatically beyond a survey frequency of every four years. The actual probability should be interpreted cautiously as it is dependent on the model structure and parameters and these have not been assessed for this population. Furthermore, the acceptable level of risk is a value judgement.

5.4 Discussion

There are a number of management recommendations that are reasonably clear from this risk assessment. Firstly, in more mesic environments, a survey frequency of three years with a precision of 20% appears to increase the risk of overharvest only slightly, while substantially reducing survey costs. Whether the increase in risk is acceptable is a decision for management in consultation with stakeholders. Secondly, in arid environments, harvesting near the MSY (e.g. 15% for the interactive model) ideally requires annual estimates of population size with a precision of < 50%. In some regions, such as northwest South Australia and northwest Queensland, harvest rates are low (see Section 12), questioning the need for annual surveys. Figure 5.7 suggests that reducing the quota to 10% would largely offset the risks resulting in surveying less frequently.

The MSYs for these models do not necessarily translate to appropriate harvest rates to set as quotas. The harvest is strongly male-biased which shifts the MSY to a higher rate (Hacker *et al.* 2003). The relevant point from the modelling is that a reduction in harvest rate has a greater influence on risk than changing survey frequency, at least given the model structure and range of parameters examined here.

The insensitivity of risk to changes in precision at CVs < 50% is surprising, particularly given the problem encountered for wallaroos in Queensland presented in Section 4. However, the latter problem was one of an unrepresentative (i.e. biased) sample rather than poor precision, although the problem was highlighted by broad confidence intervals. The simulation modelling here assumes no bias in the population estimates. A single simulation run may use a biased estimate drawn from a lognormal distribution, but on average there is no systematic bias.

In addition to lower harvest rates, other harvest strategies could be employed to offset the risks associated with reduced survey frequency. It is well recognised that imposing a threshold density below which there is no harvest will reduce the probability of quasiextinction and optimise harvest offtake if coupled with increasing harvest rates above the threshold (Engen *et al.* 1997; Milner-Gulland *et al.* 2001). The problem is that the temporal variation in harvest offtake increases with the density at which the threshold is set, and this was modelled for kangaroos by Pople (2003). This is also discussed in Section 8, where a low threshold is recommended. Although it is effectively in force presently because of economic constraints, it would guard against an increase in the value of kangaroo products allowing shooters to operate at lower densities.

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Section 6

Hauser, C. E., Pople, A. R., and Possingham, H. P. (in press). Should managed populations be monitored every year? *Ecological Applications*.

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Should managed populations be monitored every year?

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Abstract:

We often need to estimate the size of wild populations to determine the appropriate management action, for example to set a harvest quota. Monitoring is usually planned under the assumption that it must be carried out at fixed intervals in time, typically annually before the harvest quota is set. However, monitoring can be very expensive and we should weigh the cost of monitoring against the improvement it makes in decision-making. A less costly alternative to monitoring annually is to estimate population size using a population model and information from previous surveys. In this paper, the problem of monitoring frequency is posed within a decision theory framework. We discover that a monitoring regime that varies according to the state of the system can out-perform fixed interval monitoring. This idea is illustrated using data for a red kangaroo population in South Australia. Whether or not one should monitor in a given year is dependent on the estimated population density in the previous year, the uncertainty in that population estimate, and past rainfall. In particular, monitoring is important when the estimated population density in the previous year is very uncertain. This may occur if monitoring has not taken place for several years, or if rainfall has been above average. Monitoring is also important when previous information suggests that the population is near critical thresholds in population abundance. However monitoring is less important when management can have little impact on the population.

Keywords: monitoring, decision theory, optimization, harvesting, red kangaroo, rangelands

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Introduction

Wildlife management requires periodic monitoring to ensure informed decision making (Walters 1986, Possingham et al. 2001). Monitoring wildlife populations for management has two functions (Yoccoz et al. 2001). First, it is essential for circumstances where decisions are determined by the estimated size (and more generally state) of the population - state-dependent decision making (Pollock et al. 2002). Second, it provides an understanding of system dynamics, which can be used in future decision making (Walters and Hilborn 1978).

Previous authors concerned with how we should monitor have focused on trend detection (e.g. Kendall et al. 1992, Eggeman et al. 1997, Forcada 2000, Tyre et al. 2003), recognizing the relationship between power, effect size and sample size in space and time. Some studies have devised monitoring procedures that maximize power to detect trends (Taylor and Gerrodette 1993, Hayward et al. 2002, Pollock et al. 2002). However to determine the optimal monitoring strategy we need to know what power or accuracy is necessary to make good management decisions. Di Stefano (2003) argues that acceptable Type I and Type II errors should be set by considering their relative costs. Yet it is only recently that authors (Yokomizo, Yamashita and Iwasa 2003, Field et al. 2004) have explicitly considered the costs and outcomes of monitoring as part of management. While decision theory tools are often used in the fields of harvesting, conservation and control (Shea et al. 1998), there has been little optimization of monitoring using decision theory.

Yokomizo, Haccou and Iwasa (2003, 2004) are the first authors to combine monitoring and management within a single decision theory framework. For a declining population, they identified the monitoring and conservation effort that minimized the total cost of monitoring, conservation effort and extinction risk. They found that if prior information is highly uncertain or indicates that the population is small, then more effort should be spent on monitoring. The optimal conservation effort is large when the population estimate after monitoring is small, but effort is relatively independent of the uncertainty around the estimate. Results were more complex over a time horizon of more than one period.

When management is framed within decision theory, the traditional approach is to use the same monitoring effort before each management decision is made. Yokomizo, Haccou and Iwasa (2003, 2004) challenge this practice by integrating the costs of monitoring in the optimization. If we are confident about our understanding of system dynamics, then we might be able to use our system model and previous data to make a reasonable prediction of the system state before monitoring even takes place. If monitoring is a costly procedure then we must determine whether the extra information it provides outweighs this expense. How much better is the state-dependent decision we make when we compare our observed state to our model-based prediction?

In this paper we investigate the optimal monitoring of a harvested population. We integrate the costs and likely outcomes of monitoring within the framework of decision theory. Our focus is the management of commercially harvested red kangaroo (*Macropus rufus*) populations in South Australia, but there are broader applications to all wildlife populations. In our model population fluctuations are caused by variable rainfall and its effect on food availability (Caughley 1987). While quotas are currently set using a population estimate derived from an expensive survey, it may be preferable in some circumstances to use freely available rainfall data and a model-based prediction of population size to set the harvest quota. We expect there to be a trade off between the reduced cost of using a modeled prediction for the harvest decision and the increased risk of making a bad harvest decision.

Problem Definition

Here we provide some background information on management of the red kangaroo in Australia with a particular emphasis on devising an integrated measure of the "value" of different kangaroo densities to society. We will also describe the components of the problem formulation, including the population model.

(a) Background to case study

In South Australia, aerial surveys of the pastoral zone (~240 000 km^2) are conducted annually by the state government conservation agency to estimate the abundance of three kangaroo species. In this paper we use density, harvest and rainfall data for just one of the species, the red kangaroo, for the North-east Pastoral Kangaroo Management Region (~31 000 km^2) from 1978 to 2002 (Grigg et al. 1999, Jonzén et al. 2004). Similar surveys are conducted in other Australian states. Vast areas are surveyed incurring considerable costs. In South Australia, population estimates are used by the conservation agency to set regional quotas for commercial harvest throughout the state in the following year. In the last decade, annual harvest in the region has ranged between 12% and 22% of the estimated population in the previous survey.

Various stakeholders have different interests in kangaroo management. There is a desire for commercially viable harvests, control of kangaroo density to reduce grazing pressure, and maintenance of populations at levels consistent with social and cultural values (Pople and McLeod 2000, Grigg and Pople 2001). Kangaroos have historically been harvested for their skins, which produce fine-grade, valuable leather. More recently, their value has increased with an expansion of markets for kangaroo meat for human consumption in addition to lower value pet meat. Kangaroos also compete with domestic livestock, particularly sheep, damage crops and hamper the rehabilitation of degraded vegetation communities. Finally, kangaroos are an iconic group of species in Australia and conservation concerns are frequently raised, forcing management agencies to demonstrate population viability. To integrate these stakeholder values we pose a utility function that expresses the relative desirability of a range of kangaroo densities.

The current management procedure involves monitoring with the same effort each year, providing an estimate with relatively constant precision and cost. A survey of the pastoral zone of South Australia costs about AUD$50,000 and the resulting population estimate for the North-East Pastoral region has a coefficient of variation of around 20%.

We contrast the existing strategy of an annual survey with an alternative strategy where we set the quota using an estimate of density from a model and previous data. In this situation the harvest decision would be made in the face of greater uncertainty, which increases the risk of setting an inappropriate harvest quota. For example, we might incorrectly predict that the population is of moderate size when it is actually low. The moderate quota that is set will cause over-harvest, a lower average population size in the long term and hence a potential negative impact on public perception and kangaroo industry profitability. If we incorrectly predict that the population is of moderate size when it is actually high, then too many kangaroos may survive after harvest, leading to over-grazing. Our task is to weigh the risk and consequence of making such mistakes against the cost of monitoring.

(b) The population model

Previous models for population dynamics of kangaroos have generally included density-dependence and an environmental variable. The environmental variable is most commonly rainfall, a surrogate for food supply, over some previous period (Cairns and Grigg 1993, McCarthy 1996, Bayliss 1985*a*, Bayliss1985*b*) although pasture biomass has been modeled directly (Caughley 1987) . Jonzén et al. (2004) use a time series model that includes the effect of harvest and sheep population size. We use a similar approach and assume that red kangaroo density changes from year to year according to a Ricker-type function with intrinsic growth rate a, effect of density dependence b, effect of rainfall c, and process error ε_t:

$$N_{t+1} = \left(N_t - C_t\right)\exp\left(a + bN_t + cR_t + \varepsilon_t\right) \tag{1}$$

where N_t is the red kangaroo population density at the beginning of year t. The harvest removed from the population during year t is expressed as a density by the term C_t. All reproduction and natural mortality is assumed to occur after harvest. The process errors $\{\varepsilon_t, t = 0, 1, ...\}$ are independent and identically distributed normal random variables with mean zero and variance υ^2. The rainfall term R_t is the total rain falling during year t-1.

To fit this model to available data for the North-East Pastoral Kangaroo Management Region, we standardized annual rainfall using the mean and variance of the 102-year time series. Relevant rainfall data were matched to density estimates and harvest data for the region from 1978 to 2002. We obtained parameter estimates $a = 0.5316$, $b = -0.0377$, $c = 0.2264$ and $\upsilon^2 = 0.0507$ for equation (1) by assuming that there was no observation error in the data and using the least squares method (Jonzén et al. 2004).

We assume that the harvest C_t taken in year t is exactly the quota that is set. The annual harvest quota is set as a constant proportion of the point estimate for density at the beginning of the year, and we use the expected density for this point estimate. If harvest fraction h is used to set the quota, then the total harvest is

$$C_t = h\mathbf{E}\left(N_t\right).$$

We use a fixed harvest fraction of $h = 20\%$. This is currently the maximum harvest fraction set for red kangaroos in South Australia (SADEH 2002). Thus the estimation of density in year t affects the harvest taken, which in turn affects future density through equation (1). The expected density $\mathbf{E}(N_t)$, and the uncertainty of this value as a point estimate, will depend on whether or not we conducted a survey before setting the harvest quota.

(c) The objective and the utility function

The identification of an appropriate objective for a given management problem can be an enormous task in itself. It is a subjective decision that should be made by managers and other stakeholders under the guidance of social scientists. Below we describe a simple relationship between overall utility, the expected value of which we attempt to maximize, and kangaroo density. While defining a utility function and hence objective is important, this is not the central focus of this paper. Our choice is primarily to illustrate the method.

Some densities are considered more desirable than others. Low densities put the population at risk of local extinction, reduces yield and longer-term viability for harvesters and may lead to reduced visual amenity for tourists, while high densities cause over-grazing. Thus we have created a utility function that is very low as the population approaches local extinction, positive for densities of 5 to 20 individuals per square kilometer, and decreasing as density increases above 20 individuals per square kilometer. We use the utility function

$$(2) \qquad U(N) = -\alpha e^{-\beta N} - \gamma N + \delta, \qquad N \geq 0,$$

with

$\alpha = 120$, $\beta = 0.4$, $\gamma = 1$, $\delta = 20$,

where $U(N)$ is the "desirability" of kangaroo density N, and density N is measured in individuals per square kilometer. The utility does not need to be measured in monetary units, it simply reflects the relative integrated community desirability of different densities.

The utility function $U(N)$ is plotted in Figure 1. Local extinction ($N = 0$) is considered very undesirable and the utility of low densities decays exponentially as population density increases (the first term in equation (2)). As density increases utility decreases linearly as a response to increasing damage and over-grazing caused by kangaroos (the second term in equation (2)). The parameter values were chosen so that extinction was considered much more undesirable than any realistic level of property damage. Densities between 5 and 20 individuals/km^2 are most desirable.

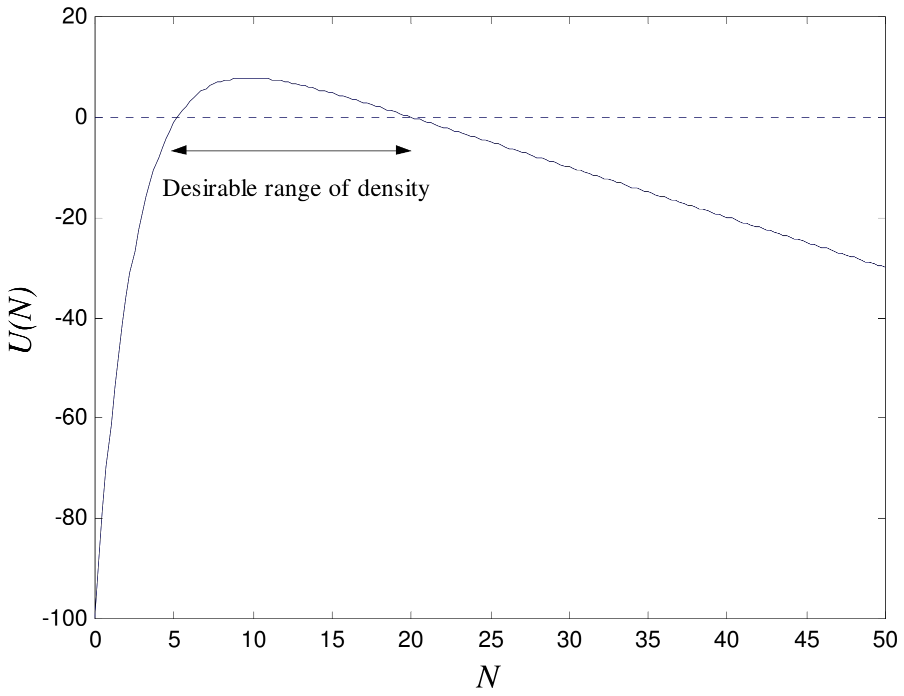

Figure 1. The relative utility, $U(N)$, of density N; as in equation (2) with $\alpha = 120$, $\beta = 0.4$, $\gamma = 1$, $\delta = 20$.

(d) The process of data collection and decision-making

Consider the decision that we must make at the beginning of year t. Regardless of whether or not we choose to conduct a survey, we must set a quota for the harvest to be taken during year t. This harvest will affect the population density at the beginning of year t+1. Our utility function $U(N)$ will give the value of this population density. The objective is to maximize the combined utility of the population density at the beginning of year t+1 and the survey decision at the beginning of year t. In making the survey decision we use equation (1) and relevant previous data. We need total rainfall during year t-2 and an estimate for density in year t-1 to predict kangaroo density in year t in the absence of a survey. Then we need rainfall during year t-1 to predict kangaroo density in year t+1, and hence calculate the expected utility.

We assume that rainfall data are obtained without cost or observation error. Each year we describe our estimation of the population by a lognormal distribution with parameters μ and σ. Therefore the probability density function for population density N is

$$f_N(n) = \frac{1}{\sqrt{2\pi\sigma^2}\, n} \exp\left[-\frac{(\ln n - \mu)^2}{2\sigma^2} \right].$$

The mean and variance of this probability density function is

$$\mathbf{E}\left(N_t\right) = e^{\mu+\sigma^2/2}, \qquad \operatorname{var}(N_t) = e^{2(\mu+\sigma^2)} - e^{2\mu+\sigma^2}.$$

We use distribution parameters μ_{t-1} and σ_{t-1}, and rainfall data R_{t-1} and R_t as state variables when making a state-dependent monitoring decision for the beginning of year t. Parameters μ_{t-1} and σ_{t-1} provide a distribution of plausible values for last year's density N_{t-1}. Rainfall data R_{t-1} and R_t can be combined with equation (1) to find plausible values for this year's density N_t, next year's density N_{t+1} and ultimately the utility $U(N_{t+1})$. The complete process of data collection and decision making is shown in Figure 2.

Assume that we have the required state variables μ_{t-1}, σ_{t-1}, R_{t-1}, R_t to make the optimal monitoring decision. Let D be a Boolean variable that indicates the monitoring decision made, where D=1 indicates that a survey is to be carried out and D=0 indicates that a harvest quota is set using a model-based prediction and previous data. Then the value of the best decision $F(\mu_{t-1}, \sigma_{t-1}, R_{t-1}, R_t)$, is

$$F\left(\mu_{t-1}, \sigma_{t-1}, R_{t-1}, R_t\right) = \max\left\{V_0, V_1\right\}$$

where

$$V_0 = \mathbf{E}\left[U\left(N_{t+1}\right) \mid D = 0\right] \tag{3}$$

$$V_1 = \mathbf{E}\left[U\left(N_{t+1}\right) \mid D = 1\right] - S. \tag{4}$$

The variable V_0 is the value of deciding not to conduct a survey. It is just the expected utility of the population density in one year's time if our quota is set using a model-based prediction of kangaroo density. The variable V_1 is the value of deciding to conduct a survey. It is the expected utility of the population density in one year's time under the assumption that a survey is conducted, with a cost, S, for the survey. This represents the expense associated with obtaining a precise population estimate. To obtain the maximum value F we choose the larger of V_0 and V_1.

Note that the expected utility of the population density at the beginning of year t+1 depends on the monitoring decision made at the beginning of year t. Choosing not to conduct precise surveys makes our density prediction increasingly uncertain each year, and hence affects the expected utility of the decision.

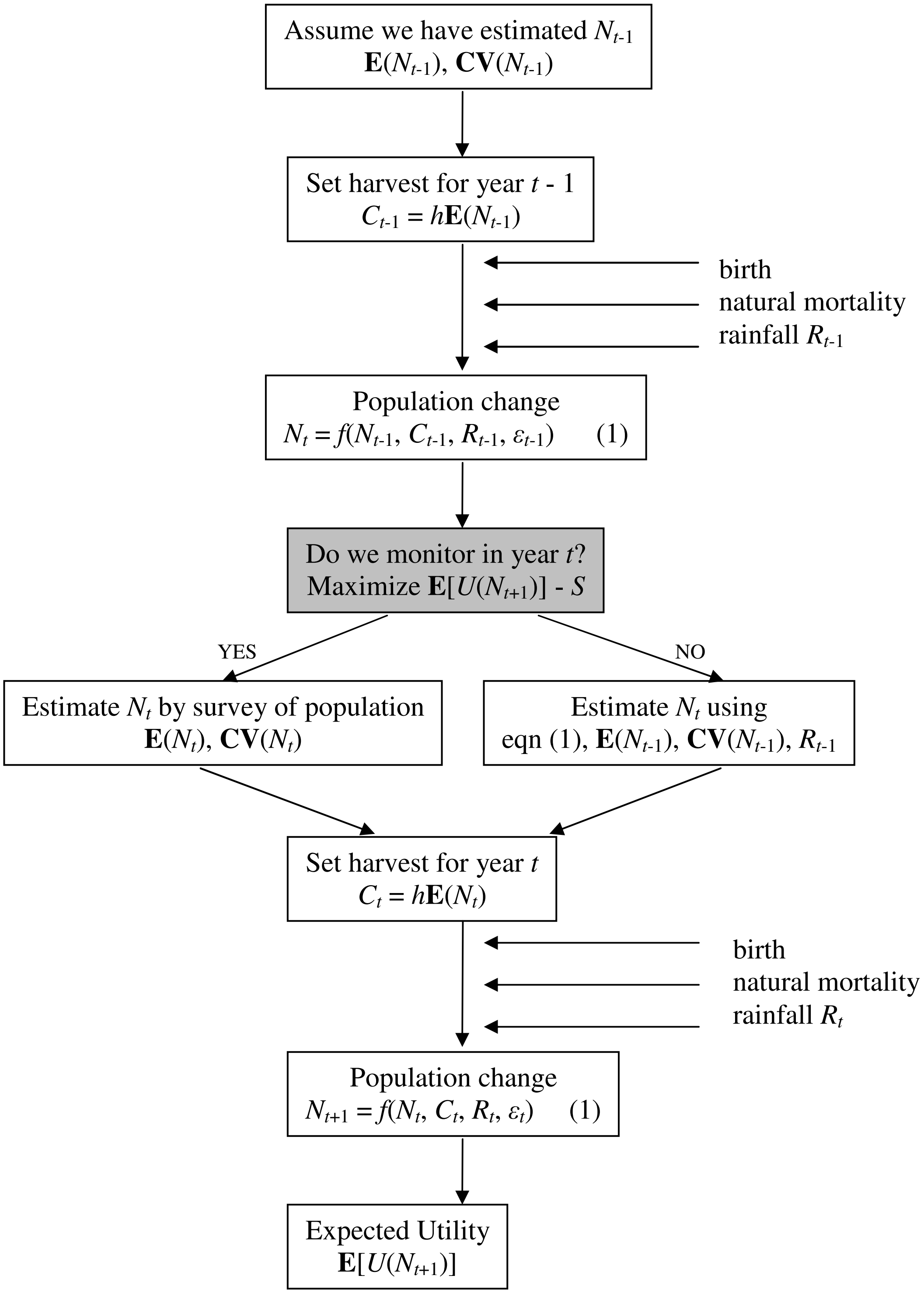

Figure 2.The process of data collection and optimization to make a survey decision for the beginning of year t. Note that to describe the distribution of the population in year t-1, we use the expected value $\mathbf{E}(N_{t-1})$ and coefficient of variance $\mathbf{CV}(N_{t-1})$, not the parameters μ_{t-1} and σ_{t-1}.

(e) Expected value of not conducting a survey

Equation (3) gives the value of deciding not to conduct a survey this year:

$$V_0 = \mathbf{E}\left[U\left(N_{t+1}\right) \mid D = 0\right].$$

That is, we wish to find the expected utility of next year's kangaroo density under the decision that we do not conduct a survey of kangaroos this year. If we have a probability distribution for population density next year under this decision $\Pr(N_{t+1}=n \mid D=0)$ then

$$V_0 = \int_0^\infty U(n) \Pr(N_{t+1} = n \mid D = 0) dn .$$

We can use equation (1) and rainfall R_t to find a distribution for next year's kangaroo density conditional on current density $\Pr(N_{t+1}=n \mid N_t=m)$. This is useful if we have a probability distribution for current population density under the decision that a survey is not conducted $\Pr(N_t=m \mid D=0)$. Then

$$V_0 = \int_0^\infty U(n) \int_0^\infty \Pr(N_{t+1} = n \mid N_t = m) \Pr(N_t = m \mid D = 0) dm dn .$$

Since we know last year's density comes from a lognormal(μ_{t-1}, σ_{t-1}) distribution, then we can use equation (1) and rainfall R_{t-1} to find the probability distribution for the current population density conditional on the population density last year $\Pr(N_t=m \mid N_{t-1}=l)$. So the expected utility next year if a survey is not carried out is

$$(5) \qquad V_0 = \int_0^\infty U(n) \int_0^\infty \Pr(N_{t+1} = n \mid N_t = m) \int_0^\infty \Pr(N_t = m \mid N_{t-1} = l) \Pr(N_{t-1} = l) dl dm dn$$

The probability distributions used in equation (5) are described in the Appendix.

The triple integral (5) is efficiently approximated by simulation. For each combination of state variables μ_{t-1}, σ_{t-1}, R_{t-1}, and R_t we first draw a large number K of lognormal(μ_{t-1}, σ_{t-1}) random variables to approximate our distribution for last year's density N_{t-1}. Then we draw K Normal(0, υ^2) random variables to represent process error ε_{t-1}. These are combined in equation (1) with rainfall R_{t-1} to approximate the distribution for current density N_t. The harvest over year t-1 is

$$C_{t-1} = h\mathbf{E}(N_{t-1}) = h \exp\left(\mu_{t-1} + \frac{1}{2}\sigma_{t-1}^2\right).$$

Similarly we draw another K Normal(0, υ^2) random variables to represent ε_t, combine them with current density N_t and rainfall R_t to approximate a distribution for next year's density N_{t+1}. Harvest over year t is the fraction h of the mean of all K values for N_t. For each of the K random variables we have for N_{t+1} we find $U(N_{t+1})$. The mean of these utilities is an approximation for V_0.

(f) Expected value of conducting a survey
Equation (4) gives the expected value of conducting a survey this year:

$$V_1 = \mathbf{E}\left[U\left(N_{t+1}\right) \mid D=1\right] - S .$$

We can use the same argument as in the previous section to show that

$$V_1 = \int_0^\infty U(n) \int_0^\infty \Pr(N_{t+1} = n \mid \hat{N}_t = \hat{m}) \int_0^\infty \Pr(\hat{N}_t = \hat{m} \mid D=1) d\hat{m} dn - S ,$$

where we have added hats to the distribution for current density N_t. These indicate that the distributions are derived from observation of the actual system, not from a predictive model.

Now we find plausible current densities from the survey. We do not yet know the outcome of the survey but we can say something about its precision. We assume that all surveys have a coefficient of variation of 20%, which is comparable to the precision of surveys conducted from 1978 to 2002 (Grigg et al. 1999, Jonzén et al. 2004). That is,

$$\mathbf{CV}(N_t) = \frac{\mathbf{SD}(N_t)}{\mathbf{E}(N_t)} = 0.2$$

where **CV** denotes coefficient of variation, **SD** denotes standard deviation and **E** denotes expected value. Since we describe likely values for N_t by a lognormal probability distribution with parameters μ_t and σ_t, then the above equation can be solved in terms of these parameters to find that $\sigma_t^2 = \ln 1.04$.

However, we still do not know the outcome of μ_t for the survey. If we assume that we know the true current density N_t, then the mean density $\hat{N}_t$ we observe will come from a lognormal distribution with $\mathbf{E}(\hat{N}_t) = N_t$ and $\mathbf{CV}(\hat{N}_t) = 0.2$. Hence the probability of getting an estimated density of $\hat{m}$ animals given we carry out a survey is

$$\Pr(\hat{N}_t = \hat{m} \mid D=1) = \int_0^\infty \Pr(\hat{N}_t = \hat{m} \mid N_t = m) \Pr(N_t = m) dm .$$

As in the previous section we can find a distribution for likely current density through modeling using

$$\Pr(N_t = m) = \int_0^\infty \Pr(N_t = m \mid N_{t-1} = l) \Pr(N_{t-1} = l) dl .$$

The actual probability distributions are included in the Appendix.

We again use simulation to approximate this integral. For each combination of state variables μ_{t-1}, σ_{t-1}, R_{t-1}, and R_t we use the same method outlined for expected utility when a survey is not conducted, to obtain K random variables that describe the distribution for current density. For each of these K random variables N_t we draw a lognormal random variable with mean N_t and coefficient of variation 0.2. This gives us a distribution for likely survey estimates $\hat{N}_t$. Then we draw K Normal$(0, \upsilon^2)$ random variables to represent ε_t, combine them with current estimate $\hat{N}_t$ and rainfall R_t to approximate a distribution for next year's density N_{t+1}. This sets the harvest $C_t = h\hat{N}_t$. For each of the K random variables we have for N_{t+1} we find $U(N_{t+1})$. The mean of these utilities is an approximation for $\mathbf{E}[U(N_{t+1}) \mid D=1]$.

Results

Here we first investigate the expected utility of each decision approximated by simulation with $K = 10000$. It is assumed that the last two years of rainfall have been average ($R_{t-1} = R_t = 0$) and we calculate expected utility $\mathbf{E}[U(N_{t+1}) \mid D=0]$ or $\mathbf{E}[U(N_{t+1}) \mid D=1]$ over a variety of distributions for last year's density by varying μ_{t-1} and σ_{t-1}. The Central Limit Theorem was used to find the standard error of simulations. Then we compare the utility of these decisions in the optimization under a broader range of rainfall information.

(a) Expected utility without a survey

Without a survey, expected utility generally increased as the expected density last year increased, until expected density reached 30 individuals/km^2 (Figure 3). The most dramatic increase occurred as expected density increased from 0 to 5 individuals/km^2, and then expected utility was somewhat steady for expected densities above 10 individuals/km^2. Expected utility was improved as last year's estimate became more accurate (coefficient of variation decreased).

Expected utility was explored under a variety of rainfall scenarios not shown here. Rainfall did not have a large effect on expected utility, although expected utility was slightly higher if rainfall was high. Each of the rainfall state variables R_{t-1} and R_t had the same effect.

(b) Expected utility when a survey is conducted

With a survey, expected utility had a similar response to last year's density estimate as it did when a survey was not conducted (Figure 4). It increased markedly as expected density increased from 0 to 5 individuals/km^2, and then was somewhat steady for expected densities above 10 individuals/km^2. Expected utility was improved as last year's estimate became more accurate, but the effect was not as strong as for expected utility when a survey is not conducted.

Again the two rainfall state variables R_{t-1} and R_t had similar effects. High rainfall produced higher expected utility. The effect of uncertainty in last year's estimate was reduced under high rainfall.

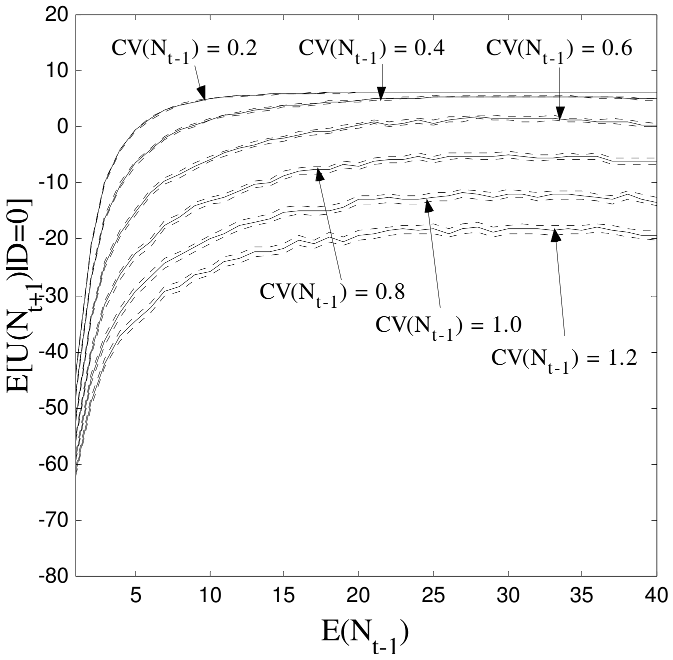

Figure 3. Estimated **E**[$U(N_{t+1})$ | D=0] (solid lines) as a function of **E**(N_{t-1}) with 95% confidence intervals on the estimations (dotted lines). Expected utilities are estimated using simulation with K=10000 and rainfall data are assumed to be $R_{t-1} = 0$, $R_t = 0$. Each solid line depicts different levels of uncertainty **CV**(N_{t-1}) (labeled).

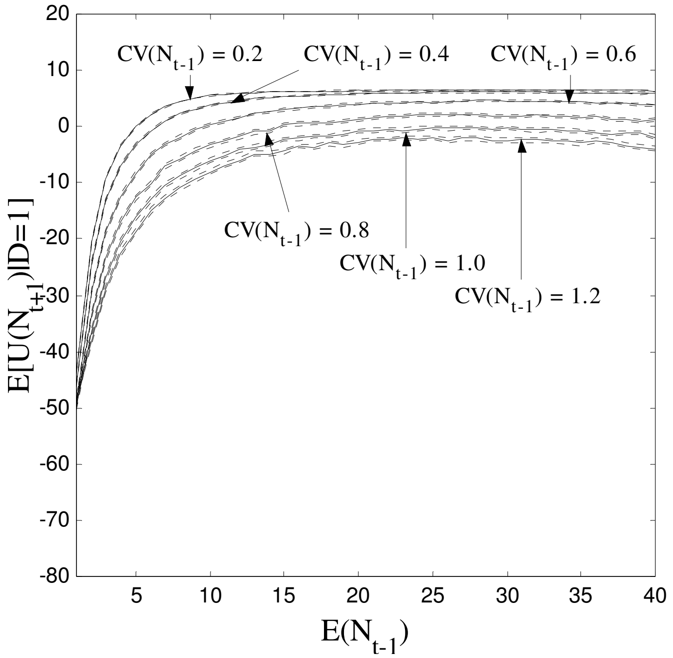

Figure 4. Estimated **E**[$U(N_{t+1})$ | D=1] (solid lines) as a function of **E**(N_{t-1}) with 95% confidence intervals on the estimations (dotted lines). Expected utilities are estimated using simulation with K=10000 and rainfall data are assumed to be $R_{t-1} = 0$, $R_t = 0$. Each solid line depicts different levels of uncertainty **CV**(N_{t-1}) (labeled).

(c) Optimal survey decision

In order to calculate V_1 and determine the optimal state-dependent survey decision, we have a cost, *S,* of carrying out a survey of the population at the beginning of year *t*. To accurately determine the trade-off between the cost of monitoring and expected utility we would have to transform the two in to one single currency. While we know the cost of a survey, it is very difficult to translate the utility of a particular kangaroo density into a monetary value. Consequently we investigated the difference between the expected utilities under each decision, ie. $\mathbf{E}[U(N_{t+1}) \mid D=1]$ -$\mathbf{E}[U(N_{t+1}) \mid D=0]$. This indicates the improvement to management that conducting a survey will make over the use of a model-based prediction. It is the maximum utility, *S*, we would be willing to pay to conduct a survey.

Figures 5, 6 and 7 show the difference between expected utilities under three combinations of recent rainfall. Other combinations of rainfall information R_{t-1} and R_t were also considered but are not shown here. It was found that higher rainfall increased the acceptable survey cost *S* and that both rainfall state variables are equally important.

We found that the expected utility using modeling $\mathbf{E}[U(N_{t+1}) \mid D=0]$ is always less than the expected utility when a survey is conducted $\mathbf{E}[U(N_{t+1}) \mid D=1]$ (see Figures 5-7, where the plot is always nonnegative). The difference between these expected utilities increases as uncertainty in last year's estimate increases. The difference is not so great if the population was thought to be at a low density last year, especially when rainfall has been low. At higher rainfall levels we are most likely to pay for a survey when last year's density estimate was around 5 individuals/km^2.

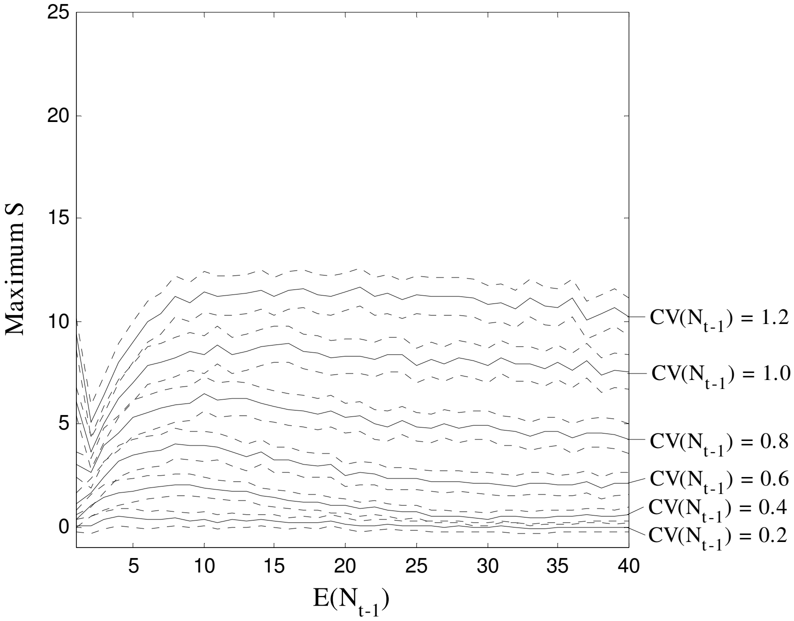

Figure 5. The maximum cost *S* for which conducting a survey is the optimal decision (solid lines). Expected utilities are estimated using simulation with K=10000 and dotted lines indicate 95% confidence intervals on the estimation. Rainfall data are assumed to be R_{t-1} = -2, R_t = -2. Each solid line depicts different levels of $\mathbf{CV}(N_{t-1})$ (labeled on right).

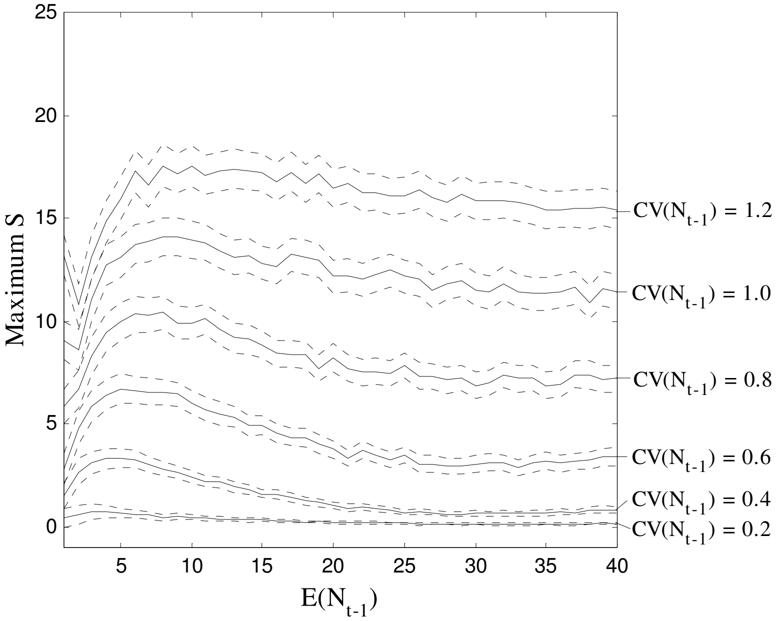

Figure 6. The maximum cost *S* for which conducting a survey is the optimal decision (solid lines). Expected utilities are estimated using simulation with *K*=10000 and dotted lines indicate 95% confidence intervals on the estimation. Rainfall data are assumed to be $R_{t-1} = 0$, $R_t = 0$. Each solid line depicts different levels of $\mathbf{CV}(N_{t-1})$ (labeled on right).

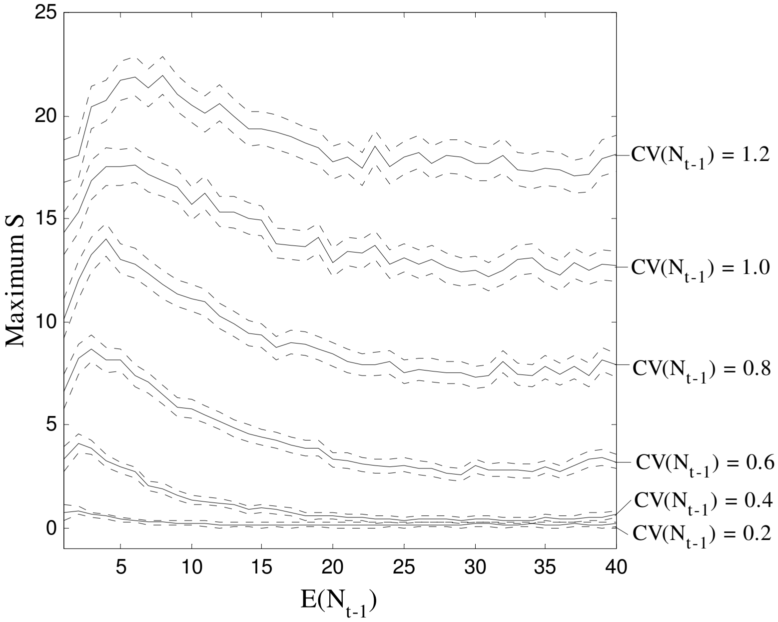

Figure 7. The maximum cost *S* for which conducting a survey is the optimal decision (solid lines). Expected utilities are estimated using simulation with *K*=10000 and dotted lines indicate 95% confidence intervals on the estimation. Rainfall data are assumed to be $R_{t-1} =2$, $R_t = 2$. Each solid line depicts different levels of $\mathbf{CV}(N_{t-1})$ (labeled on right).

Discussion

We have demonstrated that the costs and likely outcomes of monitoring can be integrated into the framework of decision theory for population management. In this way we see that it may not be optimal to use the same monitoring effort before each decision. Rather, the level of monitoring effort to be used depends on the current state of the system.

For the management of a red kangaroo population in South Australia, rainfall data and a past estimate of population density are used to determine the value of conducting a survey. Our results show that if there is no cost attached to conducting a survey then it is always better than using modeling to set harvest quotas. This is a sensible result since we would expect that collecting further data and reducing uncertainty about population density would improve management decisions, where the utility function is non-linear.

Expected utility, whether or not a survey is conducted, decreases dramatically as the estimated density last year decreases below five individuals/km^2 (Figures 3 and 4). Even if monitoring does improve management somewhat, it is unlikely that the population will increase to a higher more desirable density next year and so the population will still be at a density with low utility. In contrast, utility does not decrease significantly when density last year was estimated to be very high, suggesting the population is likely to be in a state of high utility even if monitoring does not take place. This is a consequence of the utility function, which describes low densities as much more undesirable than high densities. It may also arise from the density dependent term in equation (1), which ensures that the population is likely to decrease if it is large.

As we would expect, increasing uncertainty in last year's population density estimate increases the value of conducting a survey now. As the number of years between subsequent surveys increases, so does the uncertainty in population estimates obtained by modeling. This result indicates that eventually we must carry out a survey to reduce the uncertainty brought about by modeling year after year. This will reduce the chance of an inappropriate harvest quota.

If last year's density estimate is small (eg. below 3 individuals/km^2), then surveys are generally less valuable than if the estimate is large. This is particularly apparent when rainfall has been very low. While this appears counter-intuitive, it seems that in these circumstances the density is at a very undesirable level (see utility function in Figure 1) and management, good or bad, struggles to have a positive impact on the utility (Richards et al. 1999, Yokomizo et al. 2004).

The value of conducting a survey is larger when rainfall has been high. We believe this is a consequence of the structure of the population model in equation (1). The rainfall variable creates exponential growth and there is lognormal process error. In combination, these terms indicate that above average rainfall creates a highly uncertain increase in population density. Thus monitoring to reduce this uncertainty will improve management.

The most significant limitation of this study is that calculations are made under the assumption that equation (1) gives a true description of population dynamics. In this way we assume that modeling (skipping surveys) will give the best possible density estimate, even though the process error in equation (1) will cause uncertainty to increase from year to year. Hence our results may underestimate the value of conducting surveys. An interesting extension would be to relax this assumption by considering multiple models. Multiple hypotheses of population dynamics would allow full utilization of the second function of monitoring: understanding of system dynamics to improve future management. We expect that monitoring would become more valuable when the population is in a state that maximizes the difference between hypotheses.

We have discussed the reduced value of monitoring when management has little impact. For this red kangaroo population, a different harvest strategy might have a greater impact at very low densities. For example, taking 20% of the population estimate only when the population estimate is above 3 individuals/km^2 and allowing no harvest for population estimates below 3 individuals/km^2 may improve management. Ultimately the optimization of harvest in conjunction with monitoring is required to maximize the impact of management. Under this scenario it may be that monitoring is still of little value when population density is low and we should take conservative management action regardless of what a survey could tell us (Field et al. 2004). In a similar vein, our results do not specifically indicate an optimal survey frequency to be carried out in the long term. Simulation of a kangaroo population subject to survey decisions over a longer time frame may indicate the appropriate survey frequency.

In summary, monitoring is more valuable as the previous population estimate approaches population thresholds where the utility of population density is changing rapidly. In this example, it is at a density of five individuals/km^2, when the population becomes undesirably small. However monitoring is less valuable when management will have little impact on the population. This is the case for this kangaroo population as density declines below three individuals/km^2. The value of monitoring increases as the uncertainty around a previous population estimate increases. Environmental variables (such as rainfall, in this study) may indicate that the current state of the population is particularly uncertain, also increasing the value of monitoring. Further work on different species is needed to determine if these broader insights have general applicability.

Acknowledgments

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Appendix

Equations for V_0

Equation (5) is more fully described as:

$$\begin{aligned} V_0 &= U(0)\Pr(N_{t+1}=0) + \int_0^\infty U(n) f_{N_{t+1}}(n)\,dn \\ &= (-\alpha+\delta)\left[\Pr(N_t=0) + \Pr(N_t>0, N_{t+1}=0)\right] + \int_0^\infty (-\alpha e^{-\beta n} - \gamma n + \delta) f_{N_{t+1}}(n)\,dn, \end{aligned}$$

where

$$\Pr(N_t=0) = \int_0^{C_{t-1}} \frac{1}{\sqrt{2\pi}\sigma_{t-1} l} \exp\left[\frac{\left(\ln l - \mu_{t-1}\right)^2}{2\sigma_{t-1}^2}\right] dl, \tag{6}$$

$$\Pr(N_t>0, N_{t+1}=0) = \left[1-\Pr(N_t=0)\right]\int_0^{C_t} f_{N_t}(m)\,dm,$$

$$f_{N_{t+1}}(n) = \frac{1}{\sqrt{2\pi}\nu n}\int_{C_t}^\infty f_{N_t}(m)\exp\left\{-\frac{\left[\ln n - \ln(m-C_t) - a - bm - cR_t\right]^2}{2\upsilon^2}\right\} dm,$$

$$f_{N_t}(m) = \frac{1}{2\pi\sigma_{t-1}\nu m}\int_{C_{t-1}}^\infty \frac{1}{l}\exp\left\{-\frac{\left(\ln l - \mu_{t-1}\right)^2}{2\sigma_{t-1}^2} - \frac{\left[\ln m - \ln(l-C_{t-1}) - a - bl - cR_{t-1}\right]^2}{2\upsilon^2}\right\} dl, \tag{7}$$

$$C_t = \frac{he^{\upsilon^2/2}}{\sqrt{2\pi}\sigma_{t-1}} \int_{C_{t-1}}^{\infty} \frac{l - C_{t-1}}{l} \exp\left[a + bl + cR_{t-1} - \frac{\left(\ln l - \mu_{t-1}\right)^2}{2\sigma_{t-1}^2} \right] dl,$$

(8) $$C_{t-1} = h\exp\left(\mu_{t-1} + \frac{1}{2}\sigma_{t-1}^2 \right).$$

Equations for V_1

The variable V_1 is more fully described as:

$$\begin{aligned} V_1 &= U(0)\Pr(N_{t+1} = 0) + \int_0^\infty U(n) f_{N_{t+1}}(n)dn - S \\ &= (-\alpha + \delta)\Pr(N_t = 0) + \int_0^\infty (-\alpha e^{-\beta n} - \gamma n + \delta) f_{N_{t+1}}(n)dn - S, \end{aligned}$$

where $\Pr(N_t = 0)$ is given in equation (6),

$$f_{N_{t+1}}(n) = \frac{1}{\sqrt{2\pi}\nu n} \int_0^\infty f_{\hat{N}_t}(\hat{m}) \exp\left\{ -\frac{\left[\ln n - \ln \hat{m} - \ln(1-h) - a - b\hat{m} - cR_t\right]^2}{2\upsilon^2} \right\} d\hat{m},$$

$$f_{\hat{N}_t}(\hat{m}) = \frac{1}{\sqrt{2\pi \ln 1.04}\,\hat{m}} \int_0^\infty f_{N_t}(m) \exp\left[-\frac{\left(\ln \hat{m} - \ln m + \frac{1}{2}\ln 1.04 \right)^2}{2\ln 1.04} \right] dm,$$

and $f_{N_t}(m)$, C_{t-1} are given in equations (7), (8), respectively.

Section 7

Pople, A. R., and Fewster, R. M. (in prep.). Improving the accuracy of helicopter surveys of kangaroo populations using line transects and double counting. *Wildlife Research.*

Improving the accuracy of helicopter surveys of kangaroo populations using line transects and double counting

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Introduction

Since the mid-1980s, management of the commercial harvest of kangaroos (*Macropus* spp.) in Australia has relied on annual quotas set as a percentage of an estimate of population size (Pople and Grigg 1998). Because most harvesting occurs over the vast, relatively open, arid and semi-arid regions of Australia, population estimates have been determined primarily using aerial surveys e.g. (Caughley and Grigg 1981). Aerial surveys have traditionally used fixed-wing aircraft (e.g. Cessna) and strip transects (Caughley *et al.* 1976), but there has been an increasing use of helicopters and line transects (Clancy *et al.* 1997; Southwell and Sheppard 2000). In Queensland, where roughly 50% of the Australian kangaroo harvest is taken, kangaroo population size is determined almost solely from helicopter surveys (Lundie-Jenkins *et al.* 1999). Direct comparison of population estimates from helicopter surveys with those from fixed-wing surveys has also allowed correction for visibility bias inherent in the latter (Pople *et al.* 1998a; Pople *et al.* 1998b).

Bias in estimates of population size can lead to over or underharvesting, and so there has been considerable research effort in estimating kangaroo population size accurately (Pople 2004). However, bias in helicopter surveys using line transect methods, while recognised (Clancy *et al.* 1997), has been neither well quantified nor assessed over the range of habitats that helicopter surveys are conducted. (Clancy *et al.* 1997) found that estimates of red kangaroo (*M. rufus*) and eastern grey kangaroo (*M. giganteus*) density determined by helicopter surveys were similar to those determined from walked line transect surveys in two locations in Queensland. However, helicopter surveys underestimated the density of common wallaroos (*M. robustus*) by a factor of 2-3. Furthermore, walked line transect surveys are likely to return underestimates of kangaroo population size (Southwell 1994).

An alternative means of assessing bias in helicopter surveys is to use mark-recapture methods in combination with line transect sampling (Borchers *et al.* 1998). This involves at least two observers counting along the same transect and identifying animals that are seen by only the first observer, only the second observer or both observers. Such 'double counting' in strip transects has a history of use in aerial survey of Australian aquatic (Marsh and Sinclair 1989) and terrestrial (Bayliss and Yeomans 1989; Pople *et al.* 1998c) fauna including kangaroos (Choquenot 1995). However, if key assumptions are violated, particularly if capture probability is heterogeneous, then density estimates can be biased (Caughley and Grice 1982). Similarly, accurate density estimation from line transect sampling relies on assumptions being met, particularly animals on the line not being missed. The combination of mark-recapture and line transect methods is new and promises density estimation with minimal bias.

This study assessed the feasibility of line transect double counting in helicopter surveys of kangaroo populations and aimed to quantify bias in population estimates for three species of kangaroos at two locations in Queensland. An assessment of variability in bias amongst observers was also made. This was considered the first step to the longer-term goal of assessing bias on a broader scale, over time and with a greater range of observers.

Methods

Study area

The study was conducted in two survey blocks of approximately 10 000 km^2 centred on the southern Queensland towns of Roma, in the brigalow belt bioregion, and Charleville, in the mulga lands bioregion (Environment Australia 2000; Fig. 1). The Roma block is a mixture of tussock grasslands mostly sown to cereal crops, and *Eucalyptus, Casuarina* and conifer open grassy woodlands. Eastern grey kangaroos are abundant in the Roma district, whereas red kangaroos and common wallaroos occur at relatively low densities. The Charleville block is dominated by low *Acacia* and *Eucalyptus* woodlands with a lower stratum of tall shrubs and tussock grasses. Large areas of the original vegetation around Charleville and much of the mulga lands have been 'pulled' with tractors and chains, but not cleared, leaving areas of fallen timber and regenerating vegetation. All three species of macropod are common in the Charleville district. Sheep grazing is the principal form of land use in both blocks, with cereal crops being grown around Roma.

Helicopter line transect surveys

Double counting was conducted during the annual aerial survey of 10 blocks in 2000. A full description of this method is given by (Clancy *et al.* 1997). Briefly, a helicopter (Robinson R44) with the doors removed was flown at a ground speed of 93 km h^{-1} (50 kts), 61 m (200 ft) above the ground. Two observers (GM and GLJ) occupying the rear seats counted clusters of kangaroos seen on either side of the aircraft. The sightings of individual kangaroos were placed into 25-m distance classes up to 125 m perpendicular to the transect line, measured from directly below the observer. Sightings were recorded into micro-cassette recorders. The distance classes were delineated on aluminium poles extending perpendicularly from either side of the helicopter. The observers counted in five-minute units with a 30 s break between them.

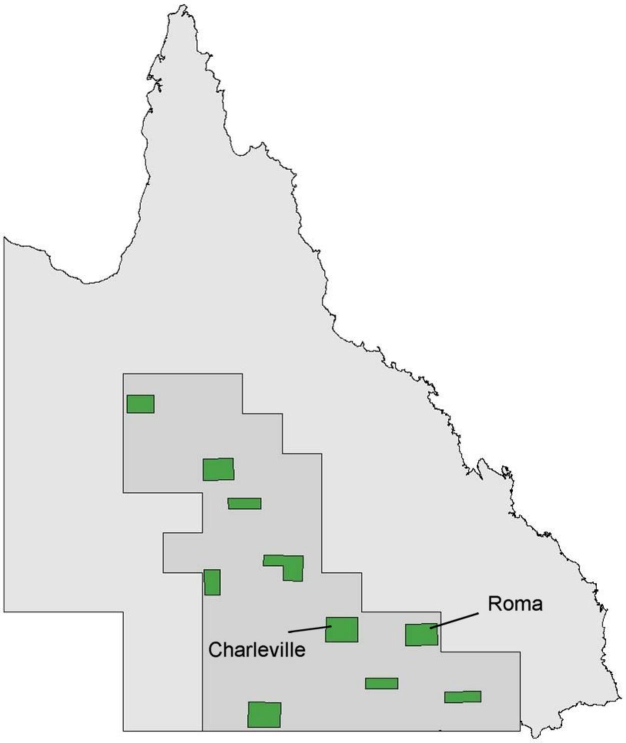


Fig. 2. Location of the survey blocks within the core survey area (dark grey; see Section 3) of Queensland.

In order to conduct a double count, a third observer (AP) counted kangaroos from the front left-hand seat next to the pilot. This observer used a separate pole extending out from the helicopter to delineate distance classes. Counts of both left-hand observers were recorded independently in continuous time into a dual-channel tape recorder. Following the survey, tapes were replayed and sightings identified as being made either by the front observer only, the rear observer only or both observers. All three observers had >100 h experience helicopter surveys of kangaroos using line transect sampling.

Eight parallel east-west transects, 80 km long and 10 km apart, were flown across each survey block. The exact distances were determined by a global positioning receiver. Surveys were conducted within the three hours after sunrise and the two hours before sunset in late May 2000. Rear seat observers swapped positions after each survey session, which usually involved two transect lines. This enabled a comparison of bias amongst the three observers.

Data analysis

In line transect sampling,

$$\hat{D} = \frac{n}{a\hat{P}_a}$$

where $\hat{D}$ is an estimator of density and $\hat{P}_a$ is the probability of detection in the surveyed area a. In strip transect sampling, transects have a fixed width $2w$ and length L, so

$a=2wL$. There is a complete census of the strip, so $\hat{P}_a = 1.0$. In line transect sampling, if $\hat{P}_a = 1.0$, then the distances to all objects recorded (100% are detected) will be uniformly distributed in the strip. If $\hat{P}_a < 1.0$, then some objects will not be detected, with fewer objects detected with increasing distance away from the line.

The four assumptions of line transect sampling, roughly in order of importance, are (Buckland *et al.* 1993):

1. Objects on the line are detected with certainty
2. Objects are detected at their initial location
3. Measurements are exact or placed in the correct distance interval
4. There is a shoulder in detectability

Line transect surveys must be designed and conducted so that these assumptions are met, otherwise estimates of density can be biased. A detection function $g(x)$ is modelled to distance data, where $g(x)$ is the probability of detecting an object, given that it is at a distance x from the randomly (or systematically) placed line. Because of assumption 1, $g(0)=1$. $g(x)$ (and therefore P_a) will vary across a range of conditions, including habitat, temperature, observer and the platform from which the method is being used (e.g. vehicle, aircraft, on foot). If $g(0)\neq 1$, but can be estimated, density can be calculated as:

$$\hat{D} = \frac{n}{a\hat{P}_a g(0)}$$

Missed objects on the line will be the result of perception bias, where objects are available for detection but are missed, or availability bias, where some objects simply cannot be detected. Perception bias can be minimised using a variety of techniques, including going slower, or g(0) can be estimated using mark-recapture as in this study. Availability bias is likely with surveys of marine mammals and burrowing animals. g(0) can be estimated for these animals using radio transmitters.

Data were analysed using the approach of Borchers *et al.* (1998). Separate analyses were conducted for each front and rear observer pair in each survey block, and separately for each kangaroo species.

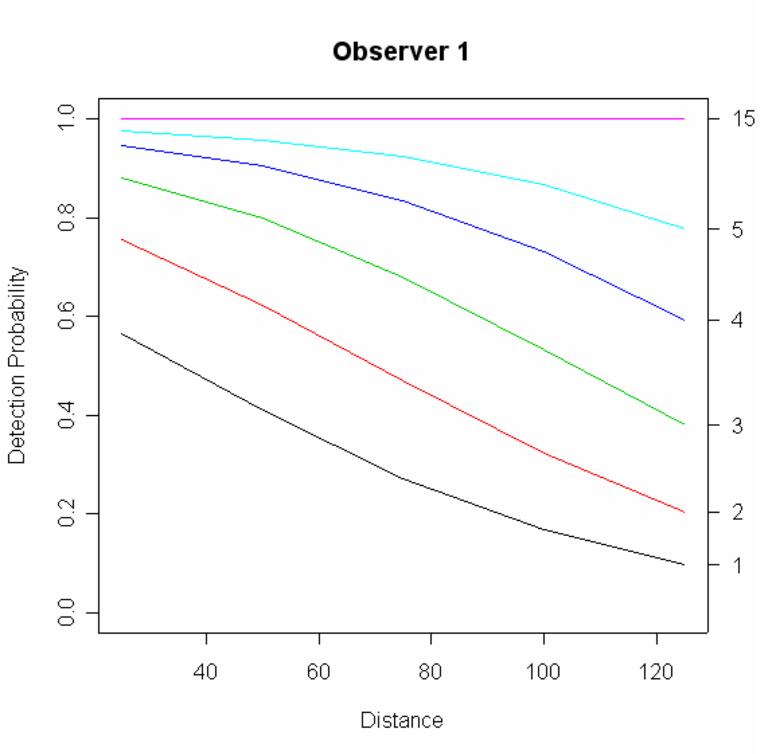
Results and Discussion

Sightings were categorised as being made by both observers when they were near simultaneous, of the same species and the same cluster size. However, because kangaroos were often moving and observers recorded sightings at slightly different times, some joint sightings were placed in different distance classes by each observer (13% of all macropod sightings at Charleville, 9% at Roma). Kangaroos form small, but loose aggregations and so some joint sightings were also recorded as different cluster sizes by the two observers (7% of all sightings at Charleville, 10% at Roma). Misidentification is also possible, particularly when there are mixed species groups, and so some joint sightings were recorded as different species (5% of all sightings at Charleville, 2% at Roma). To be consistent, if near-simultaneous sightings by both observers were in adjoining distance classes they were categorised as being the same cluster. However, if the cluster size differed by more than one, then the sighting was not considered a joint sighting. If different species were recorded near simultaneously by the two observers in the same distance class and within one of the same cluster size, then the sighting was also considered a joint sighting. In all cases, the front observer's values for joint sightings were used in the analysis. This treatment of these errors is conservative, leading to an overestimate of sighting probability on the line and therefore an underestimate of density.

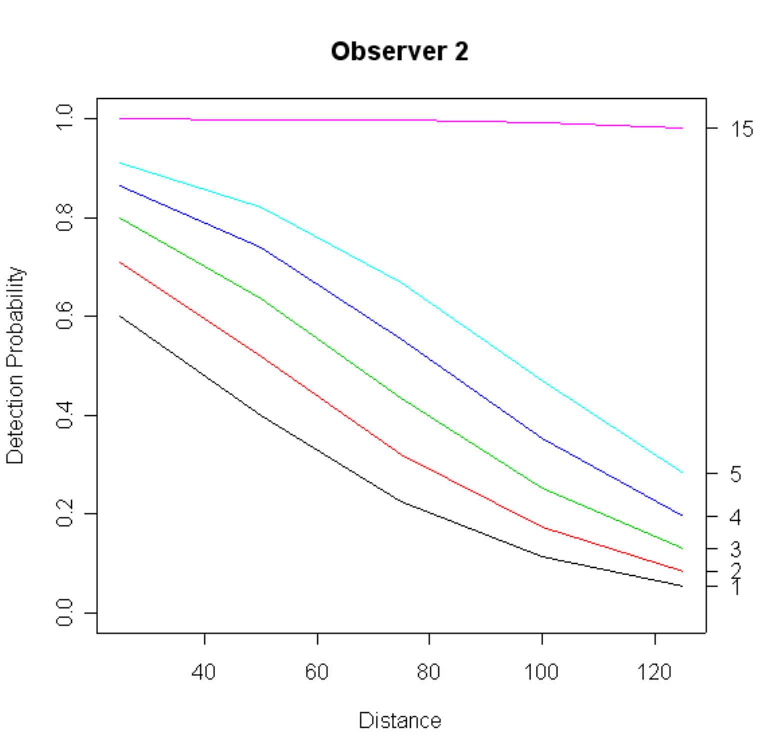
Examples of the estimated detection functions are shown in Figure 1. Not surprisingly, there is an ever steepening drop in detectability over distance with declining group size and this varies with observer. Estimates of g(0) are given in Table 1 and identify a negative bias in density estimates of up to 30%. Of concern is the variation among observers and between blocks. While detection curves are expected to vary with habitat and observer (Buckland *et al.* 1993), it had been hoped that line transect methods would reduce the variability in bias that is a concern for fixed-wing surveys (Clancy *et al.* 1997; Clancy 1999; Pople 1999). Future assessments of line transect surveys of kangaroos using a helicopter in a range of habitats and using a range of observers will reveal the extent of the variation in bias, which is clearly possible using double counting.

Table 1. Estimates of g(0) (i.e. detection probability on the transect line) for eastern grey kangaroos and red kangaroos. Estimates for Charleville B are shown in italics because they are compromised by a small sample size ($n = 62$ clusters).

Block	Observer 1	Observer 2
Eastern grey kangaroos		
Roma A	0.82	0.84
Roma B	0.69	0.92
Charleville A	0.97	0.78
Charleville B	0.81	0.94
Red kangaroos		
Charleville A	0.90	0.72
Charleville B	*0.73*	*0.75*



(*a*)



(*b*)

Fig. 2. Detection probabilities g(*x*) for different cluster sizes (1-15, right-hand y-axis) of eastern grey kangaroos at Roma A, recorded by (a) Observer 1 and (b) Observer 2.

Acknowledgements

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Section 8

Pople, A. R., Cairns, S. C., Menke, N., and Payne, N. (in press). Monitoring eastern grey kangaroos (*Macropus giganteus*) in southeastern New South Wales for harvest management. *Wildlife Research*

Monitoring eastern grey kangaroos (*Macropus giganteus*) in southeastern New South Wales for harvest management

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Running title: Eastern grey kangaroo abundance in southeast NSW

Abstract

To provide an estimate of kangaroo numbers for harvest management, a survey was designed for an area of 29,500 km^2 encompassing the agricultural and grazing lands of the Braidwood, Cooma, Goulburn, Gundagai and Yass Rural Lands Protection Board (RLPB) districts in southeast New South Wales. An aerial survey was considered more efficient than ground survey because of the size of the area and the need for regular monitoring. The relatively high relief and dense tree cover meant that a helicopter was the most suitable aerial survey platform. Tree cover and landscape relief was used to stratify the five RLPB districts into areas of probable high, medium and low kangaroo density. Based upon two levels of stratification of the area, RLPB district and density within RLPB district, and information drawn from helicopter surveys conducted in the northern tablelands of New South Wales, a survey comprising 900 km of transect line was attempted in winter 2003 with a target precision of 20%. Bad weather restricted the survey to 735 km. The survey returned an estimate of 286,600 ±32,300 eastern grey kangaroos for the whole of the proposed southeast New South Wales kangaroo management zone. In 2004, a trial harvest of slightly less than 15% of this estimate was taken. Success of the trial will be determined by the impact of harvesting on the population, landholder and industry participation, and the ability to monitor population size, harvest offtake and compliance with regulations.

Introduction

For commercial harvesting of kangaroos to occur in a region, Australian state and federal government conservation agencies require populations to be monitored (Pople and Grigg 1998). Monitoring is a critical component of wildlife management, allowing evaluation of management activities and providing information on which managers act. Monitoring of kangaroo populations, usually by aerial survey, allows managers throughout Australia to regulate the harvest by quotas that are set as proportions of population estimates (Pople 2004). It also provides a public confidence that the harvest is sustainable (McCallum 1999).

Until recently, commercial harvesting of kangaroos in New South Wales (NSW) was restricted to the inland sheep-wheat belt, the western pastoral areas and the northern tablelands. Except for parts of the northern tablelands, no commercial harvesting of kangaroos occurs east of the Great Dividing Range in NSW, nor in the central and southern tablelands. Following an expression of interest, mainly from sheep and cattle graziers, a trial commercial harvest began in the southeast of the state in 2004. A new area for commercial harvesting had not been opened in NSW since the 1980s and debate continues over the commercial use of kangaroos (Pople and Grigg 1998; Wilson 1999; Croft 2004). Negotiations for the trial harvest were therefore protracted. Landholders in this area cull kangaroos on pest destruction (shoot-and-let-lie, SLL) licences, but recognise that this is both an inefficient means of pest control and wasteful; a situation that could be redressed through the introduction of commercial harvesting. A further advantage of introducing commercial harvesting is that animals are likely to be killed more humanely by qualified field processors than if killed by landholders under SLL licences, and this can be policed to a far greater extent than a non-commercial cull (RSPCA 2002). Whether a commercial harvest can satisfy graziers' needs for reductions in kangaroo grazing pressure will depend on a number of factors including shooter access, potential supply of kangaroos within the region compared to elsewhere, and prices paid to shooters for carcasses. The broader question of the extent to which kangaroo numbers need to be reduced to ameliorate their impact, perceived or actual (Pople and McLeod 2000), is not examined here.

In NSW, aerial surveys are conducted annually by fixed-wing aircraft in the western plains where most harvesting occurs. In the northern tablelands and the Barrier Ranges north of Broken Hill, surveys are less frequent for a number of reasons. Firstly, the rugged terrain or heavy vegetation cover requires surveys to be undertaken by helicopter (Southwell and Sheppard 2000) or by ground counts (Southwell *et al.* 1995), which are costlier than surveys by fixed-wing aircraft. This increased uncertainty in population size can be offset in the Barrier Ranges by a less intensive harvest and in the more mesic environment of the northern tablelands by a kangaroo population whose dynamics are likely to be less labile (Pople *et al.* 2003)

For harvest management, a population estimate initially provides an indication of whether or not harvesting is commercially viable and worth the administrative costs in the long term. If harvesting is viable, an estimate allows quotas to be set as a proportion of population size. Population size needs to be estimated efficiently, in terms of cost and time, and with a precision (i.e. confidence interval) sufficient to keep the risk of over- or underharvest to an acceptable level. A survey will also indicate the distribution of kangaroos, allowing spatial allocation of quotas or harvesting effort.

In wildlife management, the appropriate survey frequency and precision has generally been considered with the aim of detecting trends (Caughley 1979; Harris 1986; Gerrodette 1987). In kangaroo management, harvest regulation is primarily through quotas that are set as proportions of absolute estimates of population size. Trends are of secondary importance. Imprecision in population estimates and infrequent estimates will risk applying a quota that is either too high or too low (Pople 2003). By not harvesting at the desired rate (e.g. 15%), costs are incurred to the kangaroo industry through reduced and more variable yield, and to graziers through increased competition with sheep and damage to crops. Juxtaposed to this is a social cost if kangaroos are reduced below some arbitrarily low density (i.e. quasiextinction). These costs need to be balanced against the cost of more intensive and frequent surveys (i.e. there is a trade-off). Alternative harvest strategies can also be considered in order to reduce the risk of over- or underharvest. These include harvesting at a different, and even variable, rate, regulating effort or incorporating spatial reserves.

This paper describes the monitoring program that has recently been established for eastern grey kangaroo (*Macropus giganteus*) populations in the southeast of NSW, specifically in the five Rural Lands Protection Board (RLPB) districts shown in Figure 1, and the resulting estimates of abundance and distribution from the initial survey. This area comprises rugged terrain and heavily timbered areas, making aerial survey difficult. Pople *et al.* (2003) modelled the risk of overharvest for a kangaroo population in this region under a range of survey precisions and frequency. The assessment suggested that a survey frequency of three years with a precision (i.e. standard error/mean) of 20% would increase the risk of overharvest only slightly over annual surveys with no error, while substantially reducing survey costs. Whether the increase in risk is acceptable is a decision for management to make in consultation with stakeholders. Nevertheless, this provided a target precision for this survey.

[Figure 1]

Methods

Survey feasibility

The accuracy and repeatability of aerial surveys diminishes in areas of high relief or heavy forest cover because of low and variable visibility (Southwell 1989; Clancy *et al.* 1997; Pople 1999; Southwell and Sheppard 2000). Safety may also be compromised in particularly rugged terrain. Areas of high relief or dense tree cover occur throughout the study area, but are mainly within National Parks or State Forests. Forest cover, land use and areas of high relief within the five RLPB districts that comprise the study area are shown in Figure 1. A large proportion (28%, Table 1) of the area is in National Park, particularly Kosciuszko National Park, and State Forest; areas from which commercial harvesting of kangaroos is precluded. In particular, there is dense tree cover in the northwestern area of Kosciuszko National Park and the adjoining and nearby State Forests east of Tumut, and in National Park and State Forest at the eastern edge of Braidwood RLPB district. Areas of high relief also occur on the eastern slopes of the Great Dividing Range, south from the Snowy River within Kosciuszko National Park in the southwest of the Cooma RLPB district.

[Table 1]

The composition of the study area as shown in Figure 1 is quantified in Table 1. The three density strata are described below. A small area of relatively high relief (>500 m) occurs within the area outside National Parks and State Forests. High relief areas are generally associated with dense tree cover and the combination means kangaroo density is likely to be low in these areas and harvesting is unlikely to be feasible. This area is also unlikely to be suitable for aerial survey and so was excluded from the overall survey area; effectively assuming a density of zero in areas of high relief. The impact of this small deletion would be slight.

The survey area shown in Figure 1 ranges from low, moderately timbered ranges bordering mostly open plains in the southeast, including the Cooma and Braidwood RLPB districts and around Tumut and southwest of Yass, to rolling hills of scattered woodland in the north and west. Although, the northern and western parts of the study area could be surveyed by fixed-wing aircraft, correction factors would need to be developed for this and the remaining part of the area is unsuitable for this survey method. A helicopter offers a number of advantages over fixed-wing aircraft as a platform for surveying the types of landscape found in the study area. It provides greater visibility and can fly lower and slower, which is particularly advantageous in rugged terrain and in areas with dense tree cover. The greater manoeuvrability of a helicopter allows surveys to be designed with shorter and more closely spaced transect lines, which is an advantage in heterogeneous landscapes. A helicopter also provides an appropriate platform for line transect sampling (Clancy *et al.* 1997), more so than a fixed-wing aircraft (Pople *et al.* 1998*b*), potentially allowing survey-specific correction for variations in visibility bias. The survey was therefore conducted by a helicopter using line transect sampling.

Survey design

Objective

The overall objective of designing the survey was to estimate population size in the study area from a representative sample. Precision can be greatly improved by stratifying sampling. As a rule-of-thumb, sampling effort should be allocated in proportion to the size of the population in each stratum (Thompson 1992). For this, some indication is required of the relative distribution of kangaroos amongst strata in the study area as well as knowing the area of strata. Ideally, strata should be some mappable component of the environment such as vegetation cover or soil type. However, arbitrary strata can be defined so long as they can be mapped, their areas are known and they are defined before a survey is conducted. Post-sampling stratification is possible, but it must obviously be based on information independent of the survey and it is likely to be well short of optimal.

Stratification and allocation of survey effort

Ground assessment of the study area was made in February 2003. This involved field inspection of the major environments in the study area and discussions with NSW Department of Environment and Conservation (DEC) staff and with RLPB rangers and graziers. These discussions identified likely areas of relatively high kangaroo density within the study area and likely factors determining kangaroo distribution and abundance (Pople 1989; Southwell *et al.* 1999), which could be used as a basis for stratification. The concentration of tags issued under SLL licences was also used as an indicator of kangaroo distribution.

Ground assessment of the study area supported the recognised associations between eastern grey kangaroos and partly cleared forest (cf. predominantly open or predominantly closed areas) and areas of greater pasture productivity (Hill 1981*a*, 1981*b*; Scott-Kemmis 1979). Three strata were identified and these are shown in Figure 2 and their areas given in Table 1. Relatively high kangaroo densities were predicted in the Gundagai and Yass RLPB districts and the areas of these were mapped by graziers and RLPB staff. Relatively moderate densities were expected in partly timbered areas outside this stratum. A buffer of 3 km was placed around wooded (open forest and woodland) areas (Fig. 1) to capture the grazing distribution of eastern grey kangaroos around wooded areas (Hill 1982; Taylor 1985) and to provide contiguous areas that could be surveyed from the air using transects. The remaining open areas comprised a low-density stratum. For the total survey area, 24% was high-density stratum, 59% was medium-density stratum and the remaining 17% was low-density stratum (Table 1).

[Figure 2]

Survey effort using line transects is measured by total line length. If 100 km of transect is adequate to survey a species' population in a small area, then 100 km will be adequate over a larger area, assuming similar dispersion and random sampling of transects (Buckland *et al.* 1993). Increasing line length will improve precision. The line length required for a target precision, in this case 20%, can be determined from a pilot study or drawn from surveys previously conducted in a similar environment.

The total line length desired for this survey was determined in two ways. Firstly, it was constrained by cost. In the northern tablelands of NSW, 1,480 km of systematically-placed transects were surveyed in 2001 and 2002 in three zones covering an area of 48,000 km^2 (Cairns 2003). The survey area in southeastern NSW is smaller and so a total line length of ~900 km would be in proportion to area. However, randomly placed transects (proposed here, see below) are likely to be costlier to survey than parallel transects in blocks because of increased ferry distance between lines. The second method for determining the appropriate line length involved using the precision of the survey in the northern tablelands as a guide. The relevant equation is (Buckland *et al.* 1993):

$$L_{ST} = \frac{L_{NT}\,cv(D_{NT})^2}{cv(D_{ST})^2}$$

where, $cv(D_{NT})$ and L_{NT} are the respective precision and line length of the northern tablelands survey, and $cv(D_{ST})$ and L_{ST} are the corresponding values for the proposed southern tablelands survey here. In the northern tablelands, $cv(D_{NT})$=12% for L_{NT}=1480 km (Cairns 2003). In the southern tablelands, if $cv(D_{ST})$=20%, then L_{ST} = 510 km. The precision of the northern tablelands survey was based on variability among transects in nine blocks of 3-6 parallel transects of 30-50 km each separated by 10 km. Precision is likely to have been poorer if transects were placed throughout the survey area. However, stratification is likely to improve precision, so a line length of ~500 km may be sufficient to achieve a precision of 20% and more than adequate to achieve 60-80 sightings, which is considered a minimum number for distance sampling (Buckland *et al.* 1993).

If the study area is administered as more than one zone, then each zone will require 500 km of survey line to achieve a precision of 20%. If 900 km is surveyed, then there is likely to be the option of breaking the area into two zones. A total line length of 900 km was therefore used to design the survey here.

Transects were located within strata by randomly selecting intersection points in a 10 km × 10 km grid placed over the study area. The selected point formed the midpoint of a 30 km east-west transect. If the transect extended beyond a stratum in one direction it was truncated and extended in the other direction. If it could not fit into the stratum on a gridline, the remainder of the line was placed on the neighbouring gridline to the north or south. A transect length of 30 km ensured >20 replicate lines over the study area for adequate precision and a representative sample.

Allocation of line length to strata was based on 'rough' estimates of the relative densities in each stratum. In the northern tablelands, surveys recorded areas of low (~1 kangaroo km^{-2}), medium (~5 kangaroos km^{-2}) and high (~10 kangaroos km^{-2}) density of eastern grey kangaroos (Cairns 2003). These were used as estimates of density in the strata here. The required line length in each density stratum in each RLPB district was determined by allocating the 900 km in proportion to estimated population size (Tables 2 and 3). Each RLPB district was also considered as a single stratum, because of environmental differences and to ensure good coverage in case they are used as administrative units. Only short line lengths were required in the low-density stratum, so these were usually just an extension of a line in an adjoining stratum to reduce ferry time between transects. This may introduce some bias and underestimate variance because edge habitat may be oversampled. However, the problem was likely to be only slight because density should be low in this stratum and the medium density stratum included a liberal buffer around wooded areas. The resulting survey design comprising 34 transects is shown in Figure 2.

[Table 2]
[Table 3]

Survey methods

The survey was conducted in August 2003 using a helicopter (Robinson R44) with the two rear doors removed, flown along each transect line at a ground speed of 93 km h^{-1} (50 kts) and at a height of 61 m (200 ft) above the ground. Navigation was by a global positioning system (GPS) receiver. Observers occupying the two rear seats of the helicopter counted the kangaroos seen on either side of the aircraft. Sightings of kangaroos were recorded into the 0-20 m, 20-40 m, 40-70 m, 70-100 m and 100-150 m distance classes, perpendicular to the transect line. Interval width increased with distance to reflect the greater importance of accurate measurements near the transect line, particularly to model the shoulder in the detection function (Buckland *et al*. 1993). The distance classes were delineated on aluminium booms extending from either side of the helicopter. The seating of the observers was allocated randomly for each survey session. All surveys were conducted within either two hours after sunrise or two hours before sunset.

On the longer transects (>20 km), observers counted in 5-min time blocks with a 30-s break between each block, otherwise observers counted continuously.

Sightings of clusters (groups of one or more) of eastern grey kangaroos in the different distance classes were recorded into micro-cassette recorders.

Data analysis

Distance data were analysed using the computer program DISTANCE 3.5 (Thomas *et al.* 1998) following the guidelines of Buckland *et al.* (1993). An estimate of the density of kangaroos is calculated as:

$$\hat{D} = \frac{n}{2wL\hat{P}_a}$$

where n is the number of clusters sighted, L is transect length, w is the truncation distance (i.e. 150 m) and P_a is the detection probability within a strip of area a = $2wL$. The relationship between number of sightings and perpendicular distance from the transect line is used to model the decline in detection probability away from the transect line, and thereby estimate P_a.

Six detection function models were considered in the analysis: a uniform key function, plus either a cosine or simple polynomial series expansion; a half-normal key function, plus either a cosine or Hermite polynomial series expansion; and a hazard-rate key function, plus either a cosine or simple polynomial series expansion. The most parsimonious model and number of adjustment terms in the series expansion were selected using Akaike's Information Criterion (AIC). Detection functions with marked spikes at zero distance were rejected. Densities of kangaroos were calculated as densities of clusters multiplied by mean cluster size. Average cluster size was adjusted downwards for the decline in probability of seeing smaller clusters with distance from the transect line. This was done by regressing $\log_e$(observed cluster size) against detection probability and then estimating average cluster size when detection probability is certain (i.e. on the transect line)(Buckland *et al.* 1993). Variance formulae for density estimates are given by Buckland *et al.* (1993). Post-stratification by observer, seating position within the aircraft and side-of-aircraft was also assessed, but only if numbers of clusters within any strata were >40. Side-of-aircraft differences were expected because of the difficulty in sighting animals when looking towards the sun (i.e. from the northern side of aircraft) (Pople *et al.* 1998*a*). The two rear seats give slightly different views of the transect and this may influence sightability. AIC was used to compare the more complex models of separate detection functions for each stratum with a model of a detection function pooled across strata.

Results

Four of the 34 transects could not be flown because of bad weather. These were the southern three lines in the Braidwood RLPB district and the line directly northeast of Goulburn. Based on similar habitat (Sahukar *et al.* 2003), Goulburn and Braidwood RLPB districts were therefore analysed as a single stratum. Unfortunately, the sections of transect lines in the low density stratum were not identified during the survey, so these data had to be pooled with data for the medium density stratum in each RLPB district. Density in this stratum would therefore have been underestimated slightly. For an overall estimate of abundance, the density in the low-density stratum in each RLPB district was conservatively assumed to be zero.

There were sightings of 709 clusters of eastern grey kangaroos made along 735.4 km of transect line. Average cluster size ranged 1.69-3.16 individuals among strata, while maximum cluster size ranged 12-14 among strata. Estimates of detection probability, density, total numbers and precision are shown for all strata and the entire study area in Table 4. To simplify calculations, the small high-density area in the Goulburn-Braidwood RLPB district was subsumed into the Yass RLPB district. Among density strata and RLPB districts, four different models were used as detection functions and three different types of post-stratification were employed. Detection probability also varied significantly across strata (range: 0.31-0.62). These results highlight the advantage of survey and strata-specific modelling, rather than relying on predetermined models and correction factors.

[Table 4]

Examples of fitted detection curves are given in Figures 3 and 4. The steeper detection curve and lower detection probability on the northern side of the helicopter was apparent at Cooma (Fig. 3). However, the opposite occurred along the Goulburn-Braidwood transect lines (Table 4). In the Yass high-density stratum, observer DB had a flatter detection curve than did SC (Fig. 4). There was a spike in sightings for DB at 20-40 m, suggesting greater viewing effort away from the centreline and therefore missing animals near the line. If detection probability on the transect line is <1, then density estimates will be negatively biased. However, the spike may simply have been a function of modest sample size (n=59). It is worth noting that differences in detection functions between strata do not necessarily translate into different P_a. Further, selection of one post-stratification model (e.g. side-of-aircraft) does not necessarily mean there were no effects for other post-stratification factors (e.g. observer, seating); rather they were overshadowed. However, in all analyses, the model of a detection function pooled across strata (i.e. no post-stratification) was second to the selected model according to AIC.

[Figure 3]
[Figure 4]

Discussion

To determine a continent-wide estimate of kangaroo numbers in the early 1980s, (Caughley *et al.* 1983) suggested a density of 5 eastern grey kangaroos km^{-2} for an unsurveyed area of 800,000 km^2 encompassing the eastern highlands. Since then Southwell *et al.* (1997) estimated macropod density in the northern two-thirds of this region using walked line transect surveys over 1987-92, returning a remarkably similar overall estimate of 5.3 eastern grey kangaroos km^{-2}. The survey reported here covers a largely unsurveyed portion of the eastern highlands. Comparisons between regions are difficult because of temporal variation in density and spatial variation in environmental factors driving changes in numbers. Ideally, comparisons should be made using average densities from decade-long time series that reflect the amplitude of density fluctuations in a region. Nevertheless, densities of eastern grey kangaroos in this study area are comparable to those recorded in recent helicopter surveys in the Glen Innes (8.11 kangaroos km^{-2}) and Armidale (10.23 kangaroos km^{-2}) kangaroo management zones (Cairns 2004).

Commercial harvesting in the study area was approved on a trial basis for the period 2004-2007. In addition to the ability to monitor population size, harvest offtake and compliance with regulations, the success of the trial will be determined by the impact of harvesting on the eastern grey kangaroo population as well as by landholder and industry participation (Department of Environment and Conservation 2004). A negative impact on the population would be manifest as a marked decline in numbers unexplained by environmental factors such as drought or disease. It would suggest an inability of the management system to monitor numbers, regulate the harvest or set sustainable quotas. Landholder participation can be measured as the extent to which the non-commercial take of kangaroos is reduced. Industry participation can be measured by the proportion of the available quota that is harvested.

In 2004, NSW DEC set a harvest quota for the study area of 44,000 eastern grey kangaroos, representing 15% of the population estimate of 286,600 ±32,300. The area was administered as a single kangaroo management zone. Harvesting began in March 2004 and the quota was fully allocated by September. It is anticipated that 80-90% of the quota will actually be taken.

Shoot-and-let-lie licences were considered to be only a rough guide to kangaroo distribution and abundance. There were 42,216 tags issued under SLL licences in 2003 for an area larger than the five RLPB districts comprising this new kangaroo management zone. However, compared with previous years this was unusually high, probably because of continuing dry conditions following the 2002-2003 drought. During 2004, the number of tags issued under SLL licences had declined by only 31% (Department of Environment and Conservation 2004). The fact the non-commercial take had not been further reduced following the introduction of commercial harvesting may be due to an increased demand for culling during continued dry conditions in 2004 and a lack of understanding by many landholders with the procedures associated with commercial harvesting. The previous non-commercial and 2004 commercial harvest in southeast NSW compares with a commercial take of 30-65,000 eastern grey kangaroos each year (1998-2003) in the Armidale and Glenn Innes zones (NSW DEC, unpublished data), encompassing a larger area of ~34,000 km^2 in similar terrain and vegetation and where there is a history of commercial harvesting.

Whether commercial harvesting remains viable in southeast NSW will depend on a number of factors. Quotas will decline if the population declines to a new ‘equilibrium’ or average density under harvesting. However, there may be little or no decline if harvesting simply replaces culling under SLL licences. In the short term, there is likely be an increase in abundance as the population makes an expected recovery from the drought; an increase which a proportional harvest should not inhibit.

Management recommendations

Harvest strategies other than constant proportional quotas could be employed including limiting harvest effort by restricting the number of shooters. Given that almost 30% of the area is in National Park or State Forest where harvesting and culling under SLLs are not permitted, and given that the terrain and vegetation will limit shooter access to other areas, there is a considerable safety net to guard against overharvesting. It is now well known that such spatial refuges can minimise the risk of overexploitation (Hall 1998; Lauck *et al.* 1998). To be effective, protected areas need to contain source populations that can repopulate areas depleted through harvesting. In the short term (i.e. <5 years), harvested areas adjoining National Parks and State Forests are likely to have their populations bolstered in this way. However, migration to areas remote from refuges will only occur over the longer term, perhaps >10 years. A further qualifying point is that overall kangaroo densities within these refuges are likely to be lower than in the surrounding areas. The higher densities will be on the margins of refuges, where forested areas abut open grazing lands. In short, spatial refuges in the zone should ensure regional persistence and will reduce the risk of overharvesting in the vicinity of a refuge, but be less effective with distance from a refuge.

A further safety net would be a threshold population density below which there is no harvesting. In theory, when there is uncertainty about a population’s size and dynamics, harvest offtake can be maximised and low probability of quasiextinction achieved by imposing a threshold density and allowing higher rates of harvest above the threshold (Engen *et al.* 1997; Milner-Gulland *et al.* 2001). The problem is that the temporal variation in harvest offtake increases with the density at which the threshold is set. This has been discussed for kangaroos by Pople (2003) who considered that, given that the kangaroo industry is unlikely to operate at densities below 2-5 kangaroos km^{-2}, imposing a threshold around this density would ensure that this in fact occurs. This would guard against an increase in the value of kangaroo products allowing shooters to operate at lower densities. It would also increase public confidence that the harvest is sustainable, because it would not be relying on the industry's decision to cease harvesting being determined by market forces.

A second survey for the southeast NSW management zone has been scheduled for 2006 (Department of Environment and Conservation 2004), for which survey effort should be reallocated according to the results of the 2003 survey. Some survey effort should be redirected from the Yass and Gundagai RLPB districts, where population sizes predicted prior to survey were overestimates, to the Cooma RLPB district, where the predicted population size was an underestimate (Table 2). The difference in density between the high and medium density strata in the Gundagai and Yass RLPB districts was smaller than expected, so effort in the high-density strata could be reduced. A suggested reallocation is given in Table 5, assuming 900 km is to be flown because survey cost is fixed. A shorter survey is also possible, given the goal of an overall precision of 20%. One caveat is that, while the allocation of effort in Table 5 is roughly optimal for a density estimate for the entire study area, it will not be optimal if sub areas (e.g. RLPB districts) are administered separately and each requires a precision of 20%. For example, Cooma has achieved the target with the present allocation, but Gundagai and Yass would likely have precision >20% with less effort. A further consideration is to conduct helicopter line transect surveys as double counts (Borchers *et al.* 1998), which would allow adjustment for bias due to incomplete sighting of kangaroos on the transect line.

[Table 5]

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Table 1. Areas (km^2) of five Rural Lands Protection Board (RLPB) districts proposed for commercial harvesting. Harvesting is precluded from National Parks (NPs) and State Forests (SFs) and there are some areas of high relief outside NPs and SFs that are unsuitable for aerial survey. The remaining area is divided into three strata representing areas of likely high, medium and low kangaroo density.

	Braidwood	Cooma	Goulburn	Gundagai	Yass	TOTAL
RLPB district area	5,980	11,375	6,426	9,507	6,305	39,594
High relief outside NPs and SFs	262	431	35	174	146	1,048
High density	130	0	56	3,691	3,067	6,945
Medium density	3,832	5,981	4,520	1,723	1,451	17,507
Low density	286	1,291	1,396	959	1,097	5,029
Survey area	4,248	7,271	5,973	6,373	5,615	29,481

Table 2. Predicted abundance of eastern grey kangaroos in five Rural Lands Protection Board districts in the southern tablelands of NSW. These are calculated from densities in three strata shown in Figure 2 and their areas (see Table 1). Densities are extrapolations from surveys in the northern tablelands of NSW (Cairns 2003).

Strata				**Abundance 'guess'**			
density 'guess' km^{-2}		**Braidwood**	**Cooma**	**Goulburn**	**Gundagai**	**Yass**	**TOTAL**
(High density)	**10**	1,300	0	565	36,911	30,669	69,445
(Medium density)	**5**	19,160	29,903	22,602	8,616	7,256	87,537
(Low density)	**1**	286	1,291	1,396	959	1,097	5,029
Survey area		20,746	31,194	24,563	46,486	39,023	162,011

Table 3. Allocation of survey line length (km) according to predicted abundance (see Table 2) in each stratum in each Rural Lands Protection Board district.

Strata	Braidwood	Cooma	Goulburn	Gundagai	Yass	TOTAL
High density	7	0	3	205	170	386
Medium density	106	166	126	48	40	486
Low density	2	7	8	5	6	28
Survey area	115	173	136	258	217	900

Table 4. Estimates of eastern grey kangaroo density (*D* ± s.e.) and numbers (*N* ± s.e.) in each Rural Lands Protection Board (RLPB) district. Estimates for the Goulburn and Braidwood districts have been combined. Included are the numbers of sightings (*n*), the detection function models, detection probabilities (P_a ± s.e.), and coefficients of variation (CV%) determined for each density stratum following post-stratification on the basis of side-of-aircraft (N=north or S=south), seating (LHS=left hand side or RHS=right hand side) or observer (DB or SC) or none. The density estimate for the entire study area includes the low-density stratum within each RLPB district. HzC, hazard-rate with cosine series; UC, uniform with cosine series; UP, uniform with polynomial series; HNC, half-normal with cosine series.

RLPB district	***Density stratum***	**n**	***Model***	**P_a**	**D**	**N**	***CV%***
Cooma	*Medium*						
	N	89	HzC	0.38 ±0.07	**15.97**	**95,505**	**18.2**
	S	81	UC	0.51 ±0.03			
Goulburn-Braidwood	*Medium*						
	N	65	UC	0.55 ±0.04	**9.39**	**78,459**	**33.2**
	S	50	HzC	0.31 ±0.16			
Gundagai	*Medium*	65	HNH	0.48 ±0.05	10.16	17,502	35.1
	High						
	LHS	113	HzC	0.46 ±0.06	12.21	45,050	24.0
	RHS	79	UP	0.62 ±0.04			
					11.55	**62,552**	**19.9**
Yass	*Medium*	44	HNC	0.46 ±0.06	8.54	12,388	33.7
	High						
	DB	59	UC	0.60 ±0.06	11.60	37,737	26.2
	SC	61	HNC	0.44 ±0.04			
					10.66	**50,125**	**21.4**
TOTAL					**9.72**	**286,641**	**12.3**

Table 5. Reallocation of survey line length (km) according to estimated abundance (see Table 4) in each stratum in each Rural Lands Protection Board district. The areas of high density in the Goulburn and Braidwood RLPB districts have been included in the Yass RLPB district. A density of 2 kangaroo km^{-2} is assumed in the low-density stratum

Strata	Braidwood	Cooma	Goulburn	Gundagai	Yass	TOTAL
High density	-	-	-	137	114	251
Medium density	109	290	129	53	38	618
Low density	2	8	8	6	7	31
Survey area	111	298	137	196	159	900

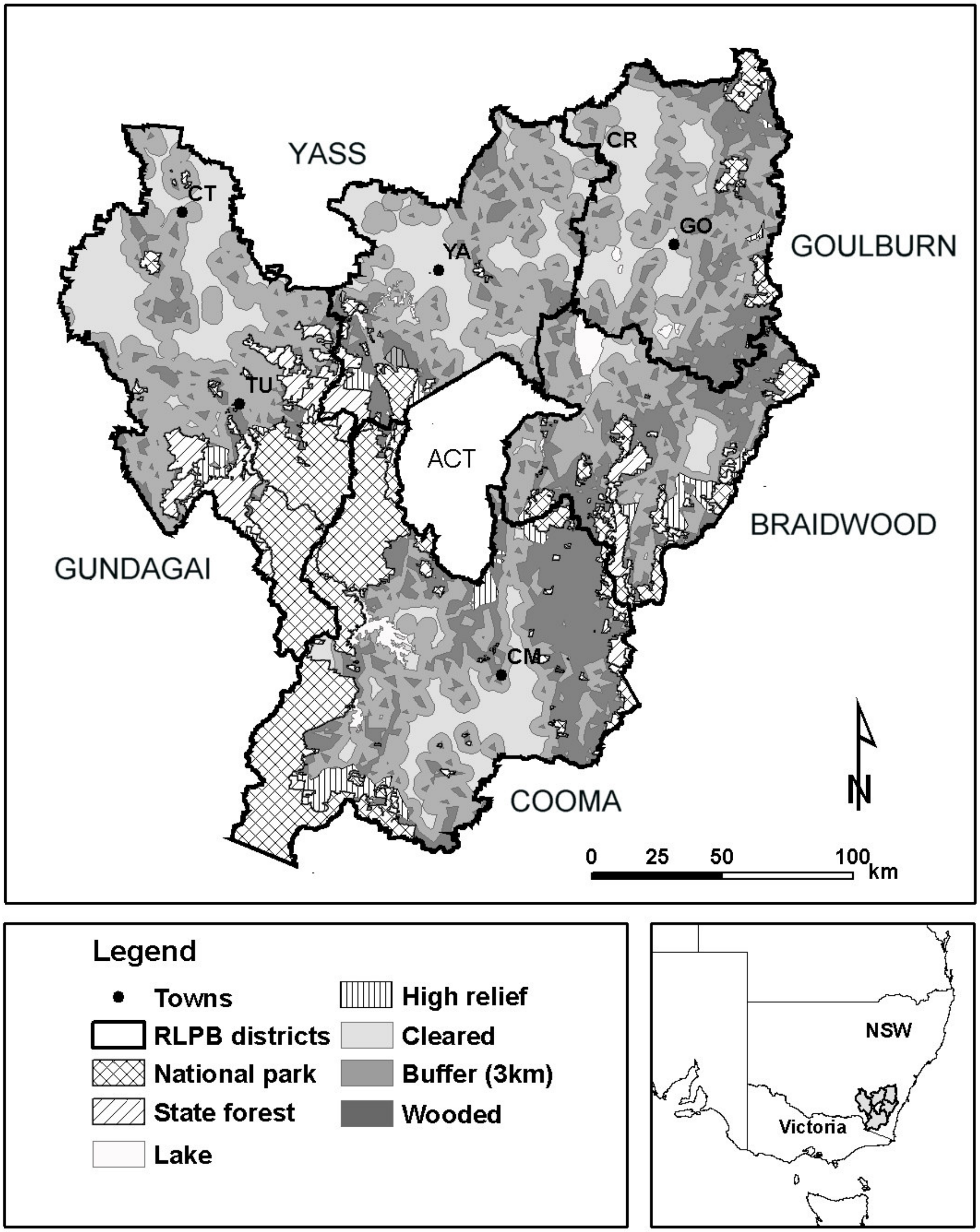
Figure captions

Fig. 1. The study area in southeastern New South Wales, which surrounds the Australian Capital Territory (ACT). CR, Crookwell; GO, Goulburn; YA, Yass; CT, Cootamundra; TU, Tumut; CM, Cooma. Areas of high relief and open forest or woodland were determined from the relief coverage (Geoscience Australia 2001), which is © Commonwealth of Australia (Geoscience Australia) 2001, and landuse coverage (Bureau of Rural Sciences 2001), © Commonwealth of Australia (National Land and Water Resources Audit) 2001.

Fig. 2. Design for the survey of kangaroos in the study area in southeastern New South Wales. The survey area is restricted to areas outside National Parks and State Forests and areas without high relief, which are shown in Figure 1. The survey area is divided into three strata according to expected kangaroo density and transects were placed randomly. CR, Crookwell; GO, Goulburn; YA, Yass; CT, Cootamundra; TU, Tumut; CM, Cooma

Fig. 3. Histogram of perpendicular distances and fitted detection function for eastern grey kangaroos in the Cooma Rural Lands Protection Board district in 2003 for the (*a*) northern (*n*=89) and (*b*) southern (*n*=81) side of the helicopter.

Fig. 4. Histogram of perpendicular distances and fitted detection function for eastern grey kangaroos in the high density strata of the Yass Rural Lands Protection Board district in 2003 for (*a*) observer DB (*n*=59) and (*b*) observer SC (*n*=61).


YASS
CT
YA
CR
GO
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CM
COOMA
N
0 25 50 100 km
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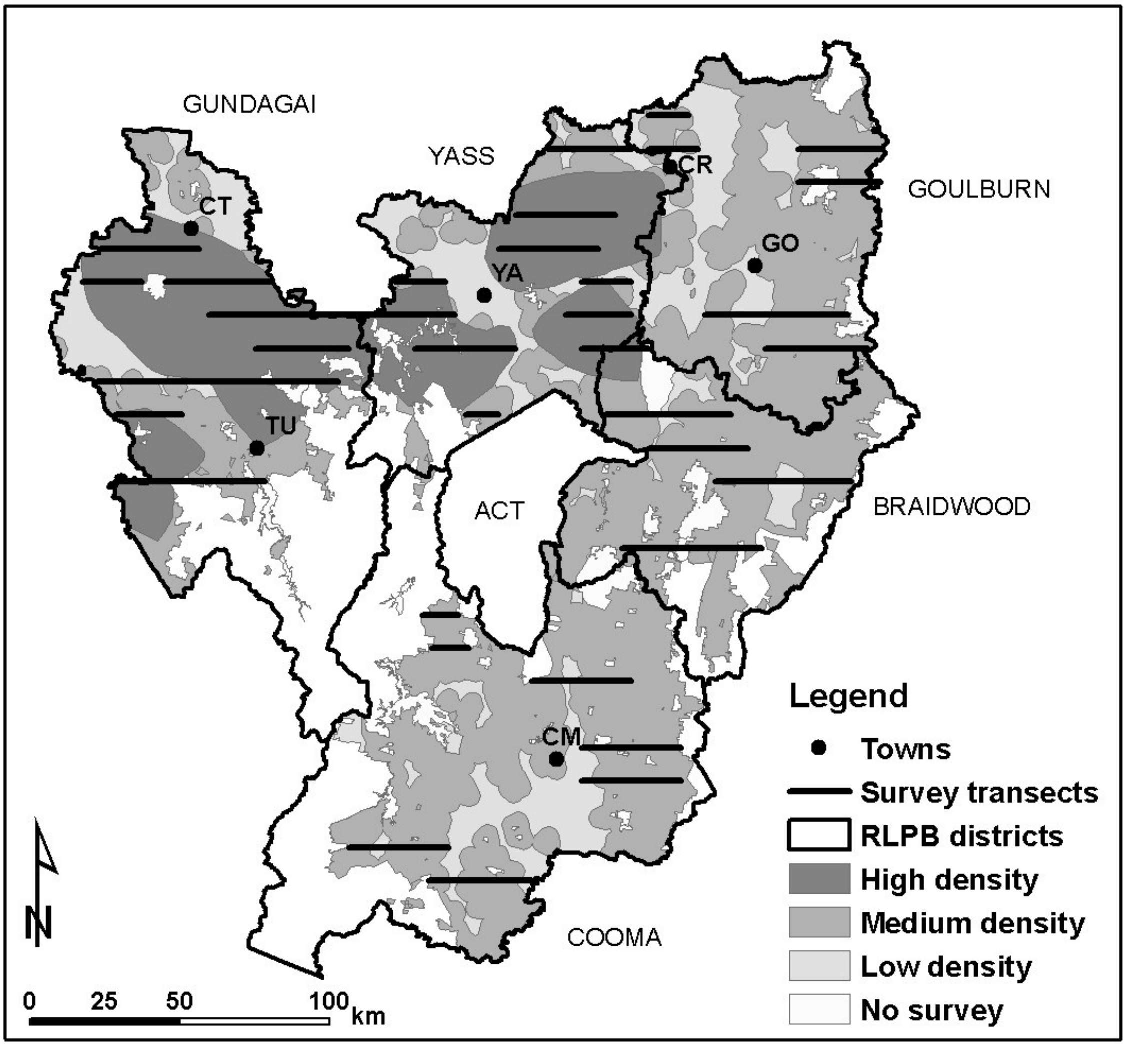
Towns
RLPB districts
National park
State forest
Lake
High relief
Cleared
Buffer (3km)
Wooded
NSW
Victoria

Figure 1


GUNDAGAI
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ACT
COOMA
CT
TU
YA
CR
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Medium density
Low density
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Figure 2

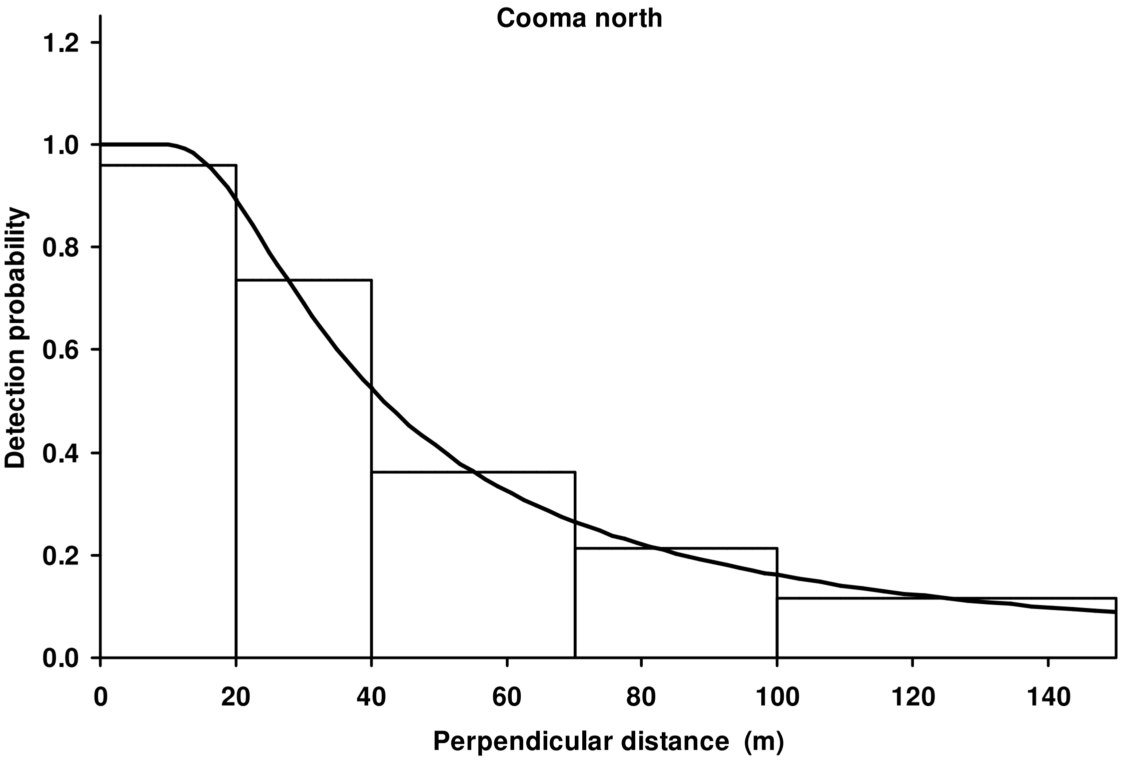


Figure 3*a*

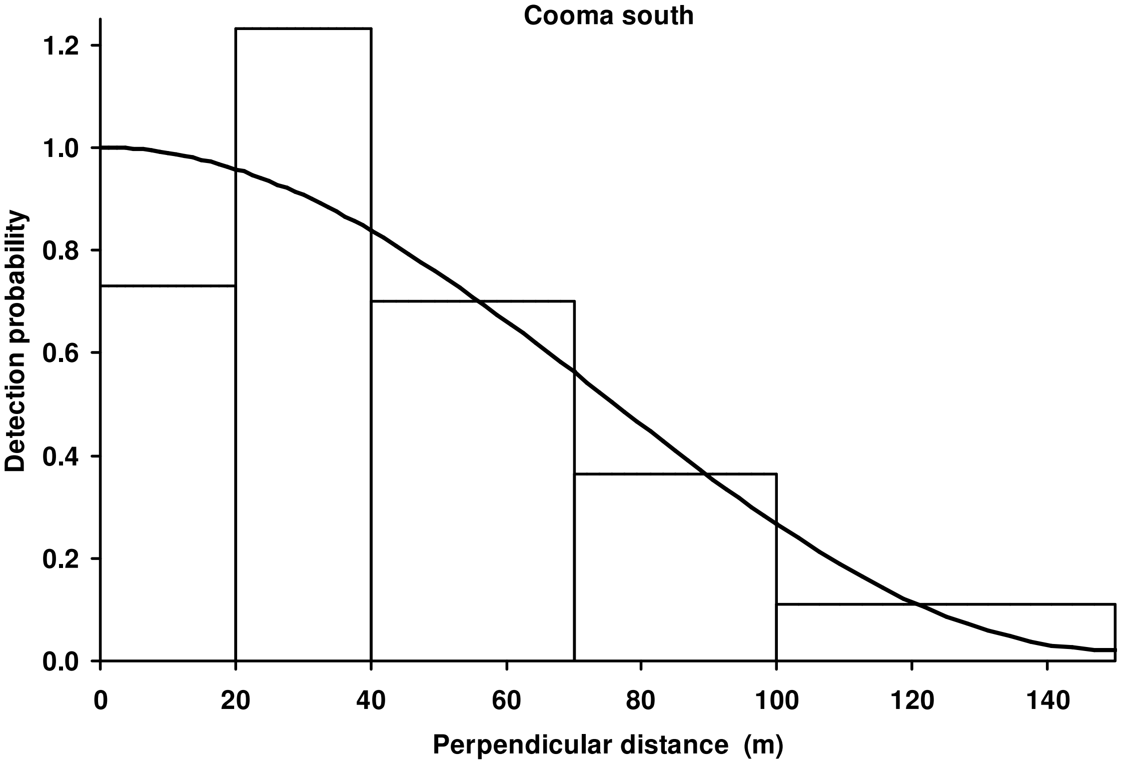


Figure 3*b*

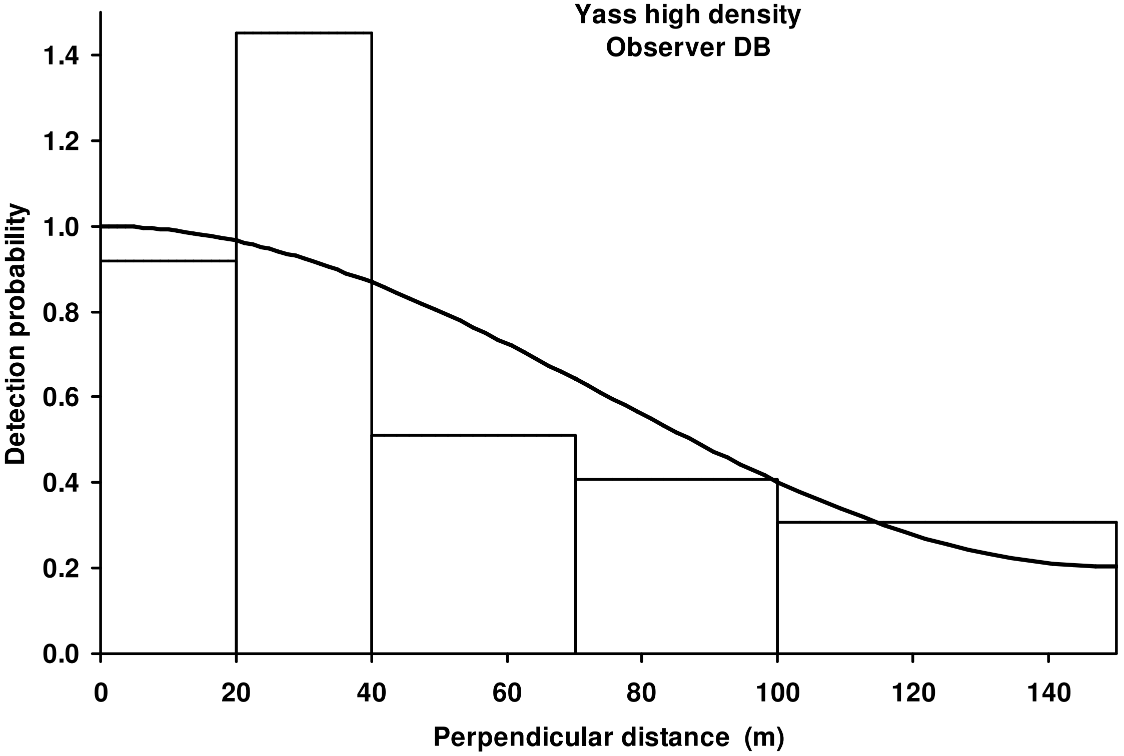


Figure 4*a*

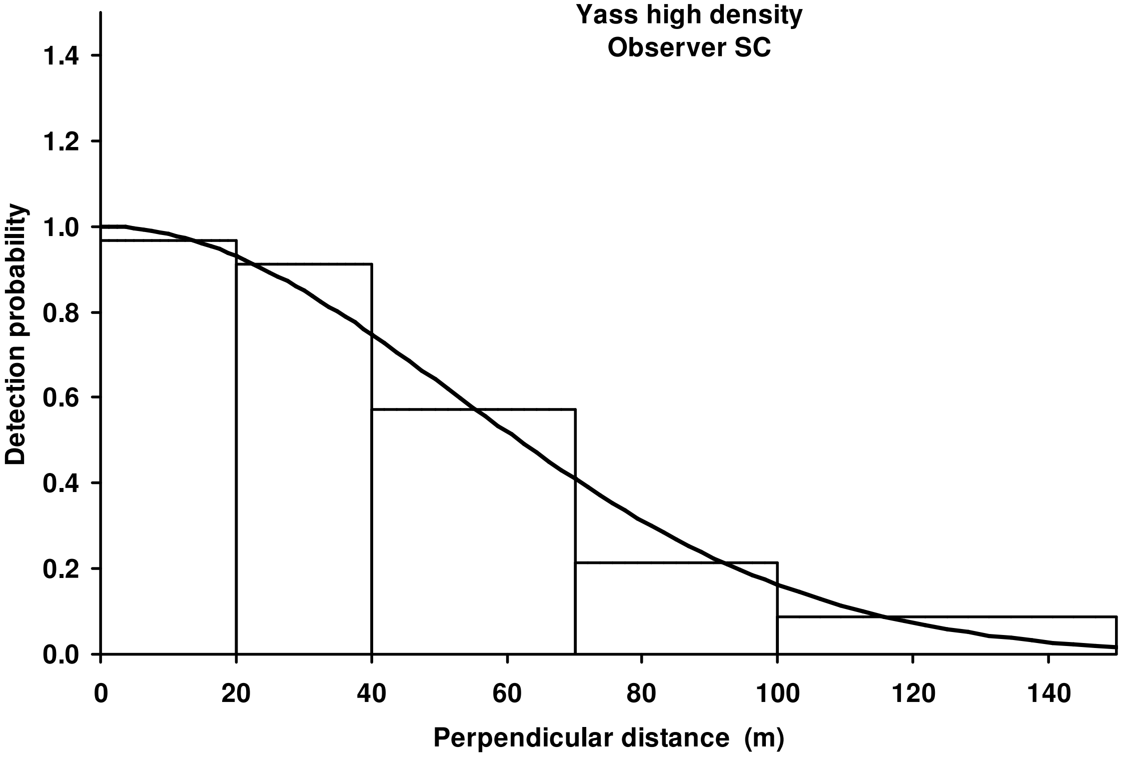


Figure 4*b*

9. Predicting kangaroo population dynamics from rainfall and satellite imagery

9.1 Introduction

The dynamics of kangaroo populations appear to be considered well understood, with the numerical response of populations to a variable, rainfall-driven food supply providing an often text book example (Caughley and Sinclair 1994; Bayliss and Choquenot 2002; Sibly and Hone 2002; Sinclair and Krebs 2002). It falls within the mechanistic paradigm described by Krebs (1995, 2002) and has been used to contrast that approach with that of the density paradigm with its emphasis on density and equilibria rather than interactions with resources (Caughley and Sinclair 1994).

This understanding has largely been through the application of aerial survey to monitoring kangaroo numbers in semi-arid and arid regions. Recent analyses of some of these survey data, particularly longer time series, suggest that the dynamics of some kangaroo populations do not fall so neatly into the mechanistic paradigm (McCarthy 1996; Jonzen *et al.* 2005; see Section 10). Cairns *et al.* (2000) also found the dynamics of western grey kangaroos in South Australia could not be as well predicted as populations in western New South Wales. It is worth noting that while populations of four species have been surveyed throughout semi-arid and arid Australia, our understanding has largely come from surveys of red and western grey kangaroos in western New South Wales and northern South Australia (e.g. Caughley *et al.* 1984; Bayliss 1985a, b, 1987; Caughley 1987; Cairns and Grigg 1993). Data from elsewhere in these species' ranges, particularly more mesic areas and northern Australia, and on eastern grey kangaroos and common wallaroos have had limited assessment.

Ideally, numerical response models for kangaroos should be based directly on food supply such as pasture biomass (Bayliss 1987). However, this has rarely been available and rainfall has been used as a surrogate. Early assessments indicated recent rainfall was a useful predictor of rate of increase in red and western grey kangaroo populations (Bayliss 1985a; Cairns and Grigg 1993), but more recent investigations with a longer time series showed rainfall with a greater lag gave a stronger correlation with rate of increase (McCarthy 1996). An alternative is to use satellite imagery which has the advantage of being directly related to the pasture response (Hobbs 1995) and being recorded throughout remote, arid areas where rainfall recording stations are sparsely located and rainfall can be patchy.

This section explores the possible determinants of rate of increase of four species of kangaroo throughout the sheep rangelands of eastern Australia. There are now time series of data extending back over 20 years across a range of environments and include a wide range of harvest rates, which is an influence that has previously been largely ignored.

9.2 Methods

9.2.1 Study area, survey and harvest data

The study area covered over 1.2 million km^2 of eastern Australia (Fig. 9.1) encompassing the South Australian pastoral zone (SAPZ), the western plains of New South Wales and

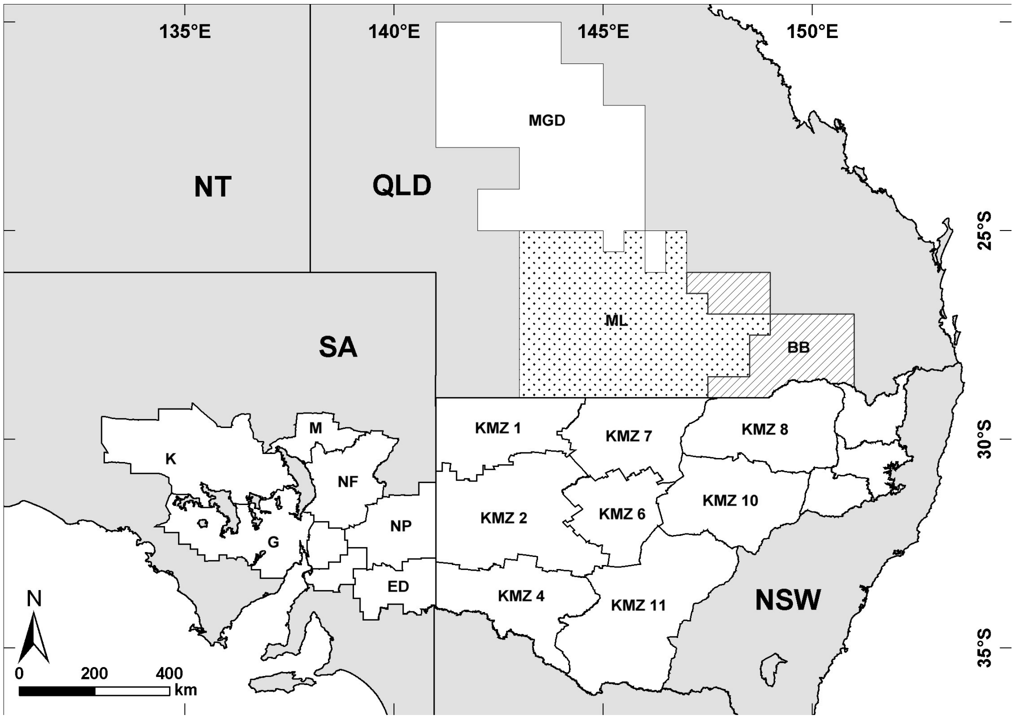


Fig. 9.1. The survey area within the sheep rangelands of eastern Australia. This area has been broken up into regions in which kangaroo harvests are managed in New South Wales (NSW, kangaroo management zones, KMZ) and South Australia (SA, soil conservation boards). Biogeographic boundaries (Environment Australia 2000) adjusted to coincide with ½° latitude and longitude lines, are shown in the Queensland (QLD) survey area. Unlabelled regions in southern SA had estimates of density that were considered too imprecise for analysis here. Similarly, unlabelled regions in eastern NSW were not examined because they lack long-term aerial survey data. Salt lakes dissect the study area in South Australia. K, Kingoonya; M, Marree; NF, North Flinders Ranges; NP, Northeast Pastoral; ED, Eastern Districts; G, Gawler; BB, Brigalow Belt; ML, Mulga Lands; MGD, Mitchell Grass Downs.

the sheep rangelands of Queensland. Aerial surveys are described in detail in Section 12. In South Australia, kangaroos are managed in soil conservation boards (SCBs). Six SCBs within the SAPZ have been extensively surveyed since 1978 and data were available up to 2003. To simplify analyses and to be consistent with the analyses of Jonzen *et al.* (2005) (see Section 10), these SCBs were pooled into three regions based on similar average rainfall: northwest (Kingoonya and Marree), northeast (North Flinders Ranges and Northeast Pastoral) and south (Eastern Districts and Gawler). In New South Wales, kangaroos are managed in kangaroo management zones (KMZs) for which survey data were available for 1984-2003. During 1975-1984, annual aerial surveys were conducted in parts of KMZ 2, 6, 8 and 10, but density estimates had to be extrapolated from monitor block (1977-1983) and map sheet (1975-6) densities. In Queensland, kangaroos have been managed without any regional division until 2003 (see Section 3). Annual aerial surveys have been conducted across a core area (roughly equivalent to the central zone, see Section 3) since 1984 and data were available up to 2003. This area was broken up into three regions broadly coinciding with biogeographic boundaries (Environment Australia 2000): mulga lands, Mitchell grass downs and brigalow belt. Since 1991, surveys have been conducted by helicopter in blocks (Fig. 9.2) and these provided obvious units for analysis, albeit for a shorter period. Helicopter surveys provided the only data on wallaroo population dynamics.

Collation of harvest data within each State is described in Section 1.

9.2.2 Satellite imagery

The Normalised Difference Vegetation Index (NDVI) is a measure of green vegetation derived from satellite multispectral image data (Tucker *et al.* 1985; Lillesand *et al.* 2004) using an advanced very high-resolution radiometer. The NDVI is calculated as the difference in the near infrared (channel 2) and visible red (channel 1) parts of the electromagnetic spectrum. Green vegetation strongly reflects near-infrared radiation but absorbs visible red light, thereby responding to changes in herbage biomass and quality (i.e. greenness). A number of studies have found a strong relationship between plant production and NDVI (e.g. Paruelo *et al.* 1997) including in the Australian rangelands (Hobbs 1995). Absolute values of NDVI and their variability at any location will also be influenced by vegetation composition and structure, topography and soil type, confounding spatial comparisons. This can partly be addressed by using the difference between the maximum and minimum NDVI (NDVI flush) within an annual growth cycle, providing an index of pasture production although it includes growth in perennial plants (Cridland *et al.* 1995). The problem can be dealt with further by standardising values at each location over a time series. Monthly NDVI images for the period July 1981 to July 2003 at a 1-km^2 resolution were obtained for the SAPZ from the Federal Department of Environment and Heritage. These were composite images representing the maximum NDVI for each month, thereby reducing contamination with cloud cover.

For each month, NDVI and NDVI flush values were averaged across pixels within each SCB. These values were then averaged over the three- (May-July) and six-month (February-July) period prior to each survey. Values were standardised for each SCB over the study period were used in analysis, allowing possible pooling of SCBs whose kangaroo populations respond similarly to NDVI.

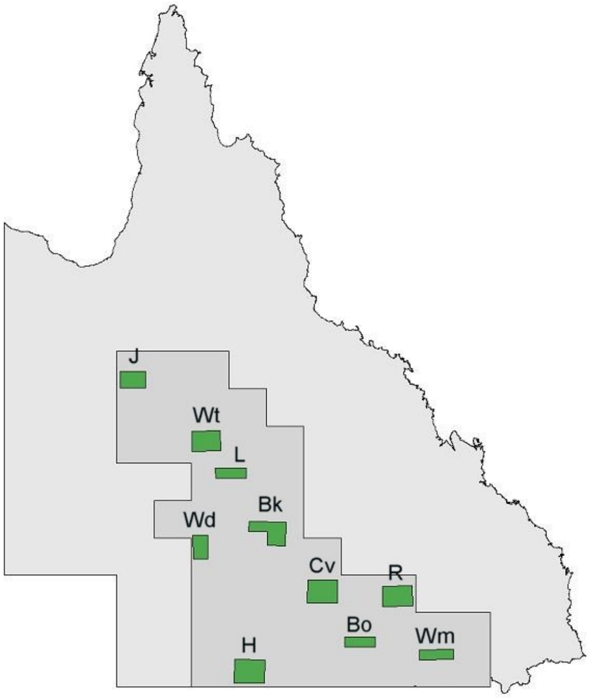


Fig. 9.2. Helicopter survey blocks (green) used monitor kangaroo populations in the core survey area (dark grey) in Queensland since 1992. J, Julia Creek; Wt, Winton; L, Longreach; Wd, Windorah; Bk, Blackall; Cv, Charleville; H, Hungerford; Bo, Bollon; R, Roma; Wm, Westmar.

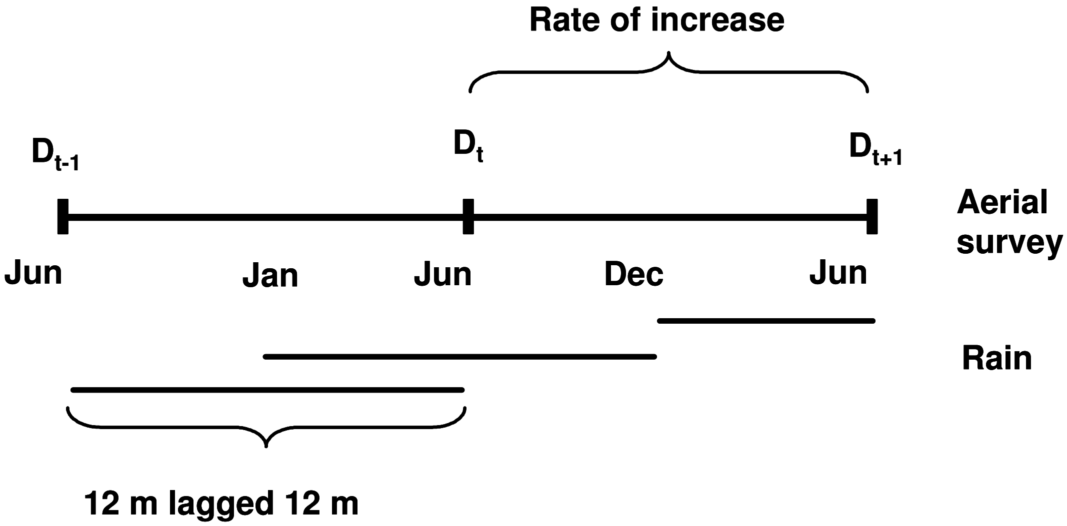


Fig. 9.3. Three rainfall periods used in analysis relative to estimates of density (D) determined by aerial survey. From left to right, the rainfalls are 12 months rain lagged 12 months (labelled), 12 months rain lagged 6 months and 6 months rain with no lag. The lag is from the second of two estimates of density which are used to calculate exponential rate of increase.

Some assessment of the ability of NDVI to monitor kangaroo food supply in the study area was possible. Photosites had been established throughout two properties, Bulgunnia (~3,100 km^2, $n = 21$) in Kingoonya SCB and Mulyungarie (~3,500 km^2, $n = 22$) in Northeast pastoral SCB. These were photographed in autumn and spring of each year since late 1992 (S. Cairns unpublished data). From a 1.5 m post, the base of another post 10 m south was photographed using low ASA colour slide film with the camera shutter set to f16 to maximise depth of field. The resulting series of photographs were digitised then ranked using the method of Noble (1977). This involves the subjective comparison of the pasture biomass (i.e. grasses, forbs and subshrubs) in each photo with all others in the series. For each property, the ranks of all photosites were averaged for each time period. The resultant trends were then compared with the NDVI averaged across each property and correlated with NDVI recorded for the same month as the photographs.

9.2.3 Rainfall

Monthly rainfall data were obtained for stations in the study area (Figs 9.1 and 9.2) from the Bureau of Meteorology. Monthly rainfall surfaces were then calculated using inverse distance weighting. For each region (Figs 9.1 and 9.2), rainfall was determined for the six months and 12 months prior to the second of two consecutive surveys and for 12 months prior to the second survey with a 12 months lag (Fig. 9.3). These periods have previously been found to correlate best with kangaroo rates of increase in northern South Australia (Cairns and Grigg 1993), in western New South Wales (Bayliss 1987) and the entire SAPZ (McCarthy 1996), respectively. Rainfall was collated for the 12 months and 24 months prior to the second survey to provide additional candidate periods for predicting rate of increase. In Queensland, rainfall has a summer peak, becoming strongly seasonal further north. Six months rainfall over the summer wet season (October-March), the winter dry season (April-September) and the summer wet season lagged 12 months prior to the second survey were therefore collated as possible determinants of kangaroo rates of increase. As with NDVI, rainfall was standardised for each region using long-term (~100 year) average and standard deviation.

9.2.4 Analysis

Annual rate of increase of kangaroos was calculated as $r = \ln(D_{t+1}/ D_t)$, where D_t and D_{t+1} are estimates of population size for consecutive surveys (Fig. 9.3). The instantaneous harvest rate hr between consecutive aerial surveys was calculated as (see Section 10):

$$hr = -\ln\left(1 - \frac{h}{\sqrt{D_t D_{t+1}}}\right) \tag{1}$$

where h is the harvest offtake between surveys. This accounts for the fact that harvesting is essentially continuous through time but the regression model treats it as a single event. It therefore must be calculated as an isolated rate equivalent to the instantaneous rate (Caughley 1977). The net rate of increase adjusted for harvest rate was calculated as:

$$nra = r + hr \tag{2}$$

This assumes the coefficient for *hr* is unity. Equation 2 assumes that harvest mortality is additional to natural mortality rather than compensatory to some extent (see Sections 5 and 10). An alternative formulation is:

$$rhr = hr \times \exp[-\exp(-a \times [rain - d])] \tag{3}$$

where *rhr* is the realised harvest rate, *a* is a parameter that could be determined using non-linear regression or assumed a particular value, *d* is a parameter determining the point of inflexion and *rain* is the interval of rainfall best predicting *nra*. This sigmoidal function (Fig. 9.4) was used to portray decreasing compensation (i.e. harvest mortality increasingly additive) with increasing rates of increase, which would be predicted for a population extrinsically regulated by food supply.

Plots of rate of increase (*nra*) against rainfall were first scrutinised for outliers and time traces examined for evidence of the ‘hysteresis’ reported by (Bayliss and Choquenot 2002) whereby populations recovering from drought respond differently to food supply. Bayliss and Choquenot (2002) reported relatively low rates of increase during recovery from drought whereas Cairns and Grigg (1993) reported the converse; the latter expected from an altered population sex and age structure. Correlations between annual rates of increase (*nr*) and candidate rainfall periods and NDVI were then examined. These correlations were then used to propose likely regression models of the form:

$$r = \text{explanatory variables} - \text{harvest rate} - D_t \tag{4}$$

where harvest rate was *hr* or *rhr* with coefficients of unity. Explanatory variables included one or two periods of rainfall, curvilinear terms, interactions and piecewise regression models (Crawley 2002). The latter involved including a recent rainfall term only when it was below a certain amount. The rationale is that survival of juveniles determines fluctuations in kangaroo numbers, as it does for large mammals in general (Gaillard *et al.* 1998). This is determined by rainfall with a substantial lag as juveniles are not readily detected from the air (Bayliss 1985b; McCarthy 1996). However, adult mortality can be substantial during drought (Robertson 1986) and immediately influence population change (Caughley *et al.* 1985), hence the requirement for a recent rainfall term. The threshold point below which to include recent rainfall was determined by plotting the deviance for models with a threshold at successively lower periods of rainfall (Crawley 2002).

Models were compared using Akaike weights from Akaike’s information criterion (AIC) (Burnham and Anderson 1998) and the best model according to Akaike weights reanalysed assuming partial compensatory mortality (*rhr*), then Akaike weights recalculated. Finally, the previous year’s density, standardised over the region’s time series, was included as an additional term in the best rainfall or NDVI model. Models with negative coefficients for rainfall or NDVI and positive coefficients for density were considered implausible and were ignored.

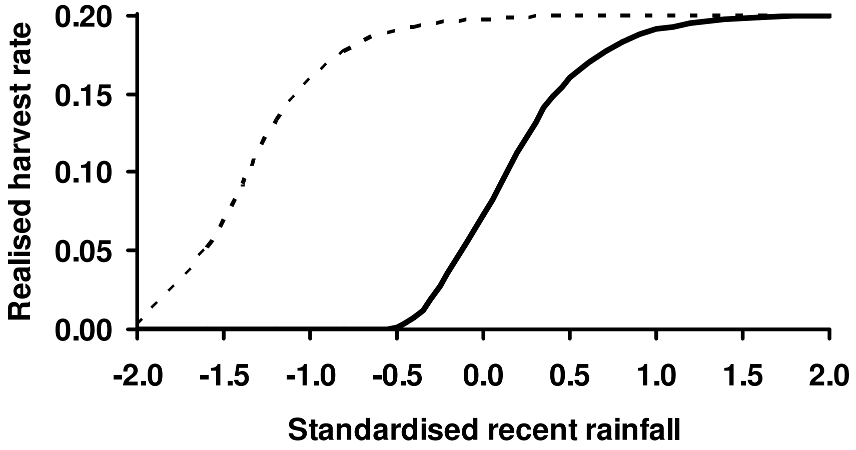


Fig. 9.4. The relationship between realised harvest rate between two density estimates (D_t and D_{t+1} in Fig. 9.3) and standardised 12 months rainfall with a 12 months lag (see Fig. 9.3) when harvest mortality is partially compensatory rather than additional to natural mortality, according to equation 3 with $a = 3$ and instantaneous harvest rate is 0.2. The solid line is more strongly compensatory ($d = 0$ in equation 3) than the dashed line ($d = -1.5$).

The geographic patterns in the determinants of kangaroo rate of increase were assessed in a number of ways. The ability of rainfall alone to predict rate of increase can be measured by the adjusted coefficient of determination (R^2), which was plotted against average annual rainfall for each region or block. Where no rainfall model was selected, the minimum R^2 for that species (always < 0) was used. The value of R^2 will vary with the length of the time series, so the comparisons are only valid within States. To enable this, the New South Wales data were examined only from 1984. To increase the number of sample points, the South Australian data were analysed for all six SCBs (Fig. 9.1). The strength of density dependence can be measured by the partial regression coefficient for the lagged density term. Where the model with density was not an improvement over a model with rainfall alone, a coefficient of zero was used. This coefficient can similarly be plotted against average annual rainfall for each region or block. Density dependence will be overestimated in the regression analysis because past density is included in both response and explanatory variables and there is unaccounted measurement error (Burgman *et al.* 1993; McCarthy 1996; Fig. 9.5). However, the interest here is not in the absolute value, but in the comparison among areas. Finally, Section 5 used a model assuming reduced kangaroo population variation in more mesic areas to compare harvest strategies and survey frequency. The basic premise of this model could be assessed by plotting the coefficient of variation (SD/mean) of kangaroo density against average annual rainfall for each region or block.

9.2.5 Simulation

Using Caughley's (1987) interactive model (see Section 5), an expected pattern of correlation between rate of increase adjusted for harvest rate (*nra*) and rainfall and past density was determined under harvesting and uncertainty. An unstructured red kangaroo population was simulated over 100 years using a weekly time step. Briefly, kangaroo rate of increase is determined by pasture biomass which in turn is determined by recent rainfall, past pasture biomass and the density of kangaroos consuming the pasture. Seasonal rainfall was drawn from a lognormal distribution using the mean and standard deviation from Menindee Post Office in western New South Wales. The population was harvested at an annual instantaneous rate of 5-20% drawn from a uniform distribution. To mimic current management practice in setting quotas, the annual harvest was calculated as a percentage of the previous winter's population estimate. That density estimate was drawn from a lognormal distribution with a mean being the modelled population density (= 'true' density) and a standard deviation ranging 0-0.6 × density. Rate of increase was also determined from these density estimates. For each level of precision in the density estimate, 1,000 iterations were performed, each providing correlations between the rate of increase (*nra*) of kangaroos and various rainfall intervals and past density.

The same exercise was performed using the coefficient of variation of rainfall for Yass in southeastern New South Wales, to mimic the dynamics of a kangaroo population in a more mesic environment (see Section 5). The model was also run for the Northeast Pastoral SCB in northern South Australia (Fig. 9.1) over 1975-2003. This allowed assessment of the likely correlations for the actual study period. Here, the model used rainfall for the Northeast Pastoral SCB, rescaled to Menindee's mean. The model was fit using least squares to the actual aerial survey, harvest and livestock data (see Section 10) by adjusting the proportion of the pasture consumed by sheep; a parameter in Caughley's (1987) model.

Finally, a single run of the model for Menindee produced a dataset of density, pasture biomass, annual rainfall, harvest offtake and rate of increase. A harvested and unharvested run using the same 100-year rainfall were examined. These data were analysed to compare the two ways of incorporating harvest rate into linear regression models predicting rate of increase (additive or partially compensatory) using Akaike weights and to estimate parameters *a* and *d* in equation 3 using non-linear least squares regression.

9.3 Results

9.3.1 Simulation

Simulations using Menindee rainfall showed the expected high correlation between rate of increase and pasture biomass. Calendar year rainfall (12.6 in Fig. 9.5) was identified as the best rainfall period predicting of rate of increase, although 12 months rainfall with lags of 0-12 months had similarly strong correlations (Fig. 9.5). As uncertainty in estimating density increased, the correlation between rainfall and rate of increase declined. In contrast, the negative correlation with the previous year's density became stronger, surpassing rainfall in the strength of the correlation coefficient around a precision (SE/mean) of 0.2. By the time precision had increased to 0.4, >5% of simulations recorded correlations < 0 for all rainfall periods examined. At a precision of 0.4, 12 months rainfall with a 12 months lag was the best predictor of *nra* in 21% of simulations, up from 0.2% when density was certain.

For the simulations at Yass, correlations with rate of increase and density, pasture biomass and rainfall showed an identical pattern to Menindee, but were about 10% stronger when there was no uncertainty in population size. However, under uncertainty the correlation with rainfall was lower at Yass than Menindee whereas the correlation with density remained stronger. Given this model, R^2 was expected to decline with increasing average annual rainfall while the strength of density dependence was expected to increase.

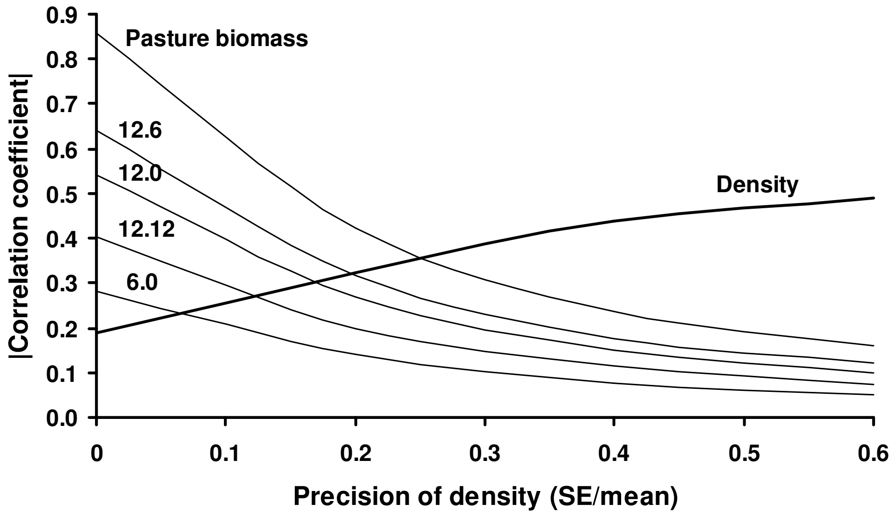


Fig. 9.5. Relationship between absolute value of the correlation coefficient between kangaroo rate of increase (adjusted for harvest rate) and pasture biomass and periods of rainfall, and precision of density estimates based on 1,000 simulations of a harvested red kangaroo population at Menindee in western New South Wales. Rainfall is coded as *x,y* where *x* is the interval of rainfall in months and *y* is the lag in months from the second of two consecutive aerial surveys (Fig. 9.3).

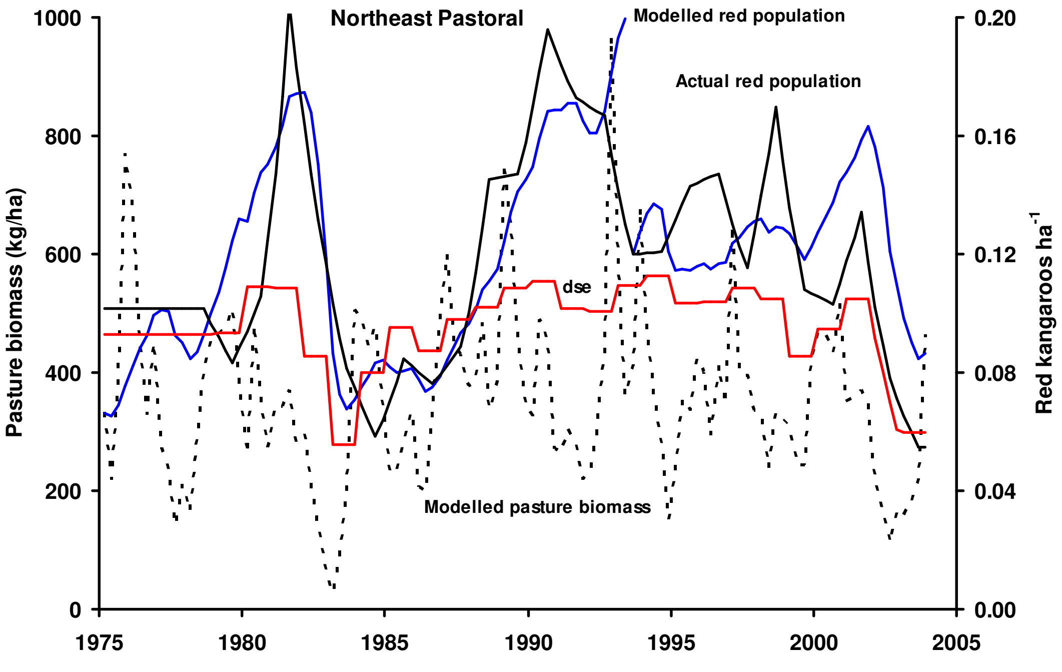


Fig.9.6. Caughley's (1987) interactive model (solid blue line) fitted to red kangaroo density estimated by aerial survey (solid black line) in Northeast Pastoral SCB (see Fig. 9.1). Kangaroo rate of increase is modelled as a function of pasture biomass (dashed black line), which in turn is a function of rainfall and grazing by kangaroos and livestock (converted to dry sheep equivalents, dse; solid red line). Both modelled and actual populations were harvested. The modelled population was reinitialised in 1993.

The fit of Caughley's (1987) model to data for Northeast Pastoral SCB was remarkably good (Fig. 9.6). However, the model needed to be reinitialised in 1993 when the population declined sharply whereas the model increased markedly on the back of high pasture biomass. The fit was poorer following 1993 than for 1978-1992, suggesting a change in pasture state. In contrast to the 100-year simulations using random rainfall, the correlations between rate of increase were strongest with 12 months rainfall immediately prior to the second survey (i.e. 12.0 *cf.* 12.6). Density had a weaker correlation with rate of increase than most rainfall periods and, again in contrast to the 100-year simulations using random rainfall, this correlation declined with poorer precision (i.e. increasing SE/mean) so that it was always weaker than most rainfall periods.

Fitting equation 3 to the data resulted in an implausible negative value for a. It was therefore fixed at 3 and parameter d fixed at 0. For a harvested population, the regression of r against rainfall and harvest rate, has a similar slope but higher intercept compared with the regression of r against rainfall without harvest rate. The regression using *rhr* has a steeper slope. Using *rhr* (partial compensatory mortality) returns a slope and intercept closer to those for the numerical response of an unharvested population (i.e. r against rainfall) than *hr* (additive mortality), but it is a poorer fit to the data than using *hr* according to R^2, and had less support according to AIC. Nevertheless, incorporating harvest rate (*hr* or *rhr*) improved models according to AIC. Finally, it is worth noting that the previous year's density is a significant term in regression models predicting r when rainfall is used as an explanatory variable but not when pasture biomass is included.

9.3.2 South Australia

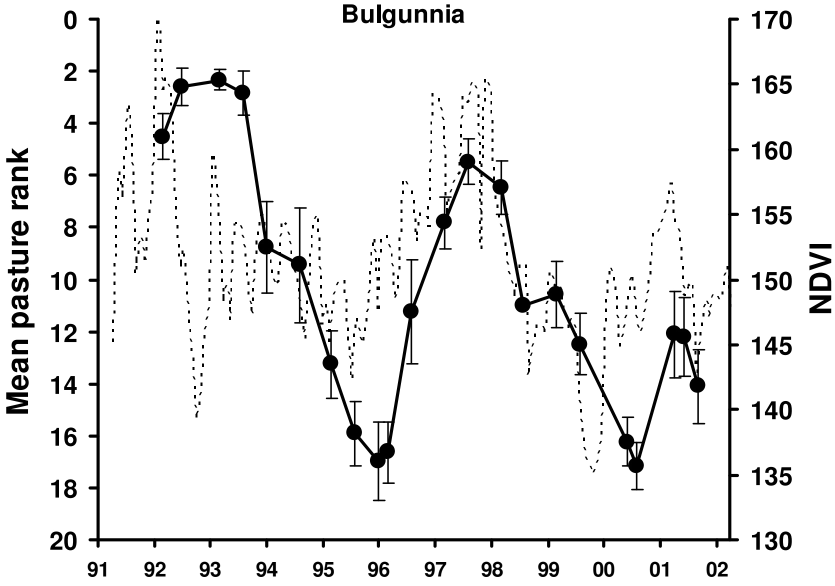
Photosites and NDVI

The relationship between the photosite ranks and NDVI are shown in Figure 9.7. There is a broad concordance between the two time series on each property and Spearman's rank correlation is significant in both cases (Bulgunnia, $r_s = 0.71$, $P < 0.01$; Mulyungarie, $r_s = 0.44$, $P < 0.05$).

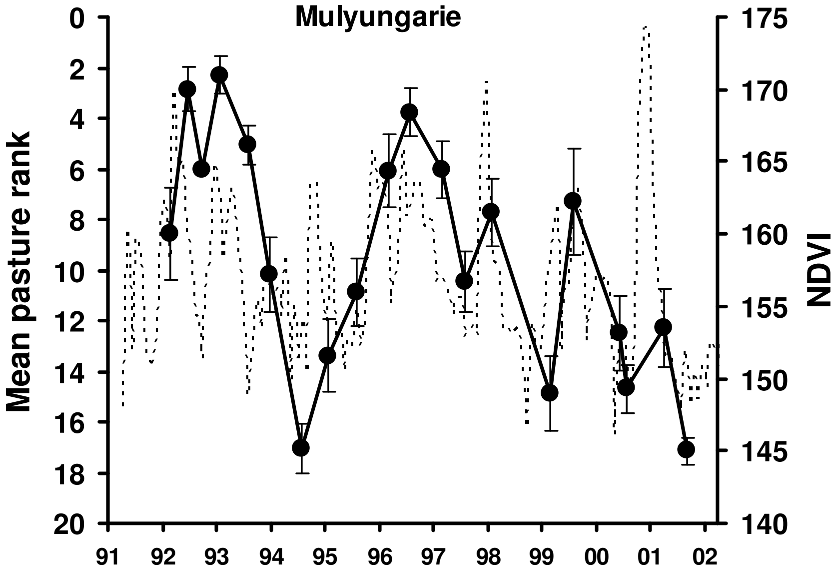
Kangaroo rate of increase

Correlations between kangaroo rate of increase and rainfall are shown in Table 9.1, highlighting the importance of 12 months rainfall with a 12 months lag for bothy species. These are consistent with the correlations for red kangaroos reported by McCarthy (1996) for the entire SAPZ, but with a shorter time series. Non-significant correlations were found for both species in regions where they occur at relatively low density (see Section 12).

Correlograms for NDVI and NDVI flush (Figs 9.8 and 9.9) show a similar pattern to rainfall. A lag of 8-12 months generally provided the strongest correlation with kangaroo rate of increase, which matches the best association with rainfall. Correlations were again strongest in regions where densities were highest, with the exception of a spike in the correlogram for western grey kangaroos in the northwest region. Correlations with NDVI flush were generally similar to those with unaltered NDVI and the 6 months interval was marginally better than 12 months. Most notably, NDVI only provided better correlations with rate of increase in the northwest region, where the correlation for western greys was more than doubled. Given these results, only rainfall was considered in subsequent regression models.



(*a*)



(*b*)

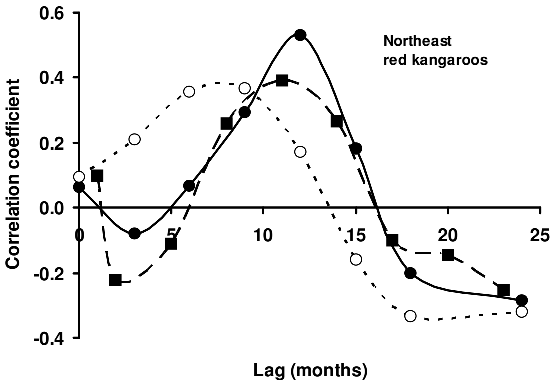
Fig. 9.7. Average (± s.e.) ranks for photosites (solid circles and line) over 1992-2002 on (a) Bulgunnia and (b) Mulyungarie in Kingoonya and Northeast SCBs, respectively. Also shown is the monthly NDVI (dotted line) over the same period averaged across each property.

Table 9.1. Correlations between red and western grey kangaroo rate of increase, adjusted for harvest rate (see text), and candidate periods of standardised rainfall in three regions in the South Australian pastoral zone. Data cover the period 1978-2003. Rainfall is coded as *x,y* where *x* is the interval of rainfall in months and *y* is the lag in months from the second of two consecutive aerial surveys (Fig. 9.3). The strongest positive correlation for each set of region and species is shown in bold. Significant positive correlations (*P* < 0.05) are italicised.

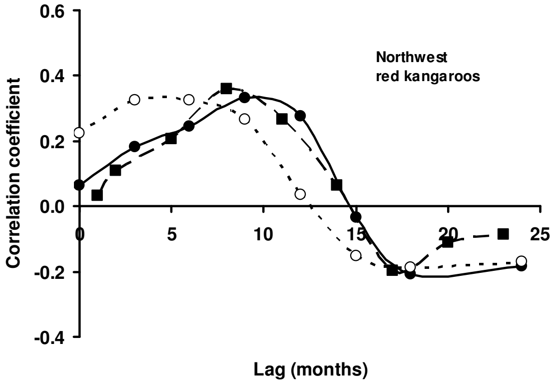
Rainfall	Northeast	Northwest	South
Red kangaroos			
6,0	0.16	0.07	-0.09
12,0	-0.03	0.03	0.02
12,6	0.17	0.13	**0.08**
12,12	***0.57***	***0.29***	0.00
24,0	*0.40*	0.22	-0.04
Western grey kangaroos			
6,0	0.04	-0.08	-0.06
12,0	0.01	-0.37	0.07
12,6	0.08	-0.26	0.11
12,12	**0.17**	**0.17**	***0.46***
24,0	0.13	-0.21	*0.32*

Table 9.2. Regressions models used to assess the influence of two rainfall periods and past density on kangaroo rate of increase in South Australia and New South Wales. Models 1-9 assume harvest mortality is additional to natural mortality, whereas model 10 assumes it is compensatory to an extent dependent on the past rainfall (see text). Rainfall is coded as *x,y*[<*b*] where *x* is the interval of rainfall in months and *y* is the lag in months from the second of two consecutive aerial surveys (Fig. 9.3) and *b* is the threshold below which to include the rainfall term in a piecewise regression. The time lag for density was 12 months.

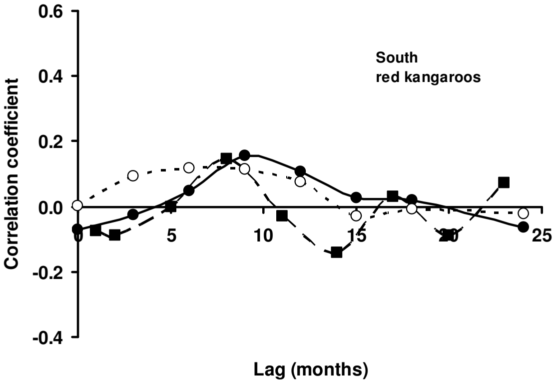
Model	Model
1	12,0
2	12,12
3	12,12 + 12,12^2
4	12,0 + 12,12
5	12,0 + 12,12 + 12,0 × 12,12
6	12,0[<*b*] + 12,12
7	12,0[<*b*] + 12,12 + 12,12^2
8	12,0[<*b*] + 12,12 + 12,0[<*b*] × 12,12
9	12,0[<*b*] + 12,12 + 12,0[<*b*] × 12,12 + 12,12^2
10	Best model(1-9) with compensatory mortality
11	Best model(1-10) - lagged density



(*a*)



(*b*)



(*c*)

Fig. 9.8. Correlations between exponential rate of increase of red kangaroos, adjusted for harvest rate (see text), and NDVI flush averaged over 6 months (solid line and circles) and NDVI averaged over 6 (dotted line and open circles) and 12 (dashed line and solid squares) months with increasing lags from the second of two consecutive aerial surveys (Fig. 9.3) in the (a) northeast, (b) northwest and (c) south pairs of SCBs in the South Australian pastoral zone.

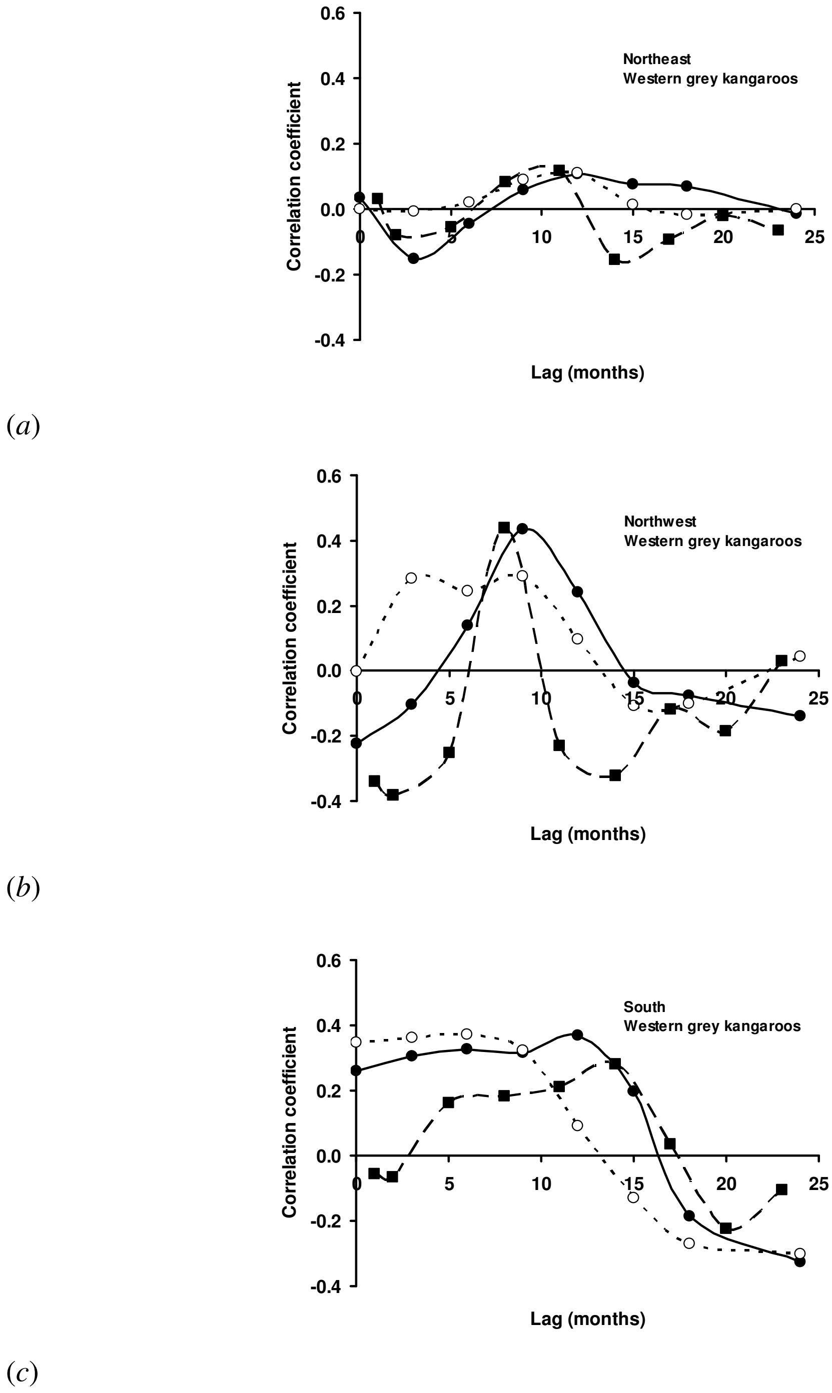


Fig. 9.9. Correlations between exponential rate of increase of western grey kangaroos, adjusted for harvest rate (see text), and NDVI flush averaged over 6 months (solid line and circles) and NDVI averaged over 6 (dotted line and open circles) and 12 (dashed line and solid squares) months with increasing lags from the second of two consecutive aerial surveys (Fig. 9.2) in the (a) northeast, (b) northwest and (c) south pairs of SCBs in the South Australian pastoral zone.

Analysis of covariance did not identify any differences in the response to rainfall (i.e. coefficient for the rainfall term) between SCBs within regions according to AIC. Nine candidate models (Table 9.2) were fitted to the data for each species in each region, initially assuming harvest mortality was additive. In the regions where each species are relatively abundant, the piecewise regression model using both recent and lagged rainfall had most support according to Akaike weights (Table 9.3). The threshold rainfall for including recent rainfall was always well below average. There was some support for a curvilinear term and an interaction between the two rainfall terms. In the lower density regions for both species, simpler models with a single rainfall term were preferred. Including harvest mortality as partially compensatory was only supported in the northwest for the low density population of western grey kangaroos. The explanatory power of the best models (i.e. R^2) was always greatest in the regions where species were at higher densities. Including lagged density in the models invariably improved the fit and support.

For each region, time traces of rates of increase against the rainfall term with the strongest correlation gave no evidence of different responses to rainfall depending on the time period (e.g. pre-drought *vs* post-drought).

9.3.3 New South Wales

Across the three species, the majority of the eight management zones also recorded strongest correlations between kangaroo rate of increase with 12 months rainfall with a 12 months lag (Table 9.4). There were species' differences, with weaker, non-significant correlations for western grey kangaroos. For red and eastern grey kangaroos, significant correlations tended to be in the higher density zones.

The same nine regression models used for South Australia (Table 9.2) were fitted to the management zone data. A piecewise regression model had the most support in over half the cases (Table 9.5) with recent rainfall only included during particularly dry periods (i.e. b generally << 0). Lagged density improved models in all cases. There was a poor fit according to R^2 for reds in the low density KMZs 10 and 11. For eastern greys the fit was poor in KMZs 4 and 6, where density is relatively moderate. The fit was poor for western greys in KMZs 4 and 6, where density is relatively high, and KMZ 10, where density is low.

Time traces again provided little support to differing responses to rainfall among time periods.

Table 9.3. Akaike weights for models 1-10 in Table 9.2 predicting rate of increase (adjusted for harvest rate) in red and western grey kangaroos in three regions in the South Australian pastoral zone. Parameter *b* for models 6-9, estimated by minimising deviance, and adjusted R^2 for the best of models 1-9 and model 11, are also shown. The model with greatest weight is shown in bold.

Model	Northeast	Northwest	South
Red kangaroos			
1	0.00	0.00	**0.22**
2	0.02	0.00	0.21
3	0.01	0.00	0.08
4	0.01	0.00	0.08
5	0.01	0.00	0.03
6	**0.32**	**0.42**	0.15
7	0.23	0.24	0.06
8	0.16	0.16	0.08
9	0.17	0.09	0.03
10	0.07	0.07	0.06
b	-0.50	-0.85	-0.60
Adj. R^2 (1-10)	0.44	0.28	0.01
Adj. R^2 (11)	0.65	0.54	0.24
Western grey kangaroos			
1	0.11		0.00
2	**0.22**	0.41	0.01
3	0.14	0.15	0.00
4	0.08		0.00
5	0.10		0.01
6	0.08		**0.42**
7	0.05		0.17
8	0.05		0.17
9	0.03		0.07
10	0.14	**0.44**	0.14
b	-0.45	-0.40	-0.90
Adj. R^2 (1-9)	0.11	0.00	0.32
Adj. R^2 (11)	0.17	0.15	0.32

Table 9.4. Correlations between red, eastern grey and western grey kangaroo rate of increase, adjusted for harvest rate (see text), and candidate periods of standardised rainfall in eight kangaroo management zones in New South Wales. Rainfall is coded as *x,y* where *x* is the interval of rainfall in months and *y* is the lag in months from the second of two consecutive aerial surveys (Fig. 9.3). KMZs 1, 4, 7 and 11 were surveyed annually over 1984-2003, whereas KMZs 2, 6, 8 and 10 were surveyed annually over the longer period of 1976-2003. The strongest positive correlation for each set of zone and species is shown in bold. Significant correlations ($P < 0.05$) are italicised.

Rainfall	KMZ 1	KMZ 2	KMZ 4	KMZ 6	KMZ 7	KMZ 8	KMZ 10	KMZ 11
Red kangaroos								
12,0	0.16	-0.02	-0.12	-0.25	0.38	0.02	-0.08	0.10
12,6	0.43	*0.41*	0.22	-0.11	**0.44**	0.14	0.00	0.09
12,12	***0.49***	***0.54***	***0.49***	**0.31**	0.33	***0.48***	**0.07**	0.18
24,0	0.45	*0.41*	0.25	0.03	0.42	0.33	0.00	**0.18**
Eastern grey kangaroos								
12,0	0.18	-0.09	-0.13	-0.04	0.16	-0.12	0.11	0.05
12,6	0.43	0.21	0.20	**0.31**	***0.54***	0.15	0.26	**0.26**
12,12	**0.44**	***0.38***	**0.30**	0.25	0.43	***0.59***	**0.32**	0.21
24,0	0.43	0.22	0.11	0.14	0.34	0.31	0.28	0.15
Western grey kangaroos								
12,0	0.23	-0.01	-0.19	0.18	0.37		**0.20**	-0.14
12,6	0.29	0.24	0.10	**0.36**	**0.45**		0.11	-0.13
12,12	0.30	**0.37**	**0.15**	0.12	0.32		0.04	-0.08
24,0	**0.36**	0.28	-0.03	0.20	0.40		0.15	-0.17

Table 9.5. Akaike weights for models (Table 9.2) predicting rate of increase (adjusted for harvest rate) in red and eastern and western grey kangaroos in eight kangaroo management zones in New South Wales. Parameter *b* for models 6-9, estimated by minimising deviance, and adjusted R^2 for the best of models 1-9 and model 11, are also shown. The model with greatest weight is shown in bold.

Rainfall	KMZ 1	KMZ 2	KMZ 4	KMZ 6	KMZ 7	KMZ 8	KMZ 10	KMZ 11
Red kangaroos								
1	0.02	0.00	0.02	0.05	0.00	0.00		0.16
2	**0.17**	0.01	0.20	0.08	0.00	0.15	**0.40**	0.20
3	0.09	0.00	0.07	0.06	0.00	0.07	0.22	0.10
4	0.09	0.00	0.11	0.10	0.00	0.07		0.08
5	0.08	0.00	0.07	0.08	0.00	0.05		0.03
6	0.12	**0.30**	**0.21**	0.20	**0.26**	**0.21**		0.09
7	0.05	0.19	0.08	0.11	0.13	0.08		0.05
8	0.12	0.14	0.08	0.08	0.26	0.11		0.03
9	0.15	0.12	0.03	0.04	0.13	0.04		0.02
10	0.11	0.23	0.15	**0.21**	0.20	0.20	0.38	**0.24**
b	-0.25	-0.65	-0.30	-0.70	-0.85	-0.90	-0.45	0.00
Ad.j R^2 (1-9)	0.22	0.48	0.26	0.18	0.48	0.26	-0.03	-0.04
Adj. R^2 (11)	0.30	0.50	0.48	0.29	0.53	0.48	0.39	0.56
Eastern grey kangaroos								
1	0.00	0.00	0.09	0.10	0.00		0.03	0.04
2	0.01	0.00	**0.19**	**0.22**	0.02	**0.34**	0.11	0.06
3	0.01	0.00	0.07	0.13	0.01	0.13	0.04	0.03
4	0.01	0.00	0.09	0.09	0.01		0.04	0.02
5	0.00	0.00	0.04	0.05	0.01		0.06	0.02
6	**0.31**	**0.31**	0.18	0.10	**0.25**	0.20	0.23	0.21
7	0.23	0.18	0.07	0.06	0.11	0.07	0.09	0.08
8	0.12	0.12	0.07	0.07	0.25	0.09	0.09	0.21
9	0.11	0.07	0.02	0.06	0.11	0.03	0.03	0.08
10	0.20	0.32	0.18	0.13	0.22	0.14	**0.26**	**0.23**
b	-0.35	-0.70	-0.55	-0.20	-0.85	-0.90	-0.70	-0.85
Adj. R^2 (1-9)	0.43	0.40	0.04	0.05	0.38	0.34	0.16	0.20
Adj. R^2 (11)	0.57	0.44	0.33	0.10	0.56	0.40	0.37	0.63

Table 9.5 cont.

Rainfall	KMZ 1	KMZ 2	KMZ 4	KMZ 6	KMZ 7	KMZ 8	KMZ 10	KMZ 11
1	0.02	0.00		0.18	0.00		0.25	
2	0.03	0.00	**0.35**	0.14	0.00		0.15	
3	0.01	0.00	0.14	0.05	0.00		0.06	
4	0.02	0.00		0.08	0.00		0.09	
5	0.02	0.00		0.04	0.00		0.04	
6	**0.29**	0.32	0.16	**0.20**	**0.28**		0.07	
7	0.21	0.13	0.06	0.08	0.10		0.03	
8	0.18	0.12	0.06	0.08	0.28		0.05	
9	0.08	0.05	0.02	0.03	0.10		0.02	
10	0.13	**0.38**	0.21	0.13	0.23		**0.26**	
b	-0.20	-0.70	-0.30	-0.20	-0.85		-0.70	
Adj. R^2 (1-9)	0.32	0.40	-0.02	0.05	0.70		-0.02	
Adj. R^2 (11)	0.40	0.48	0.03	0.07	0.73		0.07	0.11

9.3.4 Queensland

The three regions within the core area yielded a significant correlation between rate of increase and rainfall only for eastern grey kangaroos in the brigalow belt (Table 9.6). Calendar year rainfall and summer rainfall had the best associations with rates of increase and, notably, 12 months rainfall with a 12 months lag had a weak association in all cases. These weak associations were also a feature in the shorter time series for the helicopter survey blocks (Table 9.7), with only three of 28 time series having significant correlations between rate of increase and rainfall. Associations were particularly weak or negative for the northern blocks in the Mitchell grass downs. Furthermore, there were no intervals of rainfall that consistently gave the strongest correlations. In the Blackall and Charleville survey blocks, harvest rates were particularly high (> 50%) in some years during the study period (see Section 13) and may have been responsible for producing numerous negative correlations between rate of increase adjusted for harvest rate (*nra*) and rainfall. Correlations with simply the unadjusted rate of increase *r* are shown in Table 9.8 and identify a more plausible pattern.

Given the weak and varied relationship with rainfall, a new set of nine candidate models was proposed, covering a broader range of rainfall intervals but involving only simpler linear relationships without interactions (Table 9.9). The two species had poor relationships in the Mitchell grass downs, moderate R^2 in the mulga lands and a reasonable relationship for greys but not reds in the brigalow belt (Table 9.10). The piecewise regression model was not supported in any case and partially compensatory harvest mortality generally had slightly higher support than additive harvest mortality. Lagged density again improved the fit of all models. Models for the survey blocks generally reflected the result at the broader, regional level (Table 9.11). At Blackall and Charleville, only models with compensatory mortality were considered. Models for red kangaroos had a reasonable fit only for Hungerford and Bollon using recent rainfall. Reasonable fits were obtained for eastern grey kangaroos in all blocks south of Longreach and east of Windorah (Fig. 9.2), using a range of rainfall intervals. Reasonable fitting models were fitted for wallaroos at Blackall and Roma. Compensatory harvest mortality was supported over additive mortality in 13 out of 24 cases. Lagged density improved fit in almost all cases.

Time traces again provided little support to differing responses to rainfall among time periods, although the time series is shorter for Queensland than other states.

Table 9.6. Correlations between red and eastern grey kangaroo rate of increase, adjusted for harvest rate (see text), and candidate periods of standardised rainfall in three regions in the Queensland survey area. Data cover the period 1984-2003. Rainfall is coded as *x,y* where *x* is the interval of rainfall in months and *y* is the lag in months from the second of two consecutive aerial surveys (Fig. 9.3). The strongest positive correlation for each set of region and species is shown in bold. Significant correlations ($P < 0.05$) are italicised.

Rainfall	Brigalow belt	Mulga lands	Mitchell grass downs
Red kangaroos			
12,0	0.12	0.25	-0.21
12,5	-0.08	0.23	**0.15**
12,12	-0.33	0.02	0.13
6,2	**0.18**	**0.29**	-0.29
6,8	-0.20	-0.07	0.00
6,14	-0.23	0.28	0.09
Eastern grey kangaroos			
12,0	0.11	0.01	-0.34
12,5	***0.57***	**0.38**	0.10
12,12	0.40	0.24	0.12
6,2	0.13	0.34	-0.21
6,8	0.10	0.10	-0.09
6,14	*0.51*	0.33	**0.26**

Table 9.7. Correlations between red and eastern grey kangaroo and wallaroo rate of increase, adjusted for harvest rate (see text), and candidate periods of standardised rainfall in ten survey blocks in the Queensland survey area. Data cover the period 1991-2003. Rainfall is coded as *x,y* where *x* is the interval of rainfall in months and *y* is the lag in months from the second of two consecutive aerial surveys (Fig. 9.3). The strongest positive correlation for each set of block and species is shown in bold. Significant correlations ($P < 0.05$) are italicised. J, Julia Creek; Wt, Winton; L, Longreach; Wd, Windorah; Bk, Blackall; Cv, Charleville; H, Hungerford; Bo, Bollon; R, Roma; Wm, Westmar.

Rainfall	J	Wt	L	Wd	Bk	Cv	H	Bo	R	Wm
Red kangaroos										
12,0	-0.37	-0.38	0.03	-0.18	-0.07	0.00	***0.63***	0.23	-0.19	0.14
12,5	0.07	-0.24	**0.24**	0.01	-0.10	-0.01	0.29	**0.39**	-0.06	-0.06
12,12	0.08	-0.18	0.01	0.00	-0.14	-0.48	0.27	-0.11	-0.17	-0.28
6,2	-0.50	-0.40	-0.09	-0.15	-0.11	-0.03	*0.59*	0.38	-0.23	**0.21**
6,8	0.08	-0.09	0.22	**0.12**	-0.24	**0.14**	0.11	0.01	-0.04	-0.13
6,14	**0.09**	-0.21	-0.18	-0.04	-0.26	-0.39	0.05	-0.13	-0.14	-0.02
Eastern grey kangaroos										
12,0	-0.29	0.07	-0.07	-0.15	0.11	0.50	**0.54**	0.51	0.38	-0.11
12,5	-0.01	-0.09	**0.15**	**0.15**	-0.19	0.10	0.50	*0.70*	**0.53**	-0.11
12,12	0.25	**0.13**	-0.04	0.06	-0.39	-0.42	0.43	0.48	0.29	0.16
6,2	-0.40	0.05	-0.05	-0.12	**0.16**	0.39	0.46	***0.74***	0.45	-0.06
6,8	-0.27	-0.31	-0.04	0.02	-0.06	***0.59***	0.28	0.00	-0.04	-0.21
6,14	**0.32**	0.07	-0.04	0.07	-0.45	-0.36	0.32	*0.58*	0.43	**0.27**
Wallaroos										
12,0		-0.27	-0.36	-0.12	**0.52**	-0.21	0.06	-0.14	0.19	
12,5		0.11	-0.19	-0.65	0.06	-0.09	-0.37	0.17	0.44	
12,12		0.24	-0.35	-0.88	-0.32	-0.36	-0.21	**0.51**	0.46	
6,2		-0.33	-0.51	-0.28	0.49	-0.28	0.01	-0.21	-0.22	
6,8		**0.32**	-0.09	-0.04	0.39	-0.07	**0.13**	0.03	***0.62***	
6,14		0.26	-0.29	-0.72	-0.55	-0.25	-0.16	0.44	0.42	

Table 9.8. Correlations between red and eastern grey kangaroo and wallaroo rate of increase, unadjusted for harvest rate (see text), and candidate periods of standardised rainfall in two survey blocks in the Queensland survey area where harvest rates had been relatively high (>50%). Rainfall is coded as *x*,*y* where *x* is the interval of rainfall in months and *y* is the lag in months from the second of two consecutive aerial surveys (Fig. 9.3). The strongest positive correlation for each set of block and species is shown in bold. Significant correlations ($P < 0.05$) are italicised.

Rainfall	Blackall	Charleville
Red kangaroos		
12,0	0.31	0.37
12,5	**0.38**	0.34
12,12	0.07	-0.22
6,2	0.20	0.30
6,8	0.18	**0.51**
6,14	-0.02	-0.09
Eastern grey kangaroos		
12,0	0.53	*0.74*
12,5	0.53	0.45
12,12	0.13	0.04
6,2	0.45	*0.59*
6,8	***0.66***	***0.83***
6,14	-0.06	0.11
Wallaroos		
12,0	***0.68***	-0.01
12,5	0.43	0.05
12,12	0.06	-0.23
6,2	*0.63*	-0.11
6,8	*0.61*	**0.10**
6,14	-0.22	-0.11

Table 9.9. Regressions models used to assess the influence of two rainfall periods and past density on kangaroo rate of increase in Queensland. Models 1-9 assume harvest mortality is additional to natural mortality, whereas model 10 assumes it is compensatory to an extent dependent on the past rainfall (see text). Rainfall is coded as *x,y*[<*b*] where *x* is the interval of rainfall in months and *y* is the lag in months from the second of two consecutive aerial surveys (Fig. 9.3) and *b* is the threshold below which to include the rainfall term in a piecewise regression. The time lag for density was 12 months.

Model	Model
1	12,0
2	12,5
3	12,12
4	6,2
5	6,8
6	12,0 + 12,12
7	6,2 + 6,8
8	12,0 + 6,14
9	12,0[<*b*] + 12,12
10	Best model(1-9) with compensatory mortality
11	Best model(1-10) - lagged density

Table 9.10. Akaike weights for models 1-10 in Table 9.9 predicting rate of increase (adjusted for harvest rate) in red and eastern grey kangaroos in three regions in the Queensland survey area. Parameter *b* for model 9, estimated by minimising deviance, and adjusted R^2 for the best of models 1-9 and model 11, are also shown. The model with greatest weight is shown in bold.

Model	Brigalow belt	Mulga lands	Mitchell grass downs
Red kangaroos			
1	0.26	0.08	
2		0.07	**0.36**
3		0.04	0.35
4	0.30	0.10	
5		0.05	
6			
7			
8		0.09	
9			
10	**0.44**	**0.56**	0.29
b	-0.20	-0.40	0.00
Adj. R^2 (1-9)	0.02	0.20	0.01
Adj. R^2 (11)	0.46	0.38	0.31
Eastern grey kangaroos			
1	0.01	0.05	
2	0.41	**0.24**	0.30
3	0.05	0.09	0.32
4	0.01	0.17	
5	0.01	0.06	
6	0.02		
7	0.00	0.07	
8	0.06	0.06	
9		0.04	
10	**0.42**	0.22	**0.38**
b	-0.90	-0.80	-1.00
Adj. R^2 (1-9)	0.37	0.19	0.06
Adj. R^2 (11)	0.37	0.22	0.11

Table 9.11. Akaike weights for models 1-10 in Table 9.9 predicting rate of increase (adjusted for harvest rate) in red and eastern grey kangaroos and wallaroos in ten survey blocks in the Queensland survey area. Parameter *b* for model 9, estimated by minimising deviance, and adjusted R^2 for the best of models 1-9 and models 11, are also shown. The model with greatest weight is shown in bold. For Blackall and Charleville, harvest mortality was always assumed to be compensatory (i.e. model 10 in Table 9.9). J, Julia Creek; Wt, Winton; L, Longreach; Wd, Windorah; Bk, Blackall; Cv, Charleville; H, Hungerford; Bo, Bollon; R, Roma; Wm, Westmar.

Model	J	Wt	L	Wd	Bk	Cv	H	Bo	R	Wm
Red kangaroos										
1			0.15		0.35	**1.00**	**0.26**	0.12		0.00
2	0.24		0.21	0.37	**0.61**		0.02	0.22		
3	0.24		0.15				0.02			
4					0.04	0.00	0.17	0.21		0.00
5	0.24		0.20	**0.41**		0.00	0.01	0.09		
6			0.06				0.10			
7							0.08			
8							0.13			
9										
10	**0.28**		**0.22**	0.22			0.20	**0.37**		**1.00**
b	-0.85		-0.60	-0.25	-0.10	-1.00	-0.35	0.00		-0.35
Adj. R^2 (1-9)	-0.08		-0.03	-0.08	0.07	0.08	0.40	0.47		0.09
Adj. R^2 (11)	0.63	0.24	0.49	0.37	0.31	0.20	0.53	0.46	0.61	0.53
Eastern grey kangaroos										
1		0.20			**1.00**	0.35	0.03	0.02	0.09	
2			0.40	**0.28**		0.00	0.02	0.14	**0.26**	
3	0.49	**0.21**		0.25			0.01	0.02	0.06	0.44
4		0.20			0.00	0.04	0.02	**0.32**	0.14	
5				0.25		**0.36**	0.01	0.00		
6		0.08					0.02	0.02	0.05	
7						0.24	0.01			
8		0.07					0.08	0.05	0.09	
9		0.09					**0.41**	0.26	0.07	**0.45**
10	**0.51**	0.14	**0.60**	0.23			0.39	0.17	0.24	0.11
b	-0.85	-0.50	-0.60	-0.45	-0.20	-1.00	-0.95	0.00	-0.65	-0.85
Adj. R^2 (1-9)	-0.03	-0.15	-0.06	-0.07	0.51	0.62	0.52	0.57	0.33	0.52
Adj. R^2 (11)	0.51	0.55	0.26	0.12	0.55	0.64	0.77	0.53	0.33	0.12

Table 9.11 cont.

Model	J	Wt	L	Wd	Bk	Cv	H	Bo	R	Wm
Wallaroos										
1					**0.70**	0.20	0.22		0.06	
2		0.20				0.27		0.17	0.11	
3		0.24						0.39	0.12	
4					0.04	0.11	0.21			
5		0.27			0.26	**0.37**	0.23		**0.29**	
6									0.06	
7						0.05	0.09			
8									0.07	
9									0.06	
10		**0.29**					**0.25**	**0.44**	0.22	
b		-1.00			-0.20	-1.00	0.00	-0.55	-0.25	
Adj. R^2 (1-9)		-0.12			0.54	-0.09	-0.11	0.10	0.31	
Adj. R^2 (11)		0.70	0.36	0.60	0.58	-0.07	0.14	-0.17		

9.3.5 Geographic patterns in population dynamics

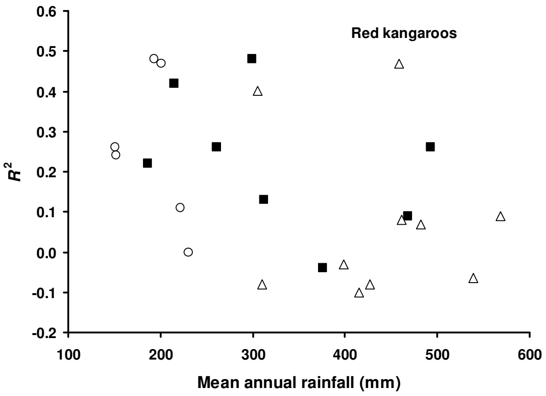
Simulations described in Section 9.3.1 suggested model fit (i.e. R^2) should decline with increasing average annual rainfall; essentially moving away from central Australia towards the coast. There is a suggestion of this for red and western grey kangaroos, despite a considerable scatter of points, but not for eastern grey kangaroos or wallaroos (Fig. 9.10). Bollon and KMZ 8 are the most obvious outliers in the plot for red kangaroos. The poor fit of models for the northern Queensland sites, relative to elsewhere, is also evident from these plots.

The strength of density dependence was expected to increase with average annual rainfall and again such a relationship is suggested for red kangaroos (Fig. 9.12*a*). Marree is an outlier in this case. For western grey kangaroos there is no hint of a pattern (Fig. 9.12*b*). For eastern greys, strong density dependence was only recorded at higher rainfall areas (Fig. 9.12*c*), but this pattern was not evident within states; reflecting a contrast between New South Wales and Queensland. For wallaroos, the pattern is not clear, but tends to be opposite to what was expected (Fig. 9.11*d*).

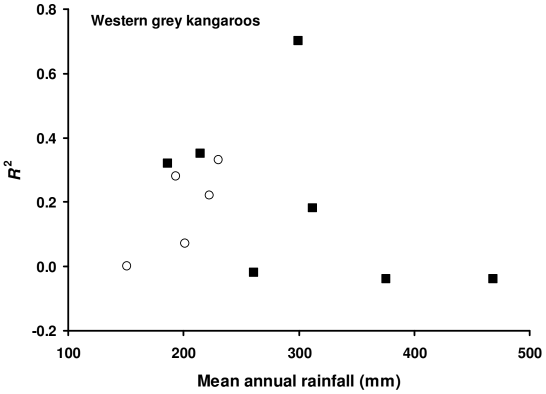
Variability in kangaroo density was expected to decline with increasing average annual rainfall. If anything, the opposite was the case for red kangaroos when states are considered separately (Fig. 9.12*a*). The data for western grey kangaroos (Fig. 9.12*b*) and eastern grey kangaroos (Fig. 9.12*c*) tend to support the hypothesis, whereas the wallaroo data (Fig. 9.12*d*) are counter to what was expected.

9.4 Discussion

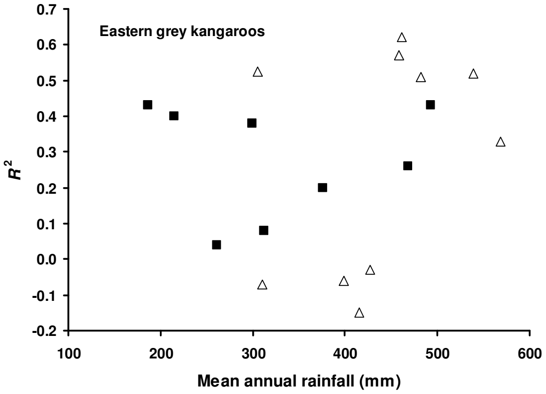
A number of aspects of kangaroo population dynamics have been clarified in this study. Firstly, the appropriate period of rainfall to predict rate of increase is best represented by two rainfall intervals, most likely reflecting mortality in all age classes during drought and variation in juvenile survival outside of drought. An age structured model should improve on this relationship. Secondly, the relationship between rainfall and rate of increase for eastern grey kangaroos and common wallaroos has been examined showing broadly similar patterns to the other two species. Thirdly, harvest rate has been incorporated into the relationships, which is clearly important for Queensland where harvest rates are higher than other states and for all states over the past 15 years as harvest rates have increased to meet quotas (see Section 13). Finally, variation in the numerical response has been documented across much of the latitudinal and longitudinal range of all four species, certainly for the areas where the harvest is concentrated.



(*a*)

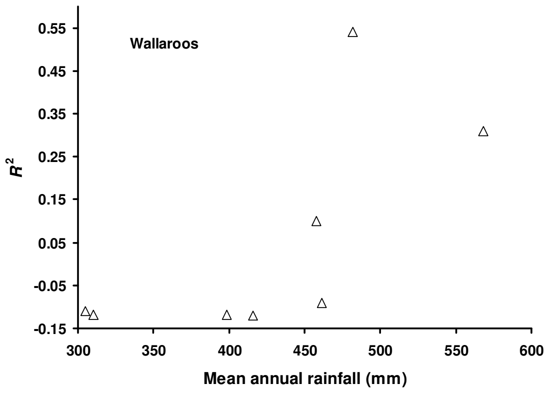


(*b*)



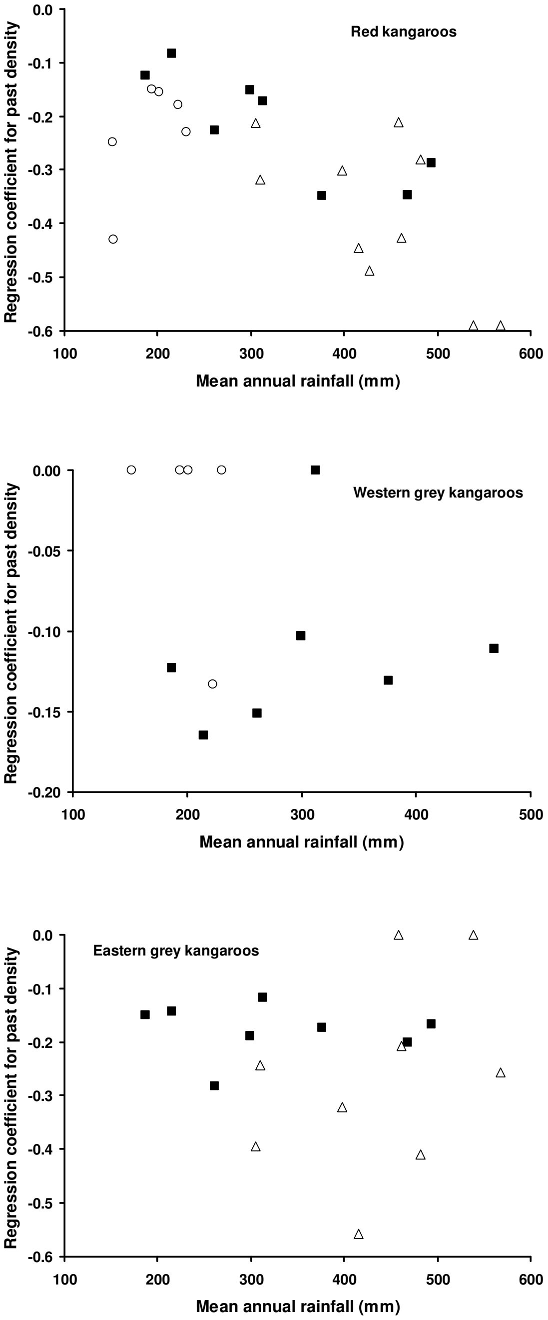
(*c*)

Fig. 9.10. Relationship between mean annual rainfall and the adjusted coefficient of determination (R^2) for the model, using only rainfall (i.e. models 1-9 in Tables 9.3, 9.5 and 9.10), that best predicts rate of increase of (a) red kangaroos, (b) western grey kangaroos, (c) eastern grey kangaroos and (d) common wallaroos. All models assume additive harvest mortality. Each point represents a region in South Australia (○), New South Wales (■) or Queensland (Δ) (see Figs 9.1 and 9.2).



(*d*)

Fig. 9.10 cont.

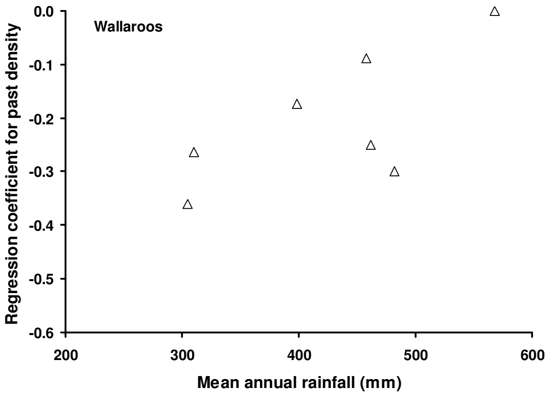


(*a*)

(*b*)

(*c*)

Fig. 9.11. Relationship between mean annual rainfall and the partial regression coefficient of the previous year's density for the model (i.e. model 11 or 12 in Tables 9.2 and 9.9) that best predicts rate of increase of (a) red kangaroos, (b) western grey kangaroos, (c) eastern grey kangaroos and (d) common wallaroos. Each point represents a region in South Australia (○), New South Wales (■) or Queensland (Δ) (see Figs 9.1 and 9.2). Points on the *x*-axis in (a) are actually -0.8 and -1.3. Coefficients of zero refer to best models excluding past density.



(*d*)

Fig. 9.11 cont.

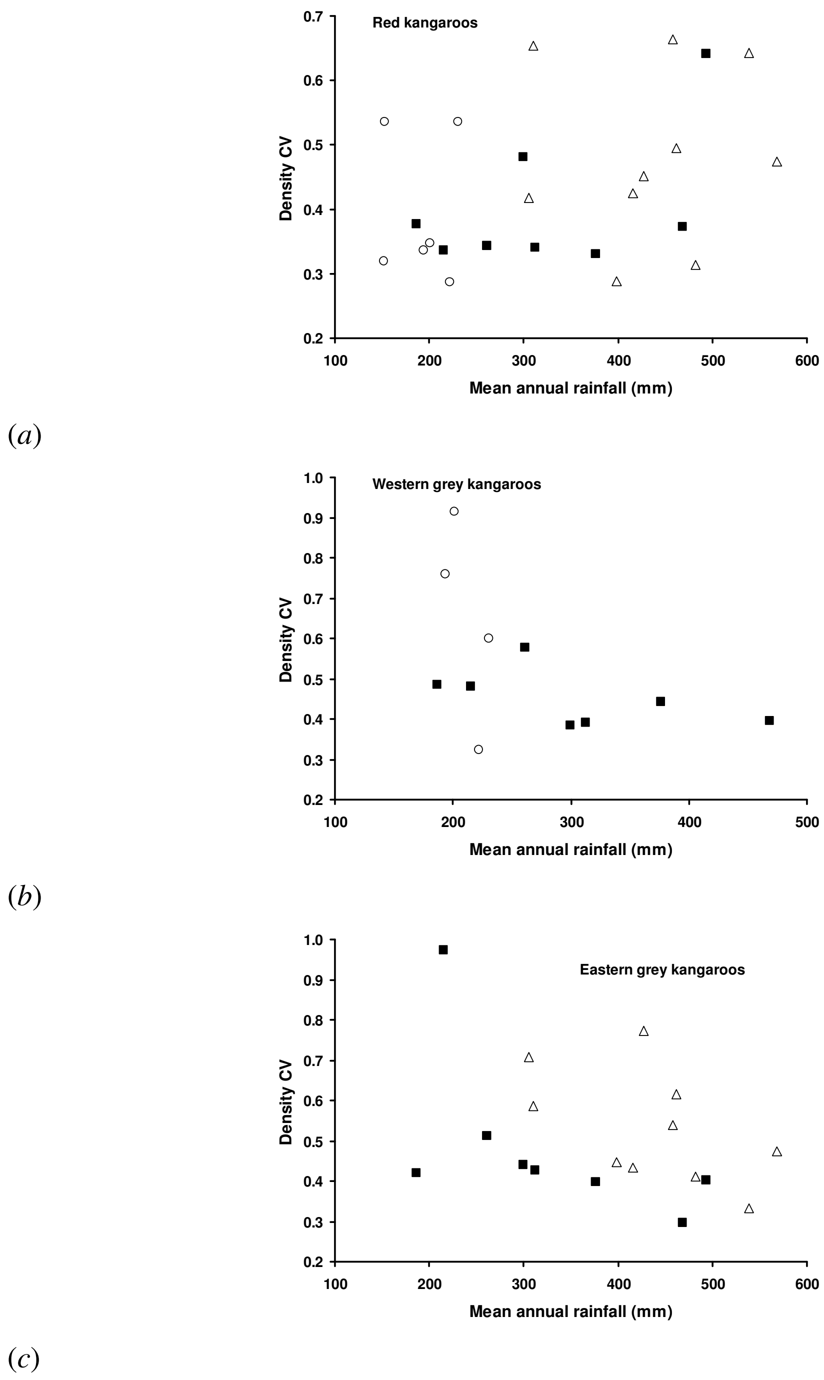
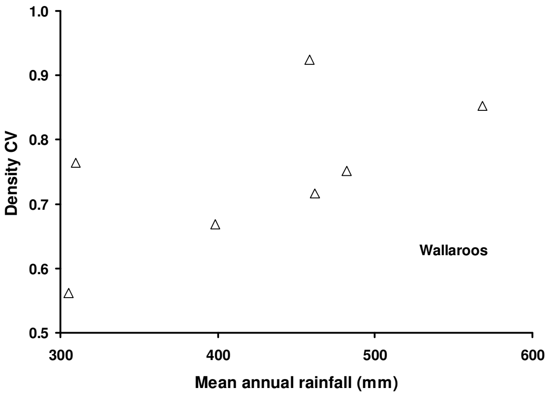


Fig. 9.12. Relationship between mean annual rainfall and variability (CV = SD/mean) in annual density of (a) red kangaroos, (b) western grey kangaroos, (c) eastern grey kangaroos and (d) common wallaroos. Each point represents a region in South Australia (○), New South Wales (■) or Queensland (Δ) (see Figs 9.1 and 9.2).



(*d*)

Fig. 9.12 cont.

The striking feature of these analyses is that the ability to predict kangaroo rate of increase using rainfall alone is poor in northern Queensland and for species in regions where they occur at low density. The latter may simply be a function of poorer precision at low density, as demonstrated with the simulation model. Precision is poor in the survey blocks in Queensland, but not generally worse in the northern blocks. The inclusion of lagged density greatly improves model fit as expected from Figure 9.5. However, this is unsatisfactory as density is only a surrogate for processes regulating the population (Krebs 2002). All the evidence points to kangaroo populations being extrinsically regulated by food supply (Caughley *et al.* 1987; Pople 1996) and so density in combination with rainfall can be considered a substitute for pasture biomass, as shown by simulation here. Unfortunately, NDVI proved no better than rainfall in predicting rate of increase, at least in South Australia. Nevertheless, NDVI may prove useful for predicting smaller-scale fluctuations in kangaroo numbers in response to patchy rainfall and resulting from movement as well as spatially-variable survival rates.

Interpretation of the geographic patterns in Figures 9.10-9.12 needs to consider the proximity of populations to the edge of each species' range, population density and the precision of density estimates. The simulation modelling demonstrated that imprecision in density estimation can, not surprisingly, mask underlying relationships and strengthen apparent density dependence. Precision (SE/mean) of density estimates of kangaroos are generally > 0.2 at a regional level (e.g. Caughley *et al.* 1977; Caughley and Grigg 1982; Cairns and Grigg 1993) and appear to be a major impediment to predicting density at this scale. It is not clear how populations are expected to behave dynamically at the edge of their range (Williams *et al.* 2003), but these species are candidates for assessment, particularly given their contrasting patterns of distributions (see Section 12). For eastern grey kangaroos, populations in the east and closer to the range core appear less variable, but are in more mesic environments. In contrast, red kangaroos in the east are on the periphery of their range and show comparable variation in density to populations at their arid core.

A good fit does not necessarily imply a model is correct. Cross-validation of these population models should be attempted, although there are some important caveats. Splitting the red kangaroo time series for Northeast Pastoral SCB into two equal time series showed Ricker (i.e. essentially the rainfall and density model fitted here) and ratio-dependent models (McCarthy 1996; see Section 10) to both predict one half of the time series well when parameterised on the other half (A. R. Pople unpublished data). The fit of Caughley's (1987) interactive model was also reasonable (Fig. 9.6). However, each model yields quite different predictions (see Section 5), again highlighting the problems of using density as a predictor of rate of increase rather than the regulating processes themselves (Krebs 2002). The partial regression coefficient for lagged density varied substantially among regions and species, but there were no clear patterns to draw generalisations. Some of this is due to variation in the strength of the relationship with rainfall. Such models are nevertheless region-specific, contrasting with the findings of Jonzen *et al.* (2005) for red kangaroos in the SAPZ (see Section 10). A more formal analysis is needed for all four species across all states.

Whether harvest mortality should be treated as additive or partially compensatory is not clear from these data, as there was empirical support for both. Simulation modelling suggested the method of analysis may not distinguish between them. The problem could be avoided if pasture biomass (i.e. kangaroo food supply) and the negative feedback with kangaroo density could be modelled directly as in Caughley's (1987) interactive model.

From a management perspective, the ability to predict kangaroo density may allow survey frequency to be altered, as outlined in Section 6. Useful predictions using rainfall are clearly possible in some regions for some species.

9.5 Acknowledgements

Wayne Rochester provided the interpolated rainfall surfaces for Queensland and South Australia and Marc Irvin collated much of the New South Wales survey data. Norbert Menke provided the maps in this section, collated the NDVI data, provided rainfall surfaces for New South Wales and updated surfaces for Queensland and South Australia and assisted with ranking photosites. Renee Sternberg digitised and ranked Stuart Cairns' time series of photographs of the South Australian photosites. We extend our gratitude to all these people.

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Section 10

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Of sheep and rain: large-scale population dynamics of the red kangaroo

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Summary

1. We analysed time-series data from populations of red kangaroos (*Macropus rufus*, Desmarest) inhabiting four areas in the pastoral zone of South Australia. We formulated a set of *a priori* models to disentangle the relative effects of the covariates: rainfall, harvesting, intraspecific competition, and domestic herbivores, on kangaroo population-growth rate.
2. The statistical framework allowed for spatial variation in the growth-rate parameters, response to covariates, and environmental variability, as well as spatially correlated error terms due to shared environment.
3. The most parsimonious model included all covariates but no area-specific parameter values, suggesting that kangaroo densities respond in the same way to the covariates across the areas.
4. The temporal dynamics were spatially correlated, even after taking into account the potentially synchronizing effect of rainfall, harvesting and domestic herbivores.
5. Counter-intuitively, we found a positive rather than negative effect of domestic herbivore density on the population-growth rate of kangaroos. We hypothesize that this effect is caused by sheep and cattle acting as a surrogate for resource availability beyond rainfall.
6. Even though our system is well studied, we must conclude that approximating resources by surrogates such as rainfall is more difficult than previously thought. This is an important message for studies of consumer-resource systems and highlights the need to be explicit about population processes when analysing population patterns.

Key-words: consumer-resource dynamics, environmental stochasticity, herbivores, population dynamics spatial correlation, herbivores, time-series analyses, environmental stochasticity, spatial correlation

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Introduction

Since the pioneering work by the Australian statistician P.A.P. Moran in the early 1950s (e.g. Moran 1953), the spatial dimension of population dynamics and especially large-scale synchrony in population fluctuations has received a lot of attention from ecologists (Royama 1992; Ranta *et al*. 1995; Bjørnstad, Ims & Lambin 1999; Koenig 1999). There is a growing interest in extending the analysis of ecological dynamics to include the spatial dimension (e.g. Bascompte & Solé 1997; Tilman & Kareiva 1997; Dieckmann, Metz & Law 2000).

The spatial distribution of individuals can be important when the primary interest is to understand temporal dynamics. For instance, populations at different spatial locations may differ in terms of demography (LaMontagne, Irvine & Crone 2002) and how they respond to environmental fluctuations, i.e. averaging across space can be misleading. The driving environmental variables may also vary across space. Hence, to be able to analyse space–time series data in a rigorous way, population models should allow for spatial variation in growth-rate parameters and environmental

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variability, as well as spatially correlated error terms (Dennis, Kemp & Taper 1998). In some cases, the populations may also be connected by dispersal, which has turned out to be challenging to estimate, but possible, from space–time series data (Lele, Taper & Gage 1998). Failure to account for spatial patterns may sometimes lead to very different conclusions about an organism's ecology, such as when estimating environment–abundance relationships (Keitt *et al*. 2002).

In this paper, we use a multivariate maximum likelihood framework to study spatio-temporal population dynamics in the red kangaroo (*Macropus rufus*, Desmarest) inhabiting the pastoral zone of South Australia. We are primarily interested in finding out to what extent kangaroo dynamics are affected by rainfall, intraspecific competition, interspecific competition with sheep and cattle, and whether there are any spatial differences in these interactions between different management areas. Previous kangaroo studies have highlighted the importance of the interactions listed above, but no attempt has been made to put them all together in a unified statistical framework.

Because kangaroos interact with sheep via resource competition (Caughley 1987; Edwards 1989) and are harvested for meat and skins (Ramsay 1994; Pople & Grigg 1998; Grigg & Pople 2001), there is a clear need for population models that can be used to evaluate alternative decisions under uncertainty. There is also a need to sort out how the different processes identified above translate into observable kangaroo dynamics and that is our major goal here. Such knowledge is important to be able to make reasonable management decisions, such as optimal harvesting in response to predicted grazing pressure and rainfall. It is also valuable on a more general level because different population processes can give rise to the same patterns in time-series data (Jonzén *et al*. 2002a; Jonzén, Ripa & Lundberg 2002b). However, the system dealt with in this paper is relatively well studied, which minimizes the risk of ignoring key processes governing a population's dynamics (Jonzén *et al*. 2002a).

It has previously been assumed that the red kangaroos inhabiting the study area make up a single large and uniform population (McCarthy 1996), but there are other studies suggesting that there may be differences between at least the western and the central and eastern regions in terms of the numerical response to rainfall (Cairns & Grigg 1993). Furthermore, the study area has been divided by the government management agency into different management regions, each with its own annual harvest quota (SADEH 2002). Hence, there are ecological as well as management reasons to increase the spatial resolution of current understanding and to study the temporal dynamics of the red kangaroo in the different management areas rather than across South Australia as a whole.

STUDY AREA AND DATA

The pastoral zone of South Australia covers approximately 282 000 km^2 in area and comprises a range of different landforms and vegetation types (Laut *et al*. 1977). The aerial survey of kangaroos in the pastoral zone of South Australia was initiated in 1978 and has been conducted annually each winter. Survey methods are described elsewhere (Caughley & Grigg 1981; Cairns & Grigg 1993).

Data on red kangaroo densities (individuals km^{-2}) in six management regions of South Australia (Fig. 1) were collected by winter aerial survey (Caughley & Grigg 1981; Grigg *et al*. 1999) between 1978 and 2002. To reduce the number of parameters that we had to estimate, we amalgamated data from pairs of similar regions, resulting in the following four major areas:

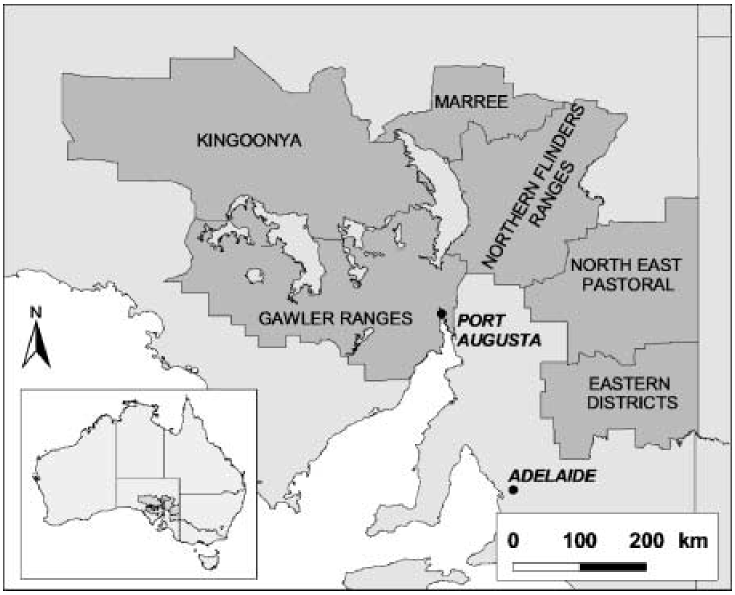

Fig. 1. Map showing the six management regions of South Australia where the analysed data were collected.

Eastern Districts, Gawler, Kingoonya / Maree, and North Flinders Ranges / North-east Pastoral, referred to as areas 1, 2, 3 and 4, respectively. The pooled regions border each other and have similar rainfall statistics.

Kangaroos are shot throughout the year and the carcasses are brought to nearby refrigeration units or dealer sites throughout the pastoral zone. The density (individuals km^{-2}) of kangaroos harvested on properties in South Australia each year were determined from shooter and dealer returns collated by the South Australian government conservation agency (currently the Department for Environment and Heritage). Records of harvested kangaroos were available only for the State as a whole in 1978 and 1979. Therefore, the proportion of the State total that was shot in each region in 1980 was used to apportion the State total in 1978 and 1979. The number of red kangaroos harvested in each region between consecutive aerial surveys was used in the analysis.

We used rainfall data from each of the management areas collected during the 12-month period prior to the start of the winter census. Rainfall during this period has been found to have the best positive correlation with the population rate of change of red kangaroos between two censuses following this 12-month period of rain, at least on the broad spatial scale of the whole pastoral zone in South Australia (McCarthy 1996).

Sheep are the predominant domestic stock in the South Australian pastoral zone, with cattle run mostly on properties in the north of the zone. Mean annual numbers of sheep and cattle on properties in the pastoral zone were determined from graziers' stock returns collated by the South Australian government department responsible for primary industries (currently Department of Water, Land and Biodiversity Conservation). Cattle numbers were converted to dry sheep equivalents by multiplying by eight, the conversion factor recommended by the Department of Water, Land and Biodiversity Conservation in South Australia (Reid 1990). Henceforth, we refer to the combined mean as Dry Sheep Equivalents (DSE), which will be expressed as a density (km^{-2}).

METHODS OF ANALYSIS

(a) Background to kangaroo modelling research

Several different models of macropod populations have been developed (reviewed by Cairns 1989) and the focus of most studies has been to document a general impact of (time-lagged) rainfall on population rate of change in the red kangaroo (e.g. Caughley, Bayliss & Giles 1984; Bayliss 1985a,b; Cairns & Grigg 1993; McCarthy 1996). Rainfall is a proxy for pasture growth and biomass and is important for predicting fluctuations in kangaroo populations. In the pastoral zone of South Australia, initial data analysis (Cairns & Grigg 1993) found that red kangaroo populations respond to rainfall at short time-lags on the scale of single management areas of 20 000–40 000 km^{-2}. However, a longer lagged effect of rainfall was found using a longer time series on a broad scale across the entire South Australian pastoral zone (McCarthy 1996).

Statistical density dependence (i.e. a relationship between population rate of change and density) was detected on a broad scale covering the entire pastoral zone of South Australia (McCarthy 1996), but the processes underlying that pattern are not fully understood. Whereas intraspecific competition for food may seem to be a logical explanation, one must also consider that kangaroos compete with sheep and cattle (Edwards 1989). The conventional wisdom is that domestic livestock density has a marked influence on the long-term density of kangaroos, but only a negligible effect on their short-term dynamics (Caughley 1987). In other words, domestic herbivore density should not affect the rate of change of kangaroos. However that has not been shown statistically. In this paper we explore different models for the impact of domestic herbivore density on kangaroo population dynamics at the regional scale.

(b) Models

Let $N_{i,(t)}$ be the kangaroo population density (individuals km^{-2}) in area i at time t for $i = \{1,2,3,4\}$ corresponding to Eastern Districts, Gawler, Kingoonya / Maree, and North Flinders Range / North-east Pastoral, respectively. We assume the mapping of density from one year to the next is described by a multivariate stochastic Ricker model (Dennis *et al.* 1998) including harvesting (H), rainfall (R) and the DSE density (S) as covariates. Hence, the full model can be written

$$N_{i,(t)} = N_{i,(t-1)} e^{(a_i + b_i N_{i,(t-1)} + c_i R_{i,(t-1)} + d_i S_{i,(t-1)} - H_{i,(t)} + E_{i,(t)})}, \qquad \text{eqn 1}$$

where a_i and b_i are constants for each area i, often referred to as a drift or location parameter and statistical density dependence, respectively. We assume the dynamics are influenced by a regionally and time-dependent environmental random variable $E_{i,(t)}$ that is drawn from a multivariate normal distribution with mean zero and variance-covariance matrix Σ. The parameters c_i and d_i capture the local response to rainfall and DSE in each area. To be able to compare the response to kangaroo density, rainfall and DSE across the areas, we standardized these time series to zero mean and unit variance.

$H_{i,(t)}$ is the instantaneous harvest mortality in area i between winter in year $t - 1$ and winter in year t calculated as

$$H_{i,(t)} \approx -\ln\left(1 - \frac{C_{i,(t)}}{\sqrt{N_{i,(t-1)} N_{i,(t)}}}\right), \qquad \text{eqn 2}$$

where $C_{i,(t)}$ is the total number of harvested animals per km^2 in each area i between consecutive aerial surveys. To approximate the annual harvest fraction, we have to divide $C_{i,(t)}$ by the geometric mean of population density in year $t - 1$ and t because harvesting is not a discrete event and population density is estimated only once every year (see Cairns & Grigg 1993). By not fitting a coefficient to the harvest term, we are assuming that the effect of harvesting is constant for a given population-growth rate, and the population-growth rate was simply adjusted for harvest rate (i.e. we assumed the coefficient was one). Estimating a coefficient (other than 1) would be seeking the level of compensation (< 1) or perhaps superadditivity (> 1) in harvesting in addition to the density dependence that was modelled, and the effect of harvesting is not the focus of this paper.

Finally, we also consider a different model structure motivated by the theory of ratio-dependent consumer–resource interactions (Arditi & Ginzburg 1989) and a previous study on red kangaroo dynamics in South Australia (McCarthy 1996). This second model is

$$N_{i,(t)} = N_{i,(t-1)} e^{\left(a_i + b_i \frac{N_{i,(t-1)}}{R_{i,(t-1)}} + d_i \frac{S_{i,(t-1)}}{R_{i,(t-1)}} - H_{i,(t)} + E_{i,(t)}\right)}, \qquad \text{eqn 3}$$

where b_i is now the regression coefficient with respect to the ratio of kangaroo density and rainfall (i.e. not standardized as above), d_i is the regression coefficient with respect to the ratio of DSE and rainfall. These ratios were standardized to mean zero and unit variance to facilitate the comparison across areas.

(c) Parameter estimation and model selection

The stochastic multivariate Ricker model with covariates (equation 1) can be considered a hybrid between an ecological and a statistical model in the sense that the parameters have an ecological interpretation, but the model can be expressed as a statistical time-series model on a logarithmic scale. If we define $\ln(N) \equiv X$, we can write equation 1 as a multivariate first-order nonlinear autoregression (NLAR) model (Tong 1990) with linear covariates on the log-scale:

$$\mathbf{X}_{(t)} = \mathbf{X}_{(t-1)} + \mathbf{a} + \mathbf{N}_{(t-1)}\mathbf{b} + \mathbf{R}_{(t-1)}\mathbf{c} + \mathbf{S}_{(t-1)}\mathbf{d} - \mathbf{H}_{(t)} + \mathbf{E}_{(t)}, \qquad \text{eqn 4}$$

where the boldface indicates that the parameters and data have vector ($\mathbf{a}$, $\mathbf{b}$, $\mathbf{c}$, $\mathbf{d}$, $\mathbf{H}_{(t)}$ and $\mathbf{E}_{(t)}$ are column vectors) or matrix ($\mathbf{N}_{(t-1)}$, $\mathbf{R}_{(t-1)}$ and $\mathbf{S}_{(t-1)}$ are diagonal matrices) structure. The likelihood function for a multivariate NLAR with Gaussian error structure is presented in Dennis *et al.* (1998) and the log-likelihood, which was used for estimating the unknown parameters, can be written as

$$\mathrm{In}\, L(\mathbf{a}, \mathbf{b}, \mathbf{c}, \mathbf{d}, \Sigma) = -0{\cdot}5mq \ln(2\pi) - 0{\cdot}5q \ln(|\Sigma|) - 0{\cdot}5 \sum_{t=1}^{q} \mathbf{Z}_\mathbf{t}' \Sigma^{-1} \mathbf{Z}_\mathbf{t}, \qquad \text{eqn 5}$$

where $\mathbf{Z}_t$ is a vector of residuals at time t, m is the number of areas ($m = 4$) and all sums are from time $t = 1$ to $t = q$ (= 25). We obtain maximum-likelihood estimates of the unknown parameters by minimizing the negative log-likelihood ($-\ln L(\mathbf{a}, \mathbf{b}, \mathbf{c}, \mathbf{d}, \Sigma)$) using the Nelder–Mead simplex algorithm (Press *et al.* 1994). For a more detailed explanation of the multivariate normal likelihood function, see Dennis *et al.* (1998).

We calculate the likelihood for each of a set of candidate models where equations 1 and 3 describe the full models assuming either additive (equation 1) or ratio-dependent (equation 3) effects of density and rainfall. We confront models with and without a term for density dependence and/or DSE, but harvesting, rainfall and a location parameter were included in all models. Each model could be further classified as having population-specific or global parameter values and the variance-covariance matrix had either zero or non-zero off-diagonal elements. Model selection was guided by the information-theoretic approach and we used the Akaike Information Criteria corrected for small sample size, AIC$_c$ (Burnham & Anderson 1998; p. 51) to rank the alternative models. We ignored observation error because we have no *a priori* reason to assume that the magnitude of the observation error should differ among the alternative models, and relative differences should therefore remain similar (LaMontagne *et al.* 2002).

Finally, we undertook a residual analysis of the best model as determined by the smallest AIC$_c$ value to make sure that the residuals were approximately normally distributed and not strongly serially correlated. For this purpose, one can treat the residuals from the four areas as approximately independent (Tong 1990). We performed Lilliefors test for goodness of fit to a normal distribution at the $\alpha = 5\%$ level (Conover 1980), and we analysed the residuals for autocorrelation by estimating the partial autocorrelation function. The critical value of the partial autocorrelation coefficient is considered significantly differently from zero at the 5% level if it is greater than $| 2/\sqrt{n} | = 0{\cdot}408$, where n is the length of the residual vector (Chatfield 1999).

Results

Inspection of the time series of kangaroo density in the four regions (Fig. 2a) shows that the four populations do not fluctuate independently. However, they are not as correlated to each other as their biotic and abiotic environments are correlated across regions, as indicated by the temporal dynamics of DSE (i.e. sheep and cattle), rainfall and the annual harvest fraction (Fig. 2b–d, Table 1). When confronting a set of alternative models, the most parsimonious model turned out to have a drift parameter and a parameter for statistical density dependence common to all areas, dry sheep equivalents as a covariate, and a variance-covariance matrix with non-zero off-diagonal elements (Table 2). Remember that rainfall and harvest were included in all models. This model provided a reasonable fit (see Fig. 3) and the assumption of normally distributed errors could not, according to Lilliefors test, be rejected in any of the four areas: Area 1 ($D^* = 0{\cdot}12$, $P > 0{\cdot}2$), Area 2 ($D^* =$

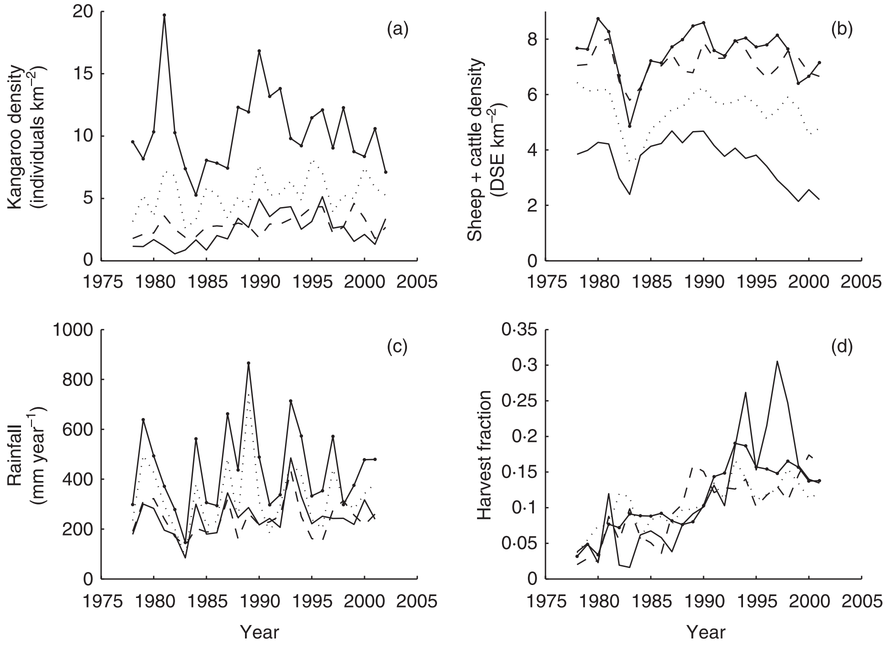

Fig. 2. The observed dynamics of (a) red kangaroo density (individuals km^{-2}), (b) sheep plus cattle density as dry sheep equivalents (DSE km^{-2}), (c) rainfall during the 12-month period prior to the first winter census of kangaroo, and (d) the annual harvest fraction. The four areas are Eastern Districts (solid lines), Gawler (dashed lines), Kingoonya/Maree (dotted lines), and North Flinders Range/North-east Pastoral (solid lines with dots).

Table 1. Spatial correlation of red kangaroo density, domestic herbivore density (as Dry Sheep Equivalent, DSE), rainfall and harvest fraction. Corr(i,j) refers to the correlation between the time series in area i and j. Area 1–4 correspond to Eastern Districts, Gawler, Kingoonya/Maree, and North Flinders Range/North-east Pastoral, respectively

	Corr(1,2)	Corr(1,3)	Corr(1,4)	Corr(2,3)	Corr(2,4)	Corr(3,4)
Kangaroo density	0·32	0·38	0·39	0·49	0·19	0·51
Sheep + cattle (as DSE)	0·44	0·47	0·62	0·78	0·71	0·84
Rainfall	0·75	0·66	0·78	0·67	0·63	0·94
Harvest fraction	0·58	0·68	0·82	0·67	0·70	0·86

Table 2. Alternative models, number of estimated parameters (K), log-likelihood (log L), Akaike Information Criteria corrected for small sample size (AIC$_c$), AIC$_c$ differences (Δ_i = AIC$_{ci}$ – min AIC$_c$) and Akaike weights (w_i) for the models where w_i – 0·01. The Σ sign (variance-covariance matrix) refers to models where the covariance in error structure is estimated. All other models assume that the variance-covariance matrix is diagonal (i.e. no covariances)

Model	Log L	K	AIC$_c$	Δ_i	w_i
$a + bN + cR + dS - H, \Sigma$	44·6	14	−56·1	0	0·53
$a + bN + cR + dS - H$	35·7	8	−53·7	2·4	0·16
$a + bN + cR + d_iS - H, \Sigma$	47·5	17	−53·1	2·9	0·12
$a + bN + cR + d_iS - H$	38·4	11	−51·6	4·4	0·06
$a + bN + c_iR + dS - H, \Sigma$	46·2	17	−50·5	5·6	0·03
$a + bN + c_iR + dS - H$	37·3	11	−49·5	6·6	0·02
$a + b_iN + cR + dS - H, \Sigma$	45·2	17	−48·5	7·6	0·01

0·07, $P > 0{\cdot}2$), Area 3 ($D^* = 0{\cdot}12$, $P > 0{\cdot}2$), Area 4 ($D^* = 0{\cdot}09$, $P > 0{\cdot}2$). There were no indications of serially correlated residuals in areas 1, 2 or 3, but the second order partial autoregressive coefficient, r_2, in area 4 exceeded the critical value: Area 1 ($r_1 = -0{\cdot}24$, $r_2 = 0{\cdot}11$), Area 2 ($r_1 = 0{\cdot}14$, $r_2 = -0{\cdot}022$), Area 3 ($r_1 = -0{\cdot}037$, $r_2 = -0{\cdot}27$), Area 4 ($r_1 = -0{\cdot}13$, $r_2 = -0{\cdot}44$). However, the proportion of the variation, R^2, explained by the best model varied from 0·07 in Kingoonya/Maree to 0·6 in Northern Flinders/North-east Pastoral, with intermediate values, 0·2, in Eastern Districts and Gawler.

The second best model was identical to the best model except that the variance-covariance matrix was diagonal (i.e. the populations were considered to be independent). The sum of the Akaike weights for the two most parsimonious models was about 0·7; hence,

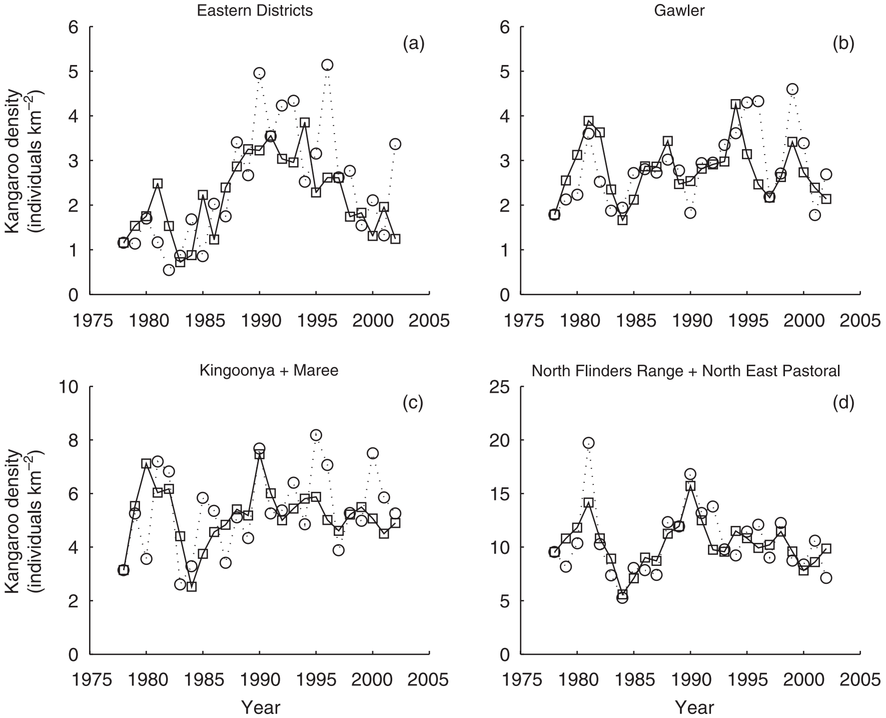

Fig. 3. The observed time series of red kangaroo density (dotted lines with circles) and the fit of the most parsimonious model (solid line with squares) for the 4 different areas.

Table 3. Maximum likelihood estimates, 95% confidence intervals, and the variance-covariance matrix when fitting the most parsimonious model $\ln\{N_{i,(t)}\} - \ln\{N_{i,(t-1)}\} = a + bN_{i,(t-1)} + cR_{i,(t-1)} + d\,\Sigma_{i,(t-1)} - H_{i,(t)} + E_{i,(t)}$ to time-series data on red kangaroo density (individuals km^{-2}) in each area i between 1978 and 2002. The parameter a is the drift parameter, b is the strength of density dependence, c is the regression coefficient with respect to rainfall, and d is the regression coefficient with respect to the density of dry sheep equivalents. All predictor variables where standardized to zero mean and unit variance. We assume that the process error has a multivariate normal distribution with a mean vector of zero and a variance-covariance matrix Σ. Correlations are given in boldface in the lower triangular of Σ

Area	*a*	*b*	*c*	*d*	Σ			
E districts	0·10	−0·25	0·088	0·13	0·26	0·05	0·01	−0·01
Gawler	0·10	−0·25	0·088	0·13	**0·40**	0·05	0·03	0·01
Kingoonya/Maree	0·10	−0·25	0·088	0·13	**0·11**	**0·51**	0·08	0·02
N Flinders R/NE Pastoral	0·10	−0·25	0·088	0·13	**−0·11**	**0·16**	**0·50**	0·03
Boundary of 95% CI								
Upper	0·038	−0·30	0·011	0·061				
Lower	0·16	−0·20	0·16	0·21				

there was strong evidence of a common dynamic structure across areas as well as an impact of DSE on the population-growth rate in the red kangaroo. Unexpectedly, the regression coefficient with respect to DSE was positive rather than the negative we would expect for competing species. Because both rainfall and DSE were standardized we can compare the corresponding regression coefficients. The positive effect of DSE on the kangaroo population-growth rate was in fact even stronger than the effect of rainfall. The maximum likelihood estimates of all parameters in the best model are given in Table 3. There was no support for ratio-dependence (Akaike weights = 0); in fact, there were 10 alternative additive models that were more parsimonious than the best ratio-dependent model.

Discussion

The sheep rangelands of southern Australia constitute a grazing system where the erratic fluctuations of rainfall and kangaroo abundance have influenced the way many ecologists think about population dynamics in large herbivores. This system has provided the inspiration for the 'mechanistic paradigm' of population-growth rate (Sibly & Hone 2002) and an emphasis on the relationship between population-growth rate and resource availability (Caughley 1976, 1987; Cairns & Grigg 1993). The general idea is that density-dependent mortality regulates population density through food-shortage (Sinclair, Dublin & Borner 1985) and, hence, the only effect of population density is to reduce the amount of available resources (see review by Bayliss & Choquenot

2002). This idea has sparked a research programme where per capita population-growth rate is assumed to be a function of available resources rather than previous population densities; the latter being the approach in classical studies of density dependence (e.g. Turchin 1999). In this paper we attempted to blend the mechanistic paradigm and classical studies of density dependence, using a time series longer than previously available for kangaroos.

Despite some model uncertainty (Table 2), there was no evidence of ratio-dependence. Models without a separate term for density dependence were not supported at all. Instead, there was strong support for region-independent density dependence (b) and the same location parameter (a). The lagged rainfall, which has been used as a surrogate for resources in previous studies, did not account for the observed feedback structure. This is in agreement with McCarthy (1996) who studied the effect of density dependence and rainfall assuming that the red kangaroos inhabiting South Australia's pastoral zone make up a single large and uniform population. The strong support for global parameter values across the four areas (i.e. no area-specific parameter values) suggests that the spatial difference in average kangaroo density between the areas (Fig. 2a) is most likely due to spatial variation in the average level of the covariates (Fig. 2b–c). Hence, rainfall, sheep and cattle density vary between areas, but populations respond to that variation in a similar way. This in turn suggests that the population structure in the four regions is not different enough to generate spatial variation in the demographic response to variation in resource abundance. What did differ among the regions, however, was the proportion of the variation explained by the best model. We conclude that a 'best model' is not necessarily a good model, but it is not clear why we explained as much as 60% in one area and only 7% in another area.

When we initiated this study, we believed that sheep and cattle densities would have a negative effect on the rate of change of red kangaroos, generating an effect not accounted for by the resource proxy. However, the effect of sheep and cattle on population rate of change in kangaroos was positive rather than negative. Does this mean that grazing by sheep and cattle has facilitative effects? No, not necessarily. One has to realize that pastoralists control sheep and cattle densities and it makes perfect sense for them to increase the sheep and cattle densities when grazing conditions are favourable. If rainfall is a good surrogate for resources, then we should be able to pick up the effect of competition. The positive effect of DSE on kangaroos suggests the contrary, and it seems that we do not yet have a clear understanding of how resource availability should be modelled in this system. This view is further supported by our results showing the occurrence of density dependence obviously not captured by the rainfall data, and the fact that there was still evidence of spatially correlated residuals (Table 2) despite the inclusion of all known sources of population synchrony in this grazing system (Table 1). Dispersal could potentially generate spatially correlated residuals, but there is no evidence of dispersal of the magnitude required for the spatial scale studied here (Priddel 1987; Croft 1991; Norbury, Norbury & Oliver 1994). More likely, we have missed an aspect of resource dynamics that is not captured by the rainfall included in the models. Future studies may show that including another rain period will solve the problem but that remains to be proven. Also, future work should explore the possibility of nonlinear effects of rainfall. How abiotic conditions work their way through the individuals to the dynamics of a population is indeed a general problem, and potentially important to our understanding of population declines observed in, for example, South African large herbivores (Ogutu & Owen-Smith 2003).

Given that kangaroo dynamics in the sheep rangelands have been studied for a long time and there exists a theory for how rainfall drives the kangaroo dynamics by generating fluctuations in the resource abundance (Caughley 1987), the conclusion that we still do not know how to approximate resource availability may seem a bit surprising. However, previous studies have focused on one or a few processes at a time, which sometimes give the false impression that we understand more than we do, especially if different processes can generate identical patterns in data (Jonzén *et al*. 2002a; Jonzén, Ripa & Lundberg 2002b). Our conclusions should alert ecologists working in less well-known systems to think carefully about what demographic and environmental processes are operating and how these processes could be expressed in mathematical terms. Only then can we get an idea about whether our models and hypotheses are supported by empirical observations.

We find ourselves in the crossfire between the proponents of models that explicitly consider resource–herbivore interactions (e.g. Choquenot & McLeod 1997) and the more pragmatic view motivated by the difficulties of measuring the resources and estimating functional relationships between the two trophic levels (e.g. Sæther 1997). We have followed the more pragmatic view, but our results indicate that we must think more carefully about the mechanistic relationships between sheep, cattle, kangaroos and their resources. Hence, if we are ever going to understand how demographic processes interact with environmental fluctuations, we need to go much further than simply model patterns in data. This calls for rigorous treatment of the problems, an understanding of the stochastic nature of the phenomena we are studying, and an embracing of flexible stochastic models with strong theoretical underpinning that can be confronted with all available relevant data.

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Section 11

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Spatial patterns of kangaroo density across the South Australian pastoral zone over 26 years: aggregation during drought and suggestions of long distance movement

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Running title: Spatial patterns of kangaroo density

Summary

1. Wildlife surveys usually focus on determining estimates of population size, and management actions such as commercial harvesting, culling and poison baiting are commonly referenced to population size alone without taking into account the way in which those animals are distributed. This paper outlines how point-based aerial survey data can be converted to continuous density surfaces using spatial analytic techniques. Using this approach, we describe and explore the spatial patterns of abundance of two species of kangaroos in an area exceeding 200,000 km^2 in South Australia over a 26-year period.
2. Densities of red and western grey kangaroos were estimated in 1-km^2 segments along aerial survey transect lines, yielding point density estimates. Universal kriging provided an unbiased interpolation of these data using the spatial autocorrelation structure described by the semivariogram. The Getis statistic identified clusters of segments of high and low kangaroo density. Residuals from the Taylor's power law relationship were used as a measure of dispersion and related to recent rainfall and greenness from satellite imagery.
3. Considerable year-to-year variation in the spatial patterns of kangaroo density was observed. In many cases, annual rates of increase over large areas were too high to be explained by vital rates alone, implying immigration from surrounding areas. These large shifts in distribution were often to areas that had received better rainfall than the surrounding areas. For both species, there was no obvious local spatial autocorrelation pattern or clustering of kangaroo density beyond that described by average density and the present set of management regions, suggesting the latter are appropriate divisions for harvest management.
4. Data for both species fitted the power law relationship extremely well. During dry times, red kangaroos but not western grey kangaroos were more aggregated, supporting past ground observations at a fine spatial scale.
5. *Synthesis and applications*. Kriged density surfaces enable estimation of kangaroo density on individual properties, which are the management units at which harvest quotas or culling approvals are allocated. These estimates will be marked improvements over systematic sampling estimates when sampling intensity is low. Predictions of shifts in kangaroo distribution using rainfall or satellite imagery will allow more accurate allocation of harvest quotas. Similarly, predictions of more even kangaroo dispersion following high rainfall will allow managers to anticipate downturns in harvest rate.

Key-words: Australia, interpolation, long-term survey, Taylor's power law, geostatistics.

Introduction

Whether the goal is conservation, sustainable use or pest control, wildlife management ideally requires regularly updated information on a population's size and distribution. Most frequently, population size is estimated from sample counts throughout a study area, but the pattern of distribution is either ignored or considered only subjectively. Typically, management actions such as setting appropriate seasonal harvest limits or undertaking poison baiting or culling are triggered by estimates of the total population without sufficient regard to its distribution pattern. This means that management actions may be focussed inappropriately, leading to wastage of money and outcomes that may be seriously sub-optimal. This paper outlines how point-based aerial survey data can be converted to continuous surfaces using spatial analytic techniques. Using this approach, we then describe and explore the spatial patterns of abundance of red kangaroos (*Macropus rufus*) and western grey kangaroos (*M. fuliginosus*) in the South Australian pastoral zone (SAPZ, 282,000 km^2) over a 26-year period.

Throughout large parts of Australia, particularly in the semi-arid rangelands, kangaroo populations are harvested sustainably for a meat and skin industry and, outside the prescribed harvest areas, culled under pest destruction permits (Pople & Grigg 1998). Annual harvest quotas are set as a percentage (typically 10-20%) of the most recent estimates of population size, usually determined by aerial survey, in management regions. For a given survey intensity, the precision (i.e. standard error/mean × 100) of a population estimate becomes poorer as the size of the area declines. In highlighting this, Caughley (1979) considered a precision of 40% inadequate, but a precision of 5% useful for kangaroo management based on the ability to detect biologically significant changes in numbers over time (Caughley, Sinclair & Wilson 1977). Given a proportional harvesting strategy rather than a strategy based on population trends, improving precision is best considered as reducing the risk of under or overharvesting (McCarthy 1996; Pople 2004). Using this framework, Pople, Cairns & Menke (2003) found that the probability of quasiextinction for a modelled, harvested kangaroo population increased dramatically above a precision of 50%. Harvest quotas can therefore be set reliably only for regions that are considerably larger than 10,000 km^2 and so precision is generally <40% (Caughley, Sinclair & Wilson 1977; Caughley & Grigg 1982; Cairns & Grigg 1993; Cairns *et al.* 2000) given the sampling intensity used in aerial surveys of kangaroos. However, pest destruction permits, tags to be attached to harvested animals and, in some cases, harvest quotas, are issued at the much finer scale of a property, largely on an *ad hoc* basis. This is important to management because harvest rate can vary substantially within regions because of variation in access, density of harvested species and distance to dealer sites where harvested animals must be taken (Sinclair 1977; Pople 1996). Clearly it would be useful if there were readily available and up-to-date information about the distribution of kangaroos within a management region, as well as the total number. To do this, the point-based data need to be translated to density surfaces. At the simplest level, counts in sampling units from aerial surveys are extrapolated to larger, contiguous blocks. Alternatively, they can be modelled with or without habitat covariates to create continuous surfaces, from which density at a broader scale can be estimated. Density surfaces modelled using geostatistics or habitat models have been produced from ground and airborne surveys of marine (e.g. Augustin *et al.* 1998; Hedley, Buckland & Borchers1999; Rivoirard *et al.* 2000) and terrestrial (e.g. Campbell & Borner 1995;

Villard & Maurer 1996; McKenney *et al*. 1998; Rempel & Kushneriuk 2003) wildlife populations. However, few if any of these have covered the same combined spatial and temporal extent as that examined in this work. It is important to distinguish between density surfaces derived from count data and maps depicting probability of occurrence that are derived from incidence models such as logistic regression (Buckland & Elston 1992; Rushton *et al*. 2004), as only some modelling techniques (e.g. generalised linear or additive models) are appropriate to both.

Previous studies on kangaroo population dynamics have focussed on changes in overall abundance rather than on changes in distribution. Fluctuations in kangaroo numbers and their relationship with food supply have been described in a number of studies (see review by Cairns 1989; McCarthy 1996; Cairns *et al*. 2000; Bayliss & Choquenot 2002; Jonzen *et al*. 2005). The underlying environmental determinants of kangaroo distribution have similarly been described in studies throughout each species' range (see review by Pople 1989). However, these studies have either been conducted on such a broad scale that movement has been ignored (e.g. Caughley *et al*. 1987), or at a scale so fine that movement is a prime focus (e.g. Newsome 1965; Priddel 1988). Short time frames, too, have constrained interpretation of data from most previous studies and, with the exception of Cairns, Pople & Grigg (1991), descriptions of broad-scale kangaroo distribution have typically covered only 1-3 years, limiting the generality of the results. Distribution data spanning long time scales (decades rather than years) also allows assessment of hypotheses specific to temporal variation. Movement of red kangaroos in particular in home ranges usually much less than 40 km^2, is influenced by temporally and spatially varying food availability (Norbury, Norbury & Oliver 1994; McCullough & McCullough 2000), which in turn may influence their broad-scale pattern of distribution as well as their dispersion. In this context, 'pattern of distribution' refers to the geographic variation in density and 'dispersion' refers more specifically to the extent of aggregation or evenness within an area (Elliott 1977).

Previous models relating kangaroo density to the environment (e.g. Short *et al*. 1983; Cairns, Pople & Grigg 1991) have not been spatially explicit, neglecting neighbourhood effects such as spatial autocorrelation that may lead to spurious relationships and fail to detect true relationships (Keitt *et al*. 2002). Inspection of the spatial structure alone in wildlife survey data can also suggest possible biotic or abiotic relationships (Perry *et al*. 2002), and identify the appropriate scale of management or analysis. In analysing the long-term spatial variations in red and western grey kangaroo density, this paper extends the analysis of Cairns, Pople & Grigg (1991) by using a considerably longer time series and geostatistical methods to explore patterns of distribution. Year-to-year changes in the dispersion of kangaroos at a finer scale are also examined. The resulting spatial and temporal patterns will allow kangaroo and land managers to better allocate harvest quotas and interpret variation in harvest offtake. These patterns should also provide insights into kangaroo ecology including how kangaroo distribution and dispersion changes through wet and dry years.

Methods

AERIAL SURVEY

Aerial surveys of kangaroos in the South Australian pastoral zone (Fig. 1) have been conducted annually since 1978 in order to determine the size of populations and thereby assist setting harvest quotas. Survey methods throughout, including the transect lines flown, have remained essentially the same as those used in the 1978 survey (Caughley & Grigg 1981; Grigg *et al.* 1999). The survey comprises a series of east-west oriented transects, 28 km apart, providing a sampling intensity of approximately 1.3% and yielding coefficients of variation of around 7% and 13% for population estimates of red and western grey kangaroos, respectively, within the entire study area (Caughley & Grigg 1981).

Figure 1

Transects were flown at a ground speed of 185 km h^{-1} by a high-wing aircraft (e.g. Cessna 172) at 76 m height. An observer on either side of the aircraft counted kangaroos in 200-m wide strips along 5-km segments (i.e. 1 km^2), each separated by a seven second break (i.e. 0.2 km) in counting. Counts of red kangaroos were adjusted for visibility bias by a factor of 2.29 in open vegetation cover, 2.36 in light cover and 2.42 in medium cover (Caughley, Sinclair & Scott-Kemmis 1976). Counts of western grey kangaroos were multiplied by 4.8 to account for visibility bias (Grigg & Pople 1999). Counts were also adjusted if air temperatures (T) exceeded 15° C at survey height by multiplying by $1/(1.474-0.0316 \times T)$ (Caughley 1989), but the need for this was uncommon. Areas higher than the 500 m contour in the Flinders Ranges were not surveyed because of the impracticality in maintaining constant height above ground in rugged terrain.

MAP PRODUCTION

Each 5 km aerial survey segment was first georeferenced to its midpoint by mapping segments relative to the start and finish of transects. A method was then required to convert these points to a spatially continuous surface. Techniques for the interpolation of spatial data have been applied extensively and the methods used for data preparation, processing and error assessment are well documented, particularly for the geosciences (Isaaks & Srivastava 1989; Cressie 1991). However, there are few reported applications of these techniques to fauna surveys, so a brief overview is presented here.

Overview of interpolation techniques

Interpolation techniques can be either deterministic or geostatistical, depending on the form of algorithm used (Fig. 2). Non-deterministic methods assume that the measured values contain an error component, and a fitted surface therefore has only one of several possible shapes. Deterministic interpolation techniques create surfaces from measured points, based on either the extent of similarity (e.g. inverse distance weighting) or the degree of smoothing (e.g. splines). Geostatistical interpolation techniques utilize the spatial autocorrelation properties of the measured points. Deterministic approaches can be split into global or local scale applications, depending on the extent to which all data points are used in the interpolation process. In global methods, the spatial distribution of the variable to be interpolated is understood to be discrete, rather than characterised by a probability and error function. Examples of global methods are trend and regression surfaces. Global methods rely on external information, including regression models with habitat covariates, and tend to be stochastic in nature, so that local variation of sample points is discarded as noise. Local methods are based on the assumption that the measured values are more correct than any globally obtained surface values, hence they calculate predictions from the measured points within neighbourhoods.

Figure 2

Selection of an appropriate interpolation technique

We considered four of the most commonly used and commercially accessible interpolation techniques, kriging, splines, triangulated irregular network and inverse distance weighting. Kriging was considered the best interpolator for our application with splines not too far behind. Kriging's major advantages are its ability to cope with data uncertainty, the inclusion of exploratory spatial analysis as part of the process, a high level of user control and the provision of error diagnostics to assess density surfaces. The nature of the input data also required a technique that would not be biased to the underlying sampling design and would allow for interpolation over an irregular grid to a pre-specified output cell size. Kriging requires more computing resources than the other methods, but this is of little concern given the ready availability of computing power and storage. Greater operator experience is also required with kriging, but this allows greater flexibility.

SPATIAL ANALYSIS OF KANGAROO DISTRIBUTION

Kriging was implemented using the Geostatistical Analyst extension to ArcGIS (ESRI 2004). GS+ (Robertson 2000) was used to calculate and compare semivariograms (eqn 2) for a range of search angles. The search angle is the axis or axes along which autocorrelation is assessed. Universal (a combination of global and local methods), anisotropic kriging, was used to estimate densities within the study area in 5 km x 5 km cells. Two forms of cross-validation were employed to allow assessment of alternative modelled density surfaces, leave-one-out cross-validation and setting aside every second survey point. Modelling of the density surface was somewhat *ad hoc*, avoiding unrealistically jagged or repetitive patterns. However, it was largely guided by goodness-of-fit to modelled points and points set aside. An adequate fit was determined by a small, standardised prediction error or residual and small root-mean-square prediction error that is similar to the average standard error (ESRI 2004). The coefficient of determination (r^2) between actual and predicted values is reported here to provide a simple measure of goodness-of-fit (Rempel & Kushneriuk 2003) and maps of the standardised residual (residual/standard error) were used to indicate the spatial variation of the fit.

Mean density surfaces were used to identify areas with consistently high or low kangaroo densities. Coefficient of variation (CV) surfaces enabled areas of high and low population variability to be identified.

Spatial structure (geostatistics)

Semivariograms and the Getis statistic (*Gi**) were used to quantify spatial patterns in kangaroo distributions and provide guidance for the interpolation. These techniques have been applied extensively in the physical sciences and epidemiology, but have so far had limited application in ecological studies (Isaaks & Srivastava 1989; Cressie 1991; Fortin 1999; Olea 1999; Dungan *et al.* 2002; Legendre *et al.* 2002). The semivariogram was used to express the strength of association between pairs of locations as a continuous function of the separating distance. The semivariogram and related functions serve as tools to separate the large and small-scale variation in a spatial phenomenon (Cressie 1991). This may be useful for kangaroo management as the effective scale of many population processes such as dispersal is not fully known and has a bearing on the appropriateness of the survey design and the appropriate scale of harvest regulation. Furthermore, the semivariogram extracts the characteristics required to derive the interpolated surfaces. The Getis statistic provides a measure of the degree of aggregation of high or low values, and can be applied as a summary measure to a series of points, or as the result of a moving window for a continuous spatial surface. These clusters can then be associated with environmental patterns, such as soil type, vegetation community, drainage catchment and areas of similar rainfall or land-use practices. The Getis statistic (eqn 2) was calculated for densities in survey segments averaged over 1978-2003 in 10 km^2 cells using the program ROOKCASE (Sawada 1999). The local semivariance was also calculated for densities in survey segments averaged over the study period in 5 km x 5 km cells using the program VESPER (Minasny, McBratney & Whelan 2002). This enabled the spatial variation in spatial autocorrelation to be assessed. Examining local semivariogram parameters such as the range can be useful in identifying the scale of dominant landscape features (Curran 2001), and so in our application they may identify broad-scale population subdivisions for mobile species such as kangaroos.

$$\gamma(h) = \frac{1}{2m}\sum_{i=1}^{m} [Z(x_i) - Z(x_i + h)]^2 \qquad \text{eqn. 1}$$

where,

$\gamma(h)$ = average semivariance at lag h
$Z(x_i)$ = kangaroo numbers at a sample or interpolated point
h = lag distance
m = number of observation pairs separated by lag h

$$Gi^*(d) = \sum_j Wij(d)Xj \Big/ \sum_j Xj \qquad \text{eqn. 2}$$

where,

Gi*(d) = Getis statistic at distance d
Wij (d) = spatial weights matrix
Xj = kangaroo numbers at a sample or interpolated point

Kangaroo dispersion (Taylor's power law)

The data also allow an assessment of the regional dispersion of both species of kangaroos. At a scale of 1-16 ha, red and eastern grey kangaroos (*M. giganteus*) are reported to exhibit a clumped distribution (e.g. Caughley 1964), with an increased aggregation during dry periods around remnant pasture (e.g. Newsome 1965). This is in agreement with oft-repeated anecdotal reports from kangaroo harvesters that kangaroos become harder to shoot following rain because they have dispersed into wooded areas (Kirkpatrick & Amos 1985), but are easier to find during dry spells when they make greater use of open areas (Hill 1979). This, in turn, is reflected in analyses of harvest returns (Prince 1984).

Kangaroos in the SAPZ are managed in regions based on district soil conservation boards (SCBs) that roughly correspond to the environmental provinces described by Laut *et al.* (1977). Six SCBs, ranging in size from 13,000 to 71,400 km^2, cover most of the survey area (Fig. 1) and were used in the analyses here. The degree of clumping in the red and western grey kangaroo populations at the scale of a 2-km^2 (= 200 ha) survey unit in each of the six SCBs was measured by the parameter b in Taylor's power law (Taylor 1961; Elliott 1977), where the variance (s^2) of a population is proportional to a fractional power (b) of the mean (m):

$$s^2 = am^b \qquad \text{eqn 3}$$

Parameters a and b were calculated from the intercept ($\log_{10}(a)$) and slope (b) of a regression of $\log_{10}(s^2)$ on $\log_{10}(m)$ of the kangaroo densities in survey units within each SCB. Each year provided a single point in the analysis. Heterogeneity of slopes and differences among intercepts was assessed in an analysis of covariance. The residuals from this relationship were then correlated with rain that had fallen in the 1, 3, 6 and 12 months prior to the winter aerial survey, and with annual exponential rate of increase (i.e. $\log_e(N_{t+1}/N_t)$). A better measure of pasture conditions may be the Normalised Difference Vegetation Index (NDVI), which is a measure of green vegetation derived from satellite multispectral image data (Tucker *et al.* 1985). An alternative is the difference between the maximum and minimum NDVI (NDVI flush) within an annual growth cycle (Cridland, Burnside & Smith 1995). The residuals were therefore also correlated with 6-weekly NDVI and NDVI flush averaged over the six months prior to survey. These measures were standardised over time to account for regional differences in mean rainfall and NDVI. Differences in slopes, and therefore dispersion, between species were similarly assessed using an analysis of covariance (Crawley 2002).

Fine-scale density estimation

Density of each kangaroo species was estimated using two methods for 162 properties, ranging in size from 20 km^2 to > 2,000 km^2, within the six SCBs. Based on systematic sampling, the density D_{ss} is simply the average of the density in survey units that fall within a property. An alternative estimate D_k comes from integrating under the interpolated density surface. These two estimates were calculated for each year. For each property, bias was calculated as $\log_e(D_{ss}/D_k)$ to place the simple ratio on a symmetric scale. Defining bias in this way assumes the interpolated density estimate is more accurate. The average bias over the 26 years was then calculated for each property and mapped. To avoid undefined values, 0.001 was added to each density estimate.

Results

KANGAROO DISTRIBUTION AND ABUNDANCE

Semivariance

Initial exploration of the data with semivariograms using GS+ indicated distinct spatial scales of aggregation for both species. As examples, Fig.3 provides semivariogram plots from the 1982 and 1995 surveys, prior to interpolation. The analysis of dispersion (see below) indicated that, over the study period, red kangaroos were most aggregated in the drought year of 1982 (Caughley, Grigg & Smith 1985) and most evenly dispersed in 1995, when rainfall prior to survey had been above average in most areas (mean ± s.e. standardised 6-months rainfall prior to survey = 0.61 ± 0.16 s.d. units across SCBs). In each semivariogram, the 90^o plot provided the most detailed information, as it is parallel to the survey line. The range value suggests a threshold distance beyond which density is no longer autocorrelated. The large ranges in 1995 reflect broad-scale correlation structures that were not appropriate for interpolation here. These values were also sensitive to the interval between flight lines and the lag distance used in their calculation.

Final modelling of density surfaces in ArcGIS was best achieved with a spherical model fitted to the semivariogram following first-order trend removal. A 45^o search angle to the principal axes appeared optimal, capturing along- and between-survey line variability, along with a search neighbourhood of 2-20 points per quadrant. The range was constrained to be > 4.5 km. Figure 4 indicates variation in the semivariogram range and kangaroo density over the study period, with 1991-4 having notably lower range than other years for red kangaroos and the mid-1980s and mid-1990s having higher values for western greys. Significant variations in spatial pattern of kangaroo distribution are evident from the fluctuating range values (14-97 km for red kangaroos, 13-63 km for western grey kangaroos), which coincide with density variations. There was considerable spatial variation in the local range for both species, but no obvious spatial clustering (Fig. 5).

Figure 3
Table 1
Figures 4 & 5

Spatial pattern

Across the entire SAPZ, numbers of both species fluctuated over a broad range over the 26-year study period (Fig. 4). The time series includes two periods of drought (1982-3 and 2002-3), when numbers declined markedly. In 1982 and 1983, mean ± s.e. standardised rainfall 12 months prior to survey was –0.67 ± 0.07 and –1.45 ± 0.10 s.d. units across SCBs and in 2002 and 2003 rainfall was -0.49 ± 0.14 and –0.64 ± 0.10 s.d. units. Despite these temporal fluctuations in density, there were relatively stable, distinct groupings of low and high densities of both species. For both species, the maps of *Gi** (Fig. 6) mirrored the maps of average, interpolated density over the study period (Fig. 7), suggesting relative stability in their pattern of distribution. Red kangaroo density has consistently been highest just south of Lake Frome in the northeastern section of the SAPZ (Fig. 7a). Density in this area has also fluctuated less than elsewhere in the SAPZ (Fig. 8a). Western grey kangaroos have a distribution and spatial pattern of variability in density almost complementary to that of red kangaroos (Figs 7b & 8b), with grey kangaroo numbers high in the Gawler Ranges and southeastern section of the SAPZ where red kangaroo densities are low. Both species show most marked fluctuations at the edge of their ranges, although this is exaggerated because of zeros in low-density areas inflating the coefficient of variation.

Figures 6- 8

Figure 9 illustrates interpolated counts from surveys conducted in 1982 and 1995. Each map enables assessment of regional to local scale (< 10 km) patterns in the distribution and population densities over the entire SAPZ, recognising that this is a snapshot of the population at the time of survey. Goodness-of-fit for each annual density surface appeared acceptable over the entire study area, with r^2 ranging 0.20-0.82. These values will be influenced by the degree of smoothing applied to the interpolation and the size of the range. Furthermore, the error surface will not be uniform and, as an example, Figure 10 identifies some discrepancies in the density surface for both species in 1995, primarily in the higher density areas that have been dampened by the interpolation. Each year differs in both the pattern of distribution of kangaroos within the study area and their dispersion (see below). This highlights the spatially dynamic nature of the system. One way of displaying this changing pattern of distribution is to map the annual exponential rate of increase of kangaroos. In some areas and in some years, the increase in numbers is so great and over such a broad scale that it cannot be explained by recruitment and survival alone. This suggests an important role for movement in broad-scale population dynamics. Figure 11a shows an interpolated surface for the exponential rates of increase for red kangaroos over 1986-7. In the eastern SAPZ there is a large, contiguous area where red kangaroo numbers have more than tripled. Measurement error contributes to this fluctuation, but the fact that it occurs over such a large contiguous block and coincides with declines elsewhere, suggests that it is real. Many of the patches of extraordinary increases in Figure 11a coincide, albeit imperfectly, with areas receiving above average rainfall in the six months prior to the aerial survey in 1987 (Figure 11b).

Figures 9-11

Kangaroo dispersion

For red kangaroos, the most parsimonious model ($r^2 = 0.90$) describing Taylor's power law included shared, rather than separate slopes ($F_{5,144} = 0.80$, $P > 0.5$), but separate intercepts for each SCB ($F_{5,149} = 11.83$, $P < 0.001$), indicating constant degree of aggregation ($b = 1.50 \pm 0.06$) across SCBs (Fig. 12). Points for the higher rainfall SCBs in southern pastoral zone fall along lines elevated from the other SCBs. This is reflected in a larger estimate for the intercept parameter (a in eqn 3) and a simpler model with two intercepts ($F_{4,149} = 1.35$, $P > 0.2$). The residuals from this relationship were not correlated with rate of increase, but correlated negatively to all rainfall and NDVI measures; most strongly to rain falling 12 months prior to survey ($r = -0.32$, 95%CI: -0.45, -0.17). The relationship has considerable scatter, but the absence of points at high rainfall and large positive residuals (= highly aggregated) (Fig. 13) is notable. Low rainfall frequently, but not always, leads to greater aggregation, but the population is always more evenly dispersed following high rainfall. These results are reflected in the temporally and spatially varying semivariogram range (Figs 4 & 5), although patterns of dispersion will not necessarily coincide with autocorrelation patterns.

Figures 12 & 13

For western grey kangaroos, there was some suggestion of heterogeneity of slopes among SCBs ($F_{4,117} = 2.16$, $P = 0.07$) due to less aggregation in the Northeast Pastoral SCB. However, the most parsimonious model ($r^2 = 0.98$) again included only separate intercepts for each SCB ($F_{4,121} = 6.63$, $P < 0.001$), indicating constant degree of aggregation (b ± s.e. = 1.35 ± 0.03) across SCBs (Fig. 14). In contrast to red kangaroos, the residuals from this relationship were not correlated with rate of increase or any rainfall or NDVI measures. Excluding Marree SCB and examining both species together, analysis of deviance indicated little support for slopes varying among species ($F_{1,241} = 0.74$, $P > 0.3$), SCBs or an interaction between the two. The most parsimonious model ($r^2 = 0.98$) included a common slope (b ± s.e. = 1.37 ± 0.03) and, hence, a similar level of aggregation across SCBs for both species.

Figure 14

FINE-SCALE DENSITY ESTIMATION

Throughout the six SCBs, density could not be estimated on 28 properties using systematic sampling because they contained no survey segments, but these were typically small properties (Fig. 15). Similarly, bias was positively correlated with logged property size for reds ($r = 0.43$, $P < 0.01$) and western greys ($r = 0.56$, $P < 0.01$). For both species, interpolated densities were generally higher than those just based on survey segments, with a mean bias (± s.e.) over 1978-2003 of -0.73 ± 0.10 (median = -0.23) for red kangaroos and -0.98 ± 0.09 (median = -0.66) for western grey kangaroos. This negative bias is obviously offset by a positive bias on properties with high-density segments. There was no obvious spatial pattern in the bias for red kangaroos, but segment-based (D_{ss}) densities of western grey kangaroos were consistently lower than interpolated density estimates (D_k) through the centre of the SAPZ (Fig. 15), which is the northern extent of the western grey kangaroo range (Fig. 5b).

Figure 15

Discussion

INTERPOLATION TECHNIQUES

Kriging was intuitive to apply, as a detailed exploratory analysis of spatial pattern within the point data set was required to establish a suitable semivariogram. In combination with the ability to assess or map the likely error in the kriged surfaces, this interpolation technique is inherently suited to exploring and mapping spatial patterns in wildlife survey data and, perhaps, modifying survey design to improve the accuracy and precision of estimates. Thus, high density areas and areas with large error could be surveyed with increased sampling intensity and, conversely, sampling could be reduced in areas of uniformly low density. However, one problem with kriging is that density cannot be extrapolated beyond the most extreme data points without making a number of assumptions or using other data such as habitat covariates. In this project, the study area is bounded by the spatial extent of the transect lines (Fig. 1). Smoothed surfaces of kangaroo density have been generated previously from aerial survey data (e.g. Caughley, Sinclair & Wilson 1977; Caughley 1987), but the interpolation method has not been identified, although it almost certainly was not kriging with its advantages described above.

An obvious alternative to kriging is spatial modelling using habitat covariates. This will be advantageous if there are discontinuities in a species' spatial pattern of density. Sharp steps in distribution are not a feature of these species' ecology (Caughley *et al.* 1988), except at the dingo fence marking the northern boundary of this study area, where predation appears to dramatically alter abundance (Pople *et al.* 2000). There are certainly discontinuities in the habitat, but these are either of little consequence to kangaroos or they occur at a much finer scale than a 1-km^2 survey segment. Assessment of the accuracy of these density surfaces could be undertaken in a number of locations using more intensive aerial surveys or ground surveys.

SPATIO-TEMPORAL PATTERNS

Conversion of point-based samples from long-term, frequent systematic surveys to a spatially extensive map of population density enables recurrent patterns in the distribution of animals to be clearly identified. Figures 7 and 8 show that the broad pattern of distribution of both red and western grey kangaroos in the SAPZ has been relatively stable. High densities of red kangaroos were consistently recorded in the northeast of the SAPZ, an area with a mosaic of soil and vegetation types, but generally dominated by low bluebush shrublands and calcareous soils and where sheep are grazed at a relatively high density (Cairns, Pople & Grigg 1991). Western greys are restricted to the less arid parts of the study area and densities were consistently high in the southwest. This area is also heterogeneous in terms of soil, landform and vegetation, with many areas of woodland interspersed with grassland and open shrubland (Cairns, Pople & Grigg 1991). There is temporal variation in this pattern for both species, particularly where they occur at relatively low density (Fig. 7). This probably reflects the vagaries of marginal habitat, despite the inflation of the CV by zeroes. Whether these areas with highly fluctuating densities experience high rates of local extinction and recolonisation or are driven just by local population dynamics, is unclear from these data.

From year-to-year there are also substantial shifts in distribution, some of which cannot be explained by birth and death alone. Even an unstable age distribution and biased sex ratio, possible in drought, can result only in a less than doubling (i.e. annual exponential rate of increase < 0.69) of population size (Bayliss 1985; Pople 1996), well short of the increases described over large areas in Figure 11a. Cairns, Pople & Grigg (1991) reported a shift in distribution of red kangaroos in the 1982-3 drought. This was largely due to spatial variation in the onset of drought, which was delayed in the west of the pastoral zone, and resulted in uneven declines in density. Uneven changes in density resulting in changes in distribution can be particularly marked during declines because of the convex shape of the numerical response of kangaroos (Davis, Pech & Catchpole 2002). What became apparent with a reanalysis of these data and over a longer time period, was that distribution shifts were also associated with increases in density. Long distance movements of > 100 km have been recorded for individual red kangaroos from tagging and radio telemetry (Bailey 1971; Bailey & Best 1992). However, these have been considered exceptions in a generally sedentary population where individuals move within home ranges of variable size (McCullough & McCullough 2000). Adult red kangaroos have been recorded ranging more widely during drought (Norbury, Norbury & Oliver 1994), and movements of up to 30 km have been reported for red kangaroos in response to patchy rainfall during prolonged dry spells, resulting in global shifts of the population (Newsome 1971; Denny 1980; Priddel 1987; Croft 1991). The data presented here lend further support to the hypothesis that large-scale movements occur to areas of higher quality food supply. However, Priddel, Wellard & Shepherd (1988) and Bayliss (1985) considered red kangaroo movement had little influence on their dynamics at a scale of 440 km^2. The results of this study suggest that populations are not closed at this scale or even greater. This apparent discrepancy from previous studies may be due to a number of factors including, the relatively short time frame and small spatial scale of many radio-tracking and tagging studies, site-specific factors such as fences and lakes which influence movement, low recapture rates of some population classes in tagging studies and a bias towards selection of adult animals in radio tracking studies.

The exceptional fit of these data to Taylor's power law is not surprising, given its fit to a broad range of taxa (Taylor, Woiwod & Perry 1978; Taylor & Woiwod 1982). A slope of between 1 and 2 has also been found for most species. We do not offer an explanation for this scaling relationship; rather we use it to detect increased aggregation of red kangaroos during dry times, supporting fine-scale observations. What is interesting is that it has been detected here at the scale of a 1-km^2 survey segment. It suggests that seasonal movements can be detected with broad-scale aerial survey and that the more extensive NDVI data may be able to predict movement and the resulting changes in spatial distribution of kangaroos.

These shifting patterns of distribution have important implications for management. Annual harvest quotas are based on surveys conducted at least six months prior to the actual harvest, by which time the geographic variation in kangaroo density may have altered. Spatial allocation of quotas needs to account for these shifts and the results here suggest this may be possible. Harvest rate appears to be influenced by dispersion of kangaroos with increased harvests when animals are aggregated (Kirkpatrick & Amos 1985). Rainfall or NDVI could be used to predict downturns in harvest offtake although the direct link between harvest rate and rainfall or NDVI needs to be quantified for the eastern Australian states.

APPROPRIATE SCALE OF MANAGEMENT AND ANALYSIS

A semivariogram range of 13-97 km indicates that spatial autocorrelation needs to be accommodated in spatial modelling with data collected within these distances. The correlation structure can be incorporated directly (Guisan & Zimmerman 2000; Keitt *et al*. 2002) or data can be pooled into larger units that are less likely to be autocorrelated (Hall 1988; Buckland & Elston 1993).

Appropriate geographic stratification of broad-scale data has been considered critical for monitoring population trends in declining populations (Villard & Maurer 1996). It will similarly be important for other management fields such as regulating harvests. The clusters of high and low densities identified by the Getis statistic are alternative strata to administrative or biogeographic boundaries. For both species, *Gi** broadly matches average density, which tends to cluster and differ in value for each SCB, providing support for one level of current kangaroo management in South Australia. Management activities such harvest regimes, survey frequency and enforcement could be tailored to these strata. At present, these activities, including the proportion of the population that is offered as a harvest quota, are uniformly undertaken or applied across SCBs within the SAPZ (SADEH 2002). However, harvest rate and variability differs among as well as within these SCBs (Jonzen *et al*. 2005), suggesting that management would be more efficient if it varied its activities accordingly (Pople, Cairns & Menke 2003; Pople 2004). The lack of clustering in the semivariogram range suggests the present management regions are not ignoring a spatial autocorrelation structure that may suggest discrete population units other than the SCBs.

In South Australia, kangaroo harvest quotas are allocated to individual properties. More widely within Australia, permits for culling are given to individual properties. Ideally, this requires fine-scale estimates of density, relative or absolute, to divide a regional quota among constituent properties, or to assess requests for culling permits by a property manager. This study highlights how kriging can overcome the imprecision and bias associated with low sampling intensities when estimating density on a fine scale. The marked differences between interpolated densities and averaged segment densities within properties highlights the gain that can accrue by taking the approach we have described in this paper.

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Table 1. Parameters, coefficients of determination (r^2) and models for the semivariograms shown in Figure 3.

	Red		Western grey	
	1982	1995	1982	1995
Range (degrees)	0.43	0.50	0.27	1.70
Nugget	107.6	67.4	24.1	117.9
Sill	215.3	134.9	113.6	235.9
r^2	0.75	0.47	0.73	0.71
Model	Exponential	Spherical	Exponential	Spherical

Figure Captions

Fig. 1. (a) The South Australian pastoral zone (hatched) showing soil conservation boards (shaded) which serve as kangaroo management regions and the location of survey segments (•) in 2003. (b) Vegetation structural formations within the survey area (Boomsma & Lewis 1980).

Fig. 2. Classification of interpolation techniques.

Fig. 3. Semivariograms for (a) red kangaroos in 1982, (b) red kangaroos in 1995, (c) western grey kangaroos in 1982 and (d) western grey kangaroos in 1995. Points represent four analysis directions (□, 0 °; ○, 45 °; ✳, 90 °; +, 135 °). X-axis units are in decimal degrees.

Fig. 4. Semivariogram range (■) and population densities (♦) (± SE) for (a) red kangaroos and (b) western grey kangaroos within the study area, 1978-2003.

Fig. 5. Map of local semivariogram range for (a) red kangaroo and (b) western grey kangaroo density, averaged over 1978-2003 within 5 km x 5 km cells, in the South Australian pastoral zone.

Fig. 6. The Getis statistic for (a) red and (b) western grey kangaroo density, averaged over 1978-2003 within 25 km x 25 km cells, in the South Australian pastoral zone.

Fig. 7. Average density of (a) red kangaroo and (b) western grey kangaroos in the South Australian pastoral zone over 1978-2003. Calculated from annual densities in 5 km x 5 km cells interpolated from densities in aerial survey segments (Fig. 1a) using universal kriging.

Fig. 8. Coefficient of variation of (a) red kangaroo and (b) western grey kangaroo density over 1978-2003. Calculated from annual densities in 5 km x 5 km cells interpolated from densities in aerial survey segments (Fig. 1a) using universal kriging.

Fig. 9. Densities of (a) red kangaroos in 1982, (b) red kangaroos in 1995, (c) western grey kangaroos in 1982 and (d) western grey kangaroos in 1995. Densities in 5 km x 5 km cells were interpolated from densities in aerial survey segments (Fig. 1a) using universal kriging. Over 1978-2003, red kangaroos were most aggregated in 1982 and most evenly dispersed in 1995. Dispersion showed less marked changes for western grey kangaroos.

Fig. 10. Standardised residuals for the density of (a) red kangaroos ($r^2 = 0.32$) and (b) western grey kangaroos ($r^2 = 0.27$) in aerial survey segments in 1995.

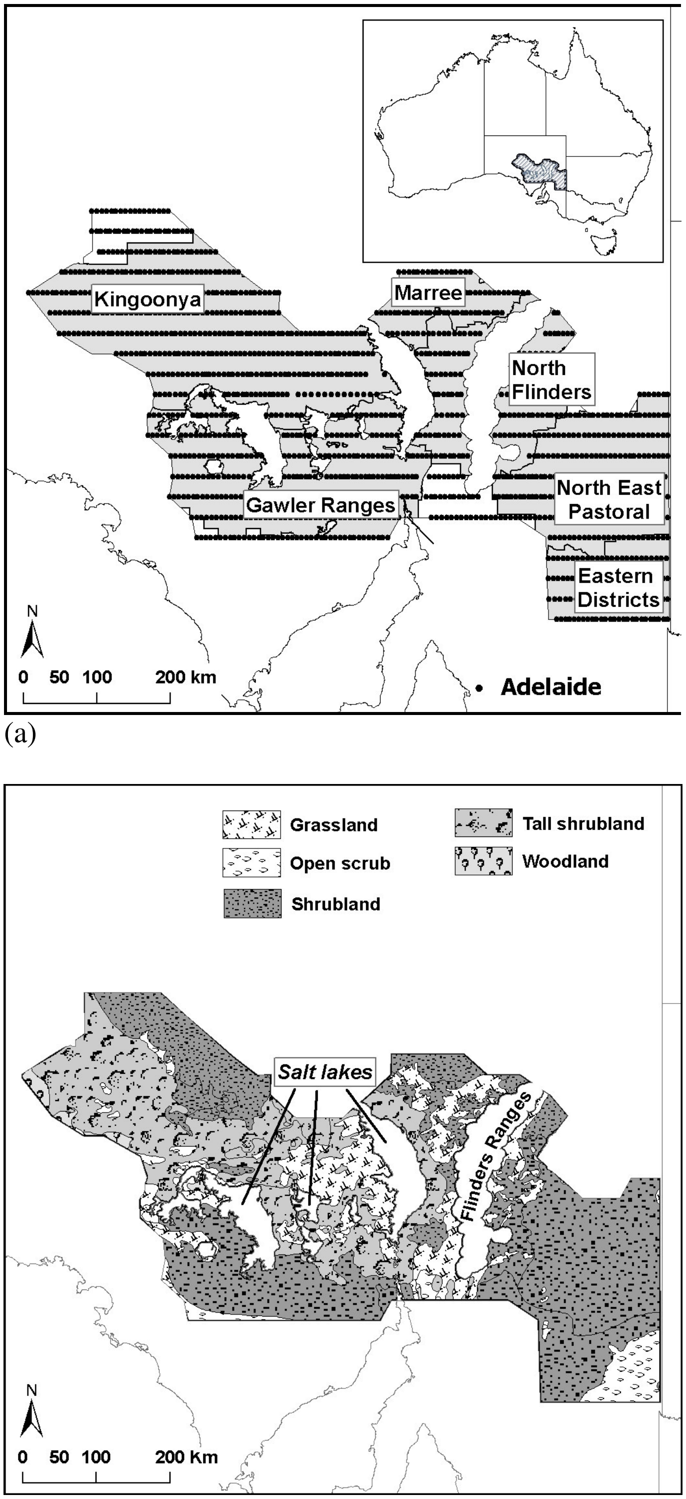
Fig.11. (a) Annual exponential rate of increase for red kangaroos over 1986-87. Calculated from annual densities in 1986 and 1987 in 5 km x 5 km cells interpolated from densities in aerial survey segments (Fig. 1a) using universal kriging. (b) Rainfall, standardised using the long-term mean and standard deviation, for January – June 1987.

Fig. 12. Relationship between $\log_{10}$(variance) and $\log_{10}$(mean) of red kangaroo density in six soil conservation boards (see Fig. 1a) for each year over 1978-2003. Fitted regression lines with a common slope are also shown. Eastern Districts (○), Gawler Ranges (□), Kingoonya (■), Marree (●), North Flinders (▲), North East Pastoral (♦).

Fig. 13. Relationship between the residuals from the regressions shown in Figure 11 (= index of aggregation) and rain falling 12 months prior to each annual aerial survey, 1978-2003. Rainfall is standardised within each soil conservation board. Eastern Districts (○), Gawler Ranges (□), Kingoonya (■), Marree (●), North Flinders (▲), North East Pastoral (♦).

Fig. 14. Relationship between $\log_{10}$(variance) and $\log_{10}$(mean) of western grey kangaroo density in six soil conservation boards (Fig. 1a) for each year over 1978-2003. Fitted regression lines with a common slope are also shown. Eastern Districts (○), Gawler Ranges (□), Kingoonya (■), Marree (●), North Flinders (▲), North East Pastoral (♦).

Fig. 15. Average bias over 1978-2003 in segment-based (Fig.1a) densities of (a) red kangaroos and (b) western grey kangaroos in properties within the South Australian pastoral zone. Bias was calculated as the $\log_e(D_{ss}/D_k)$, where D_{ss} is density based on systematic sampling and D_k is density based on interpolated density surface. 0.001 has been added to densities to avoid undefined values.


Kingoonya
Marree
North Flinders
Gawler Ranges
North East Pastoral
Eastern Districts
N
0 50 100 200 km
Adelaide
Grassland
Open scrub
Shrubland
Tall shrubland
Woodland
Salt lakes
Flinders Ranges
N
0 50 100 200 Km

(a)

(b)

Figure 1.

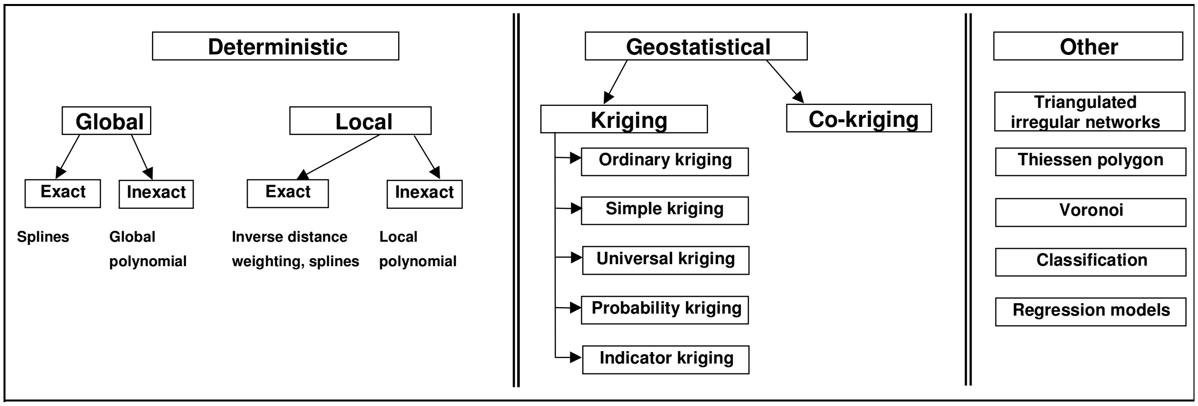
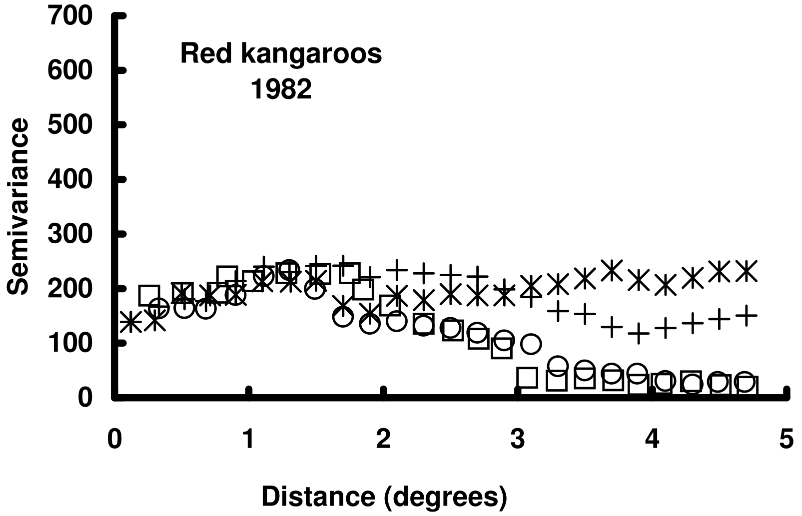
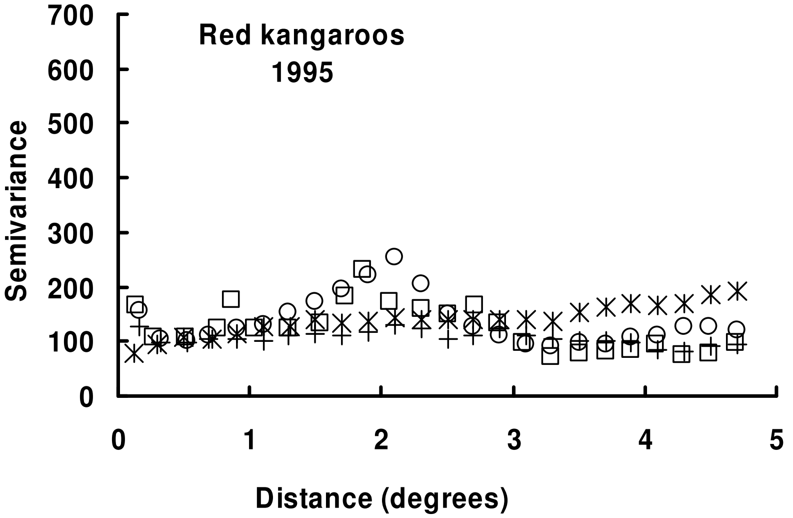

Deterministic
Global
Local
Exact
Inexact
Exact
Inexact
Splines
Global polynomial
Inverse distance weighting, splines
Local polynomial
Geostatistical
Kriging
Co-kriging
Ordinary kriging
Simple kriging
Universal kriging
Probability kriging
Indicator kriging
Other
Triangulated irregular networks
Thiessen polygon
Voronoi
Classification
Regression models

Figure 2.

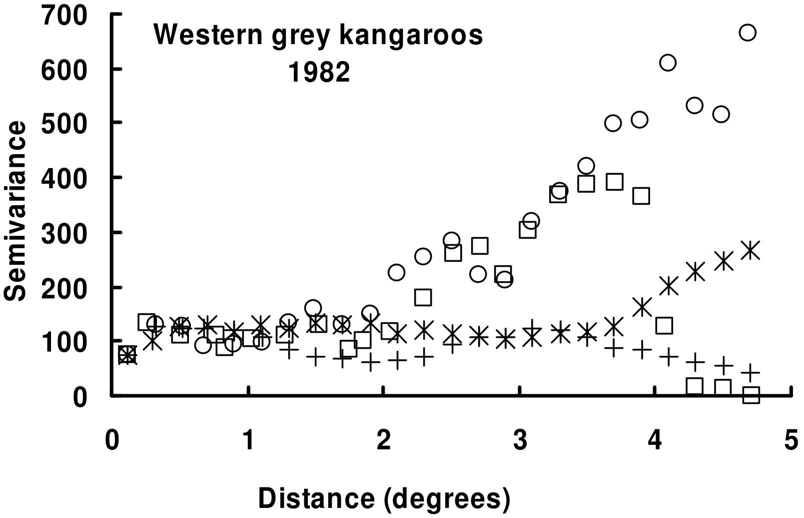

Red kangaroos
1982
Semivariance
700
600
500
400
300
200
100
0
0
1
2
3
4
5
Distance (degrees)

(a)

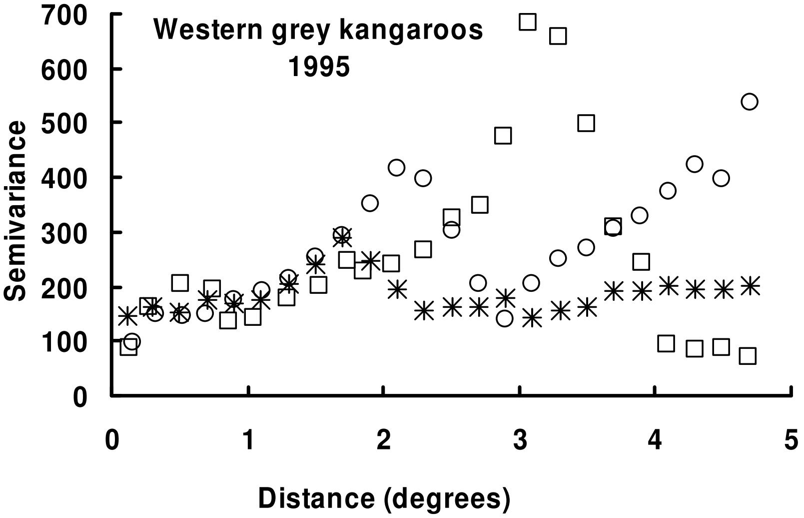

Red kangaroos
1995
Semivariance
700
600
500
400
300
200
100
0
0
1
2
3
4
5
Distance (degrees)

(b)

Figure 3.

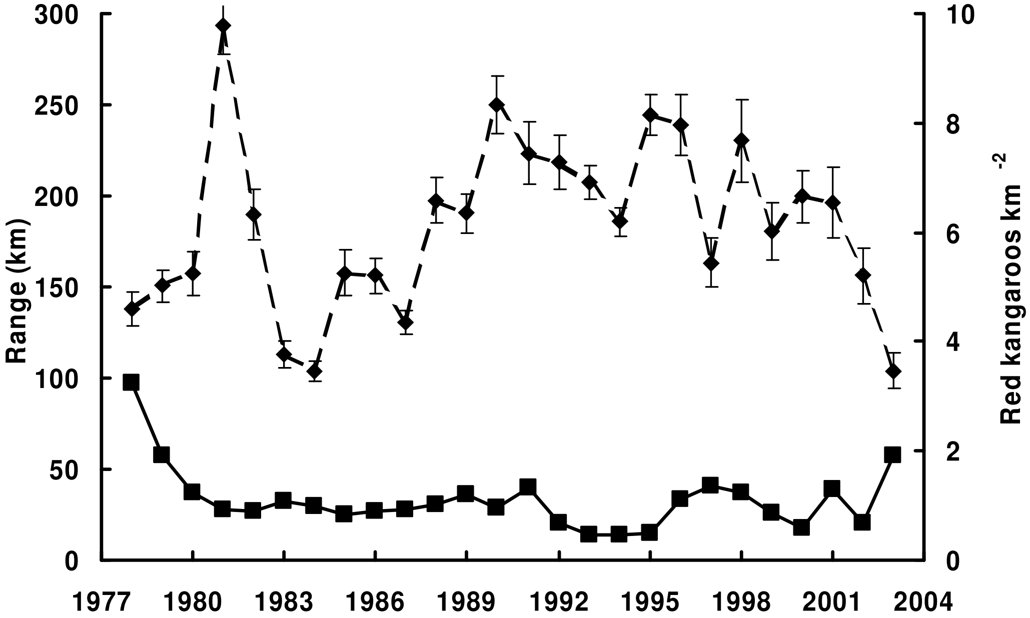


(c)

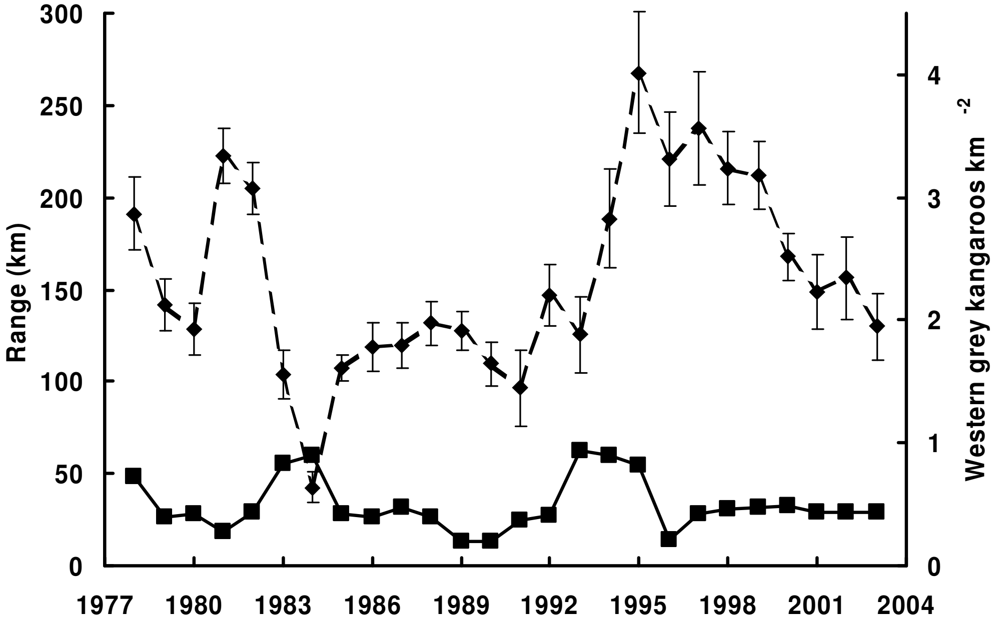


(d)

Figure 3 cont.

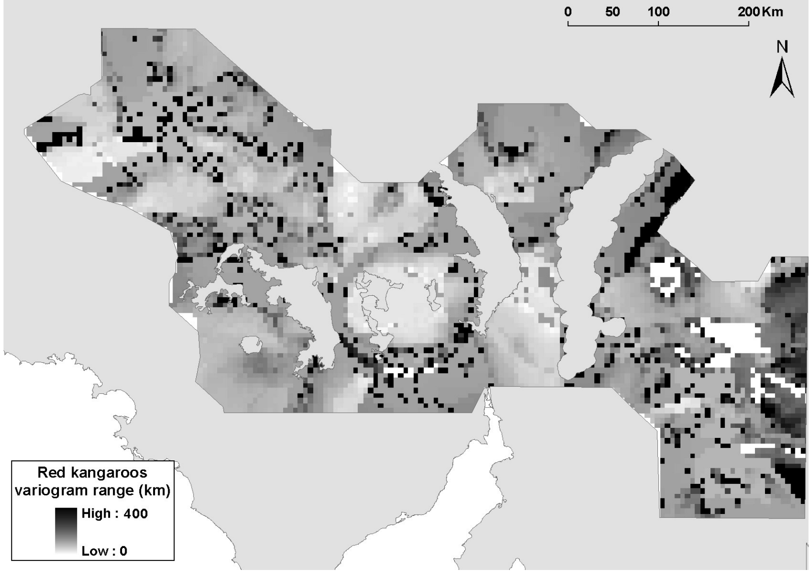

Range (km)
300
250
200
150
100
50
0
Red kangaroos km -2
10
8
6
4
2
0
1977
1980
1983
1986
1989
1992
1995
1998
2001
2004

(a)

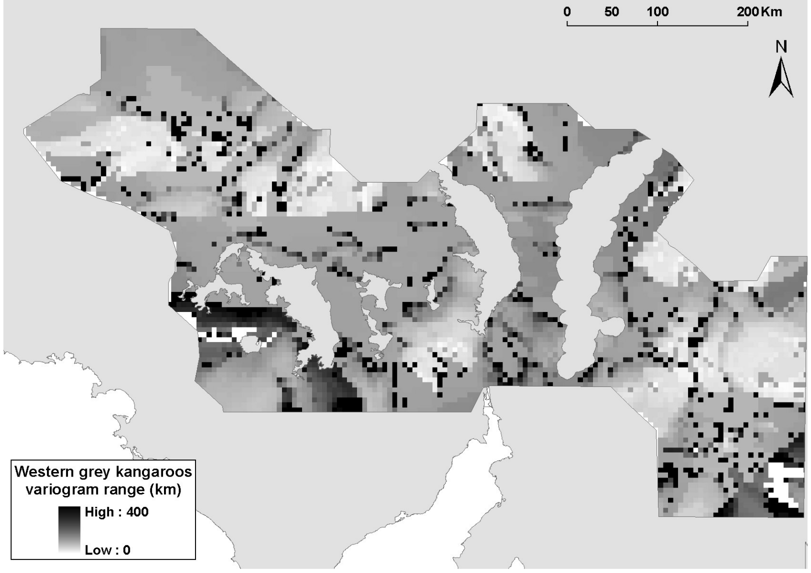

Range (km)
300
250
200
150
100
50
0
Western grey kangaroos km -2
4
3
2
1
0
1977
1980
1983
1986
1989
1992
1995
1998
2001
2004

(b)

Figure 4.

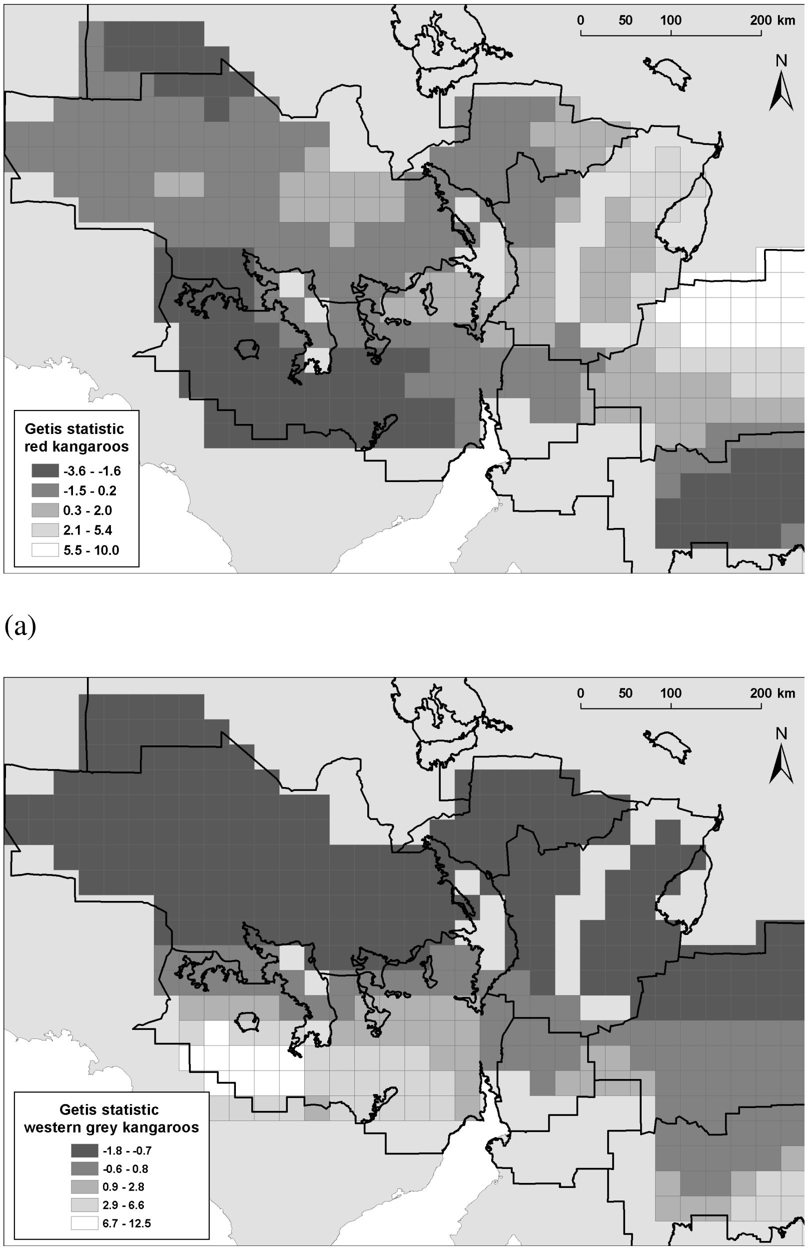

0 50 100 200 Km
N
Red kangaroos variogram range (km)
High : 400
Low : 0

(a)


0 50 100 200 Km
N
Western grey kangaroos variogram range (km)
High : 400
Low : 0

(b)

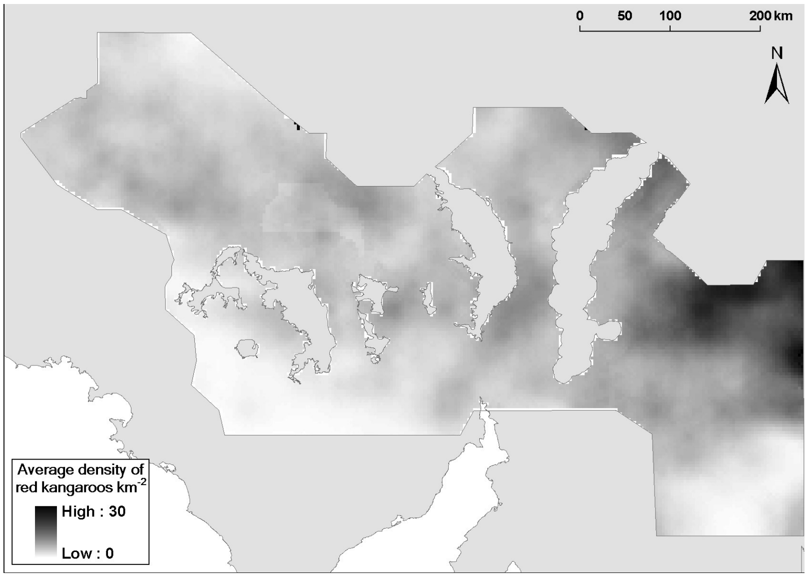
Figure 5.


0 50 100 200 km
N
Getis statistic red kangaroos
-3.6 - -1.6
-1.5 - 0.2
0.3 - 2.0
2.1 - 5.4
5.5 - 10.0
0 50 100 200 km
N
Getis statistic western grey kangaroos
-1.8 - -0.7
-0.6 - 0.8
0.9 - 2.8
2.9 - 6.6
6.7 - 12.5

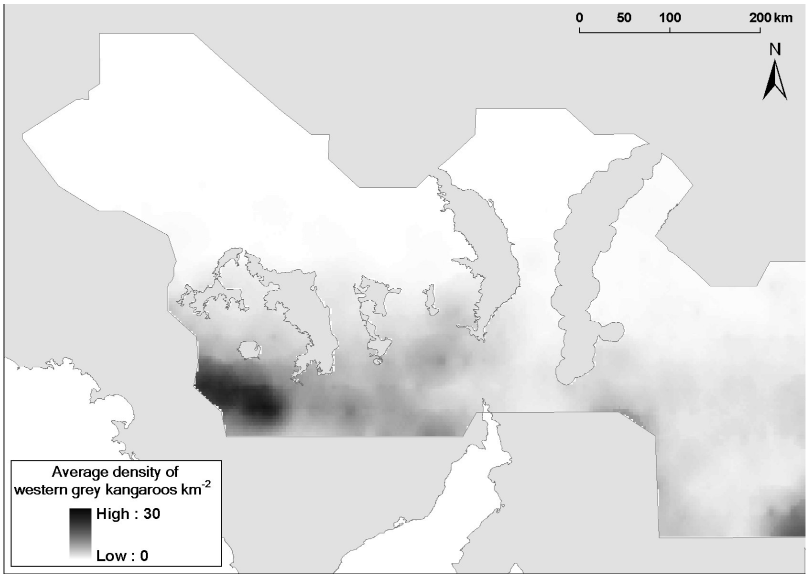
(a)

(b)

Figure 6.


0 50 100 200 km
N
Average density of red kangaroos km^{-2}
High : 30
Low : 0

(a)


0 50 100 200 km
N
Average density of western grey kangaroos km^{-2}
High : 30
Low : 0

(b)

Figure 7.

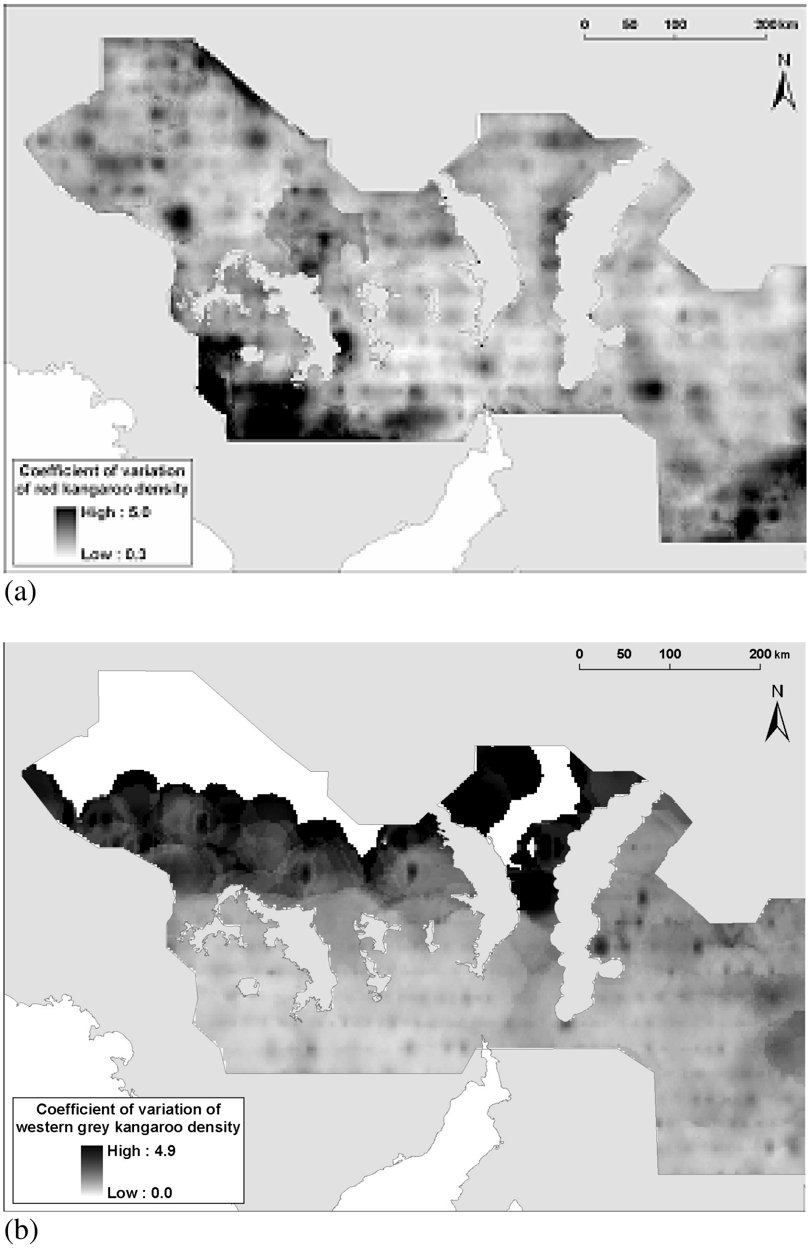
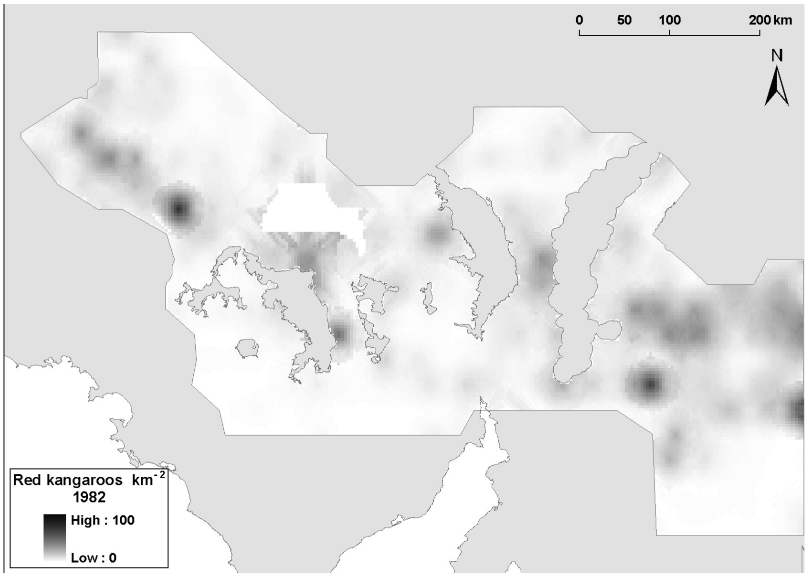
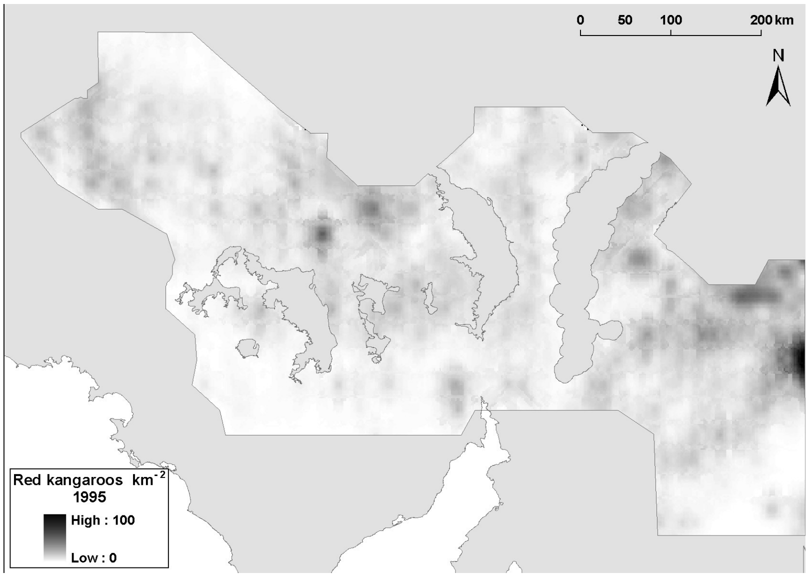

0 50 100 200 km
N
Coefficient of variation of red kangaroo density
High : 5.0
Low : 0.3
(a)
0 50 100 200 km
N
Coefficient of variation of western grey kangaroo density
High : 4.9
Low : 0.0
(b)

Figure 8.

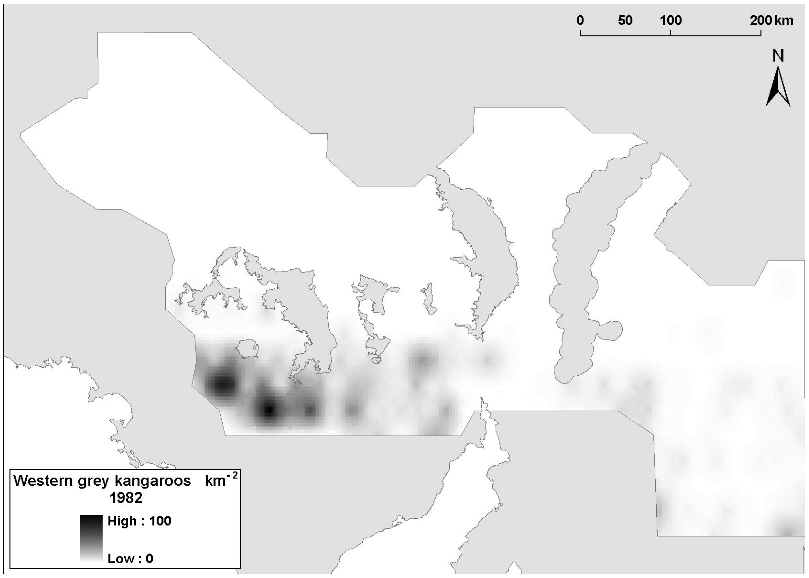

0 50 100 200 km
N
Red kangaroos km^{-2}
1982
High : 100
Low : 0

(a)

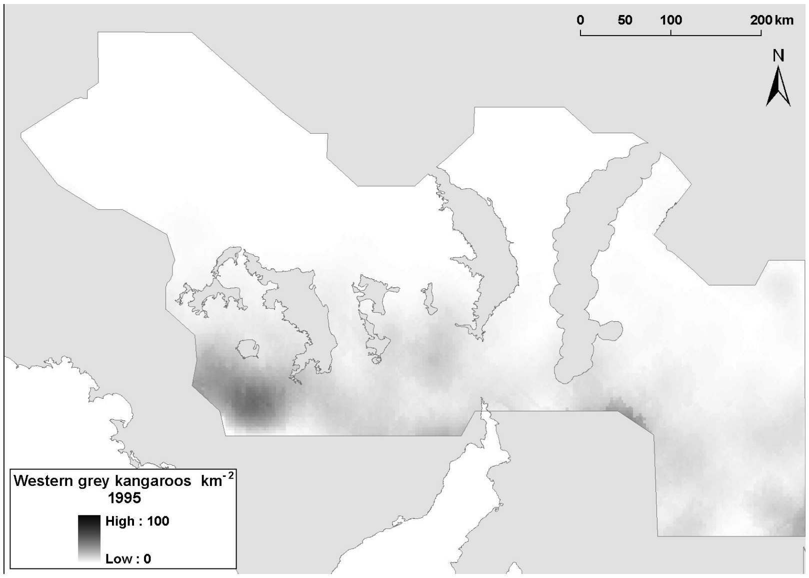

0 50 100 200 km
N
Red kangaroos km^{-2}
1995
High : 100
Low : 0

(b)

Figure 9.

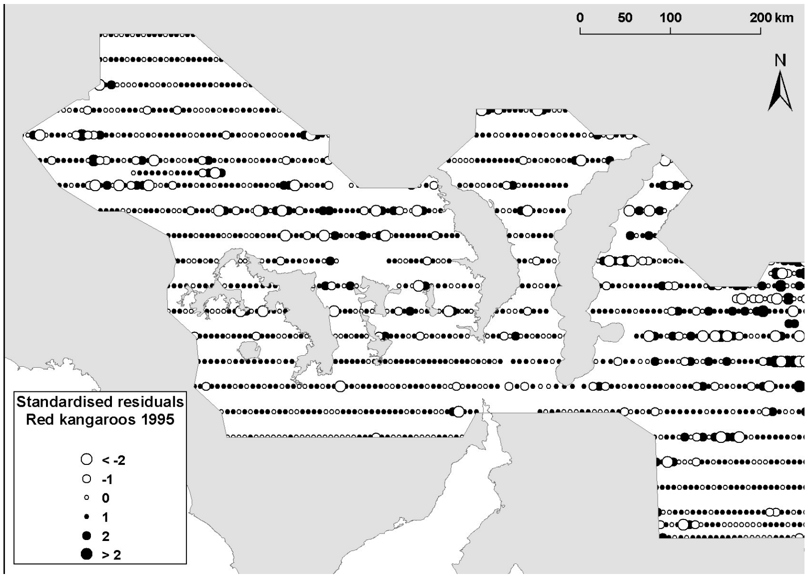


(c)

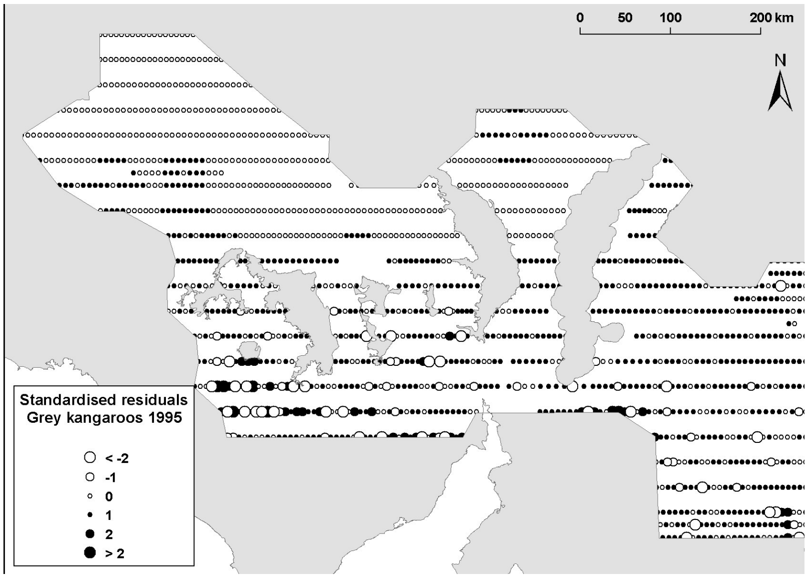


(d)

Figure 9 cont.


0
50
100
200 km
N
Standardised residuals
Red kangaroos 1995
< -2
-1
0
1
2
> 2

(a)


0
50
100
200 km
N
Standardised residuals
Grey kangaroos 1995
< -2
-1
0
1
2
> 2

(b)

Figure 10.

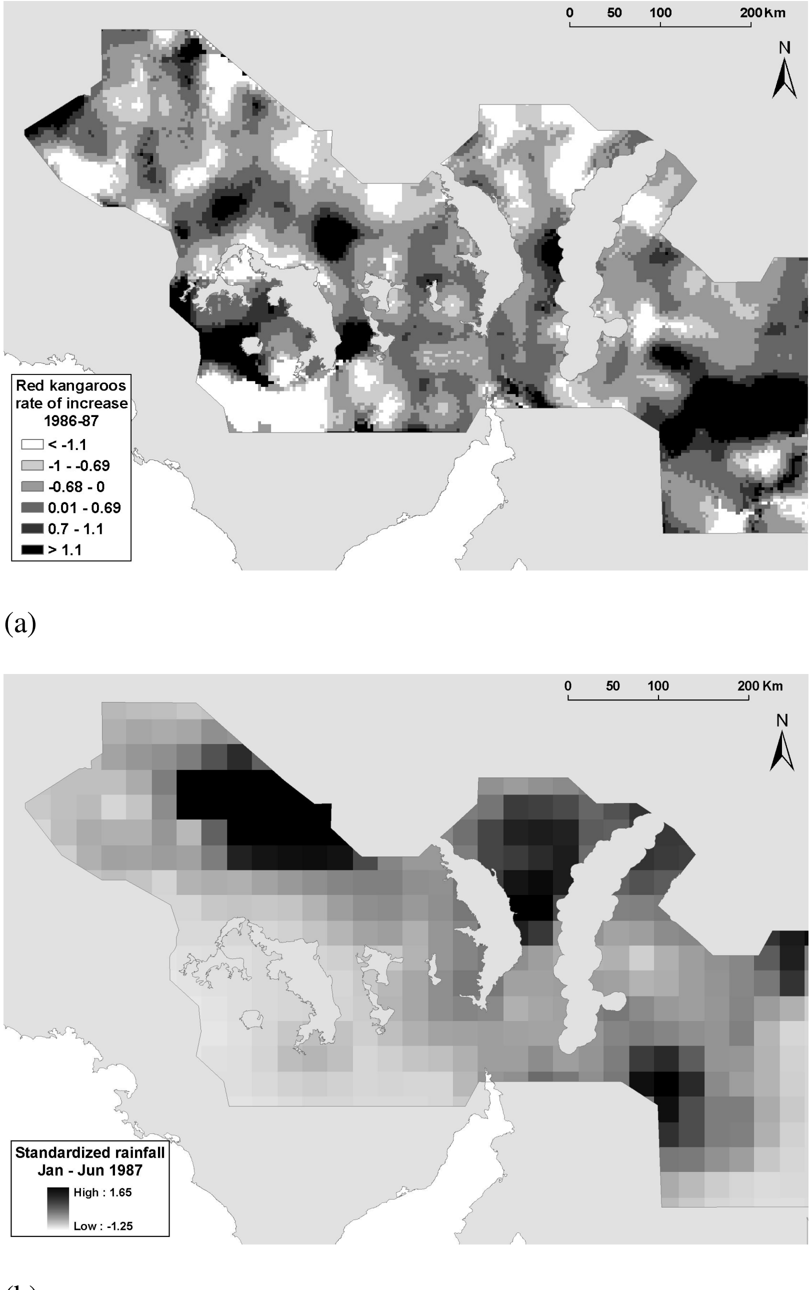

0 50 100 200 Km
N
Red kangaroos rate of increase 1986-87
< -1.1
-1 - -0.69
-0.68 - 0
0.01 - 0.69
0.7 - 1.1
> 1.1
(a)
0 50 100 200 Km
N
Standardized rainfall Jan - Jun 1987
High : 1.65
Low : -1.25
(b)

Figure 11.

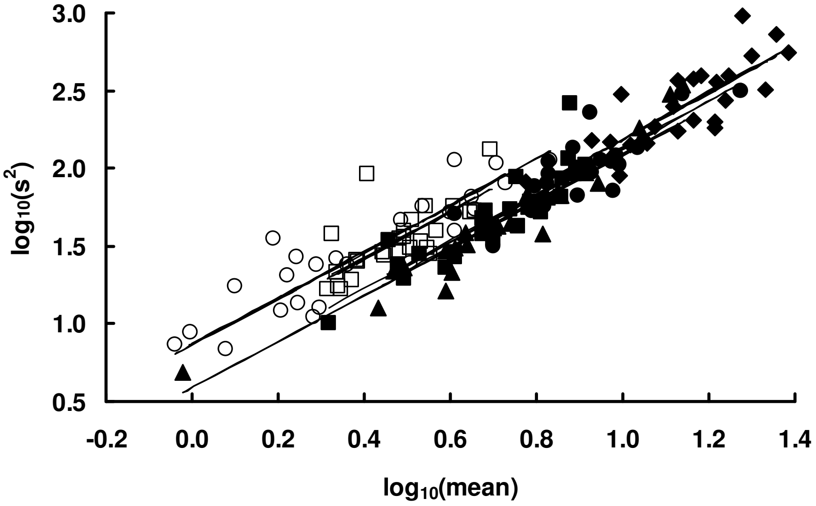


Figure 12.

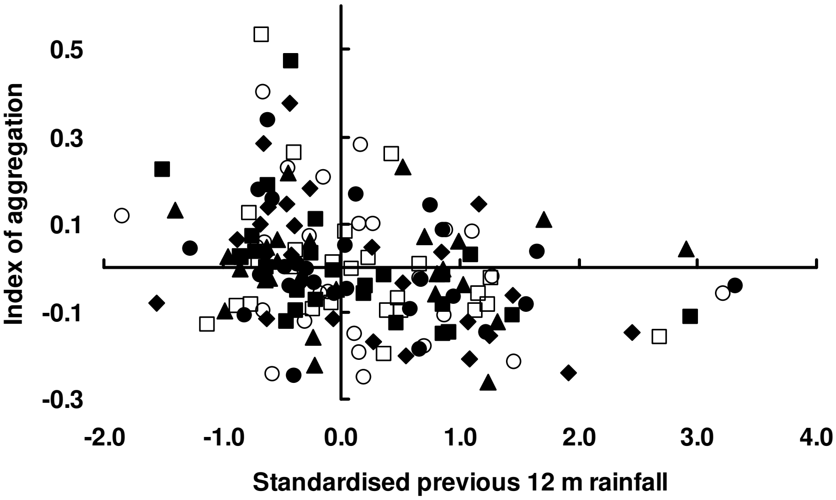


Figure 13.

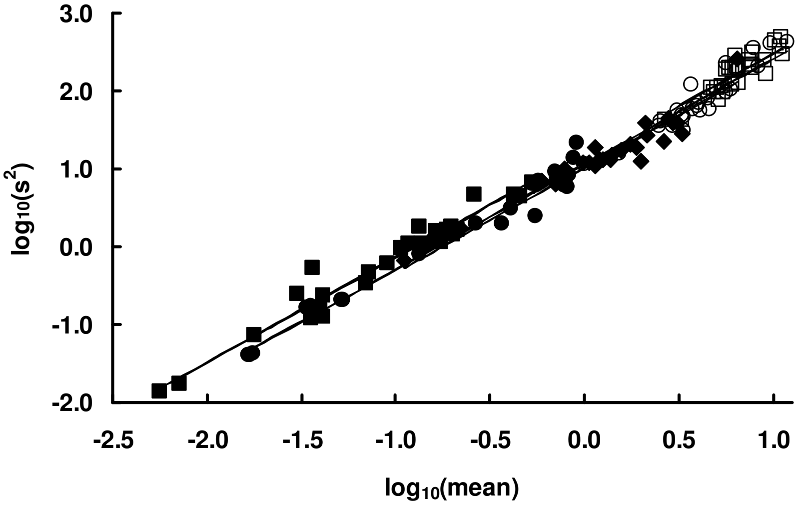
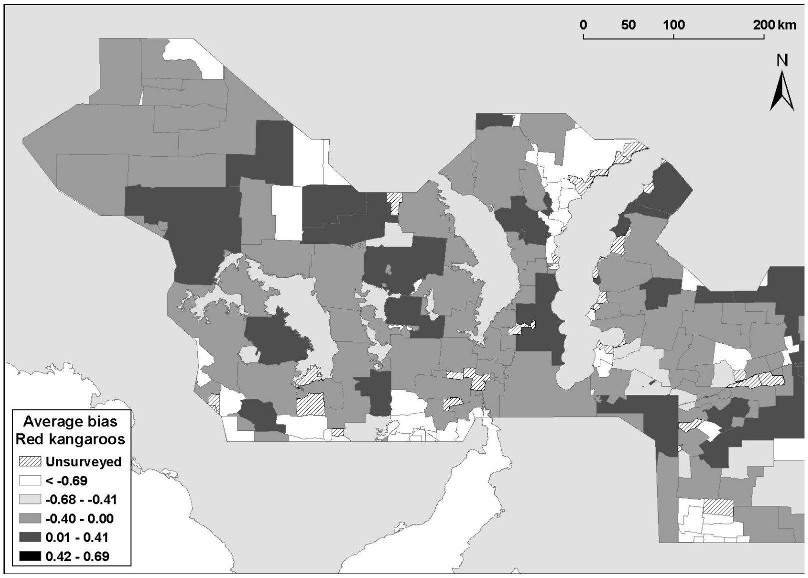
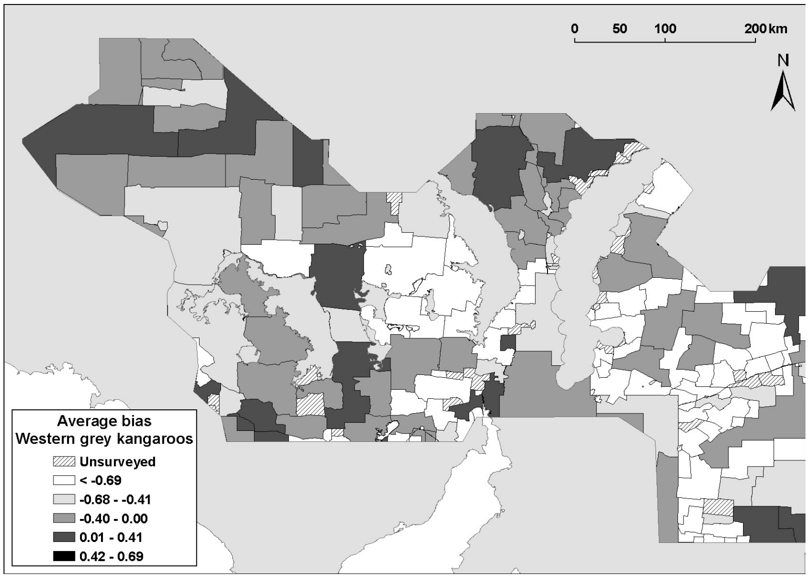


Figure 14.


0 50 100 200 km
N
Average bias
Red kangaroos
▨ Unsurveyed
< -0.69
-0.68 - -0.41
-0.40 - 0.00
0.01 - 0.41
0.42 - 0.69

(a)


0 50 100 200 km
N
Average bias
Western grey kangaroos
▨ Unsurveyed
< -0.69
-0.68 - -0.41
-0.40 - 0.00
0.01 - 0.41
0.42 - 0.69

(b)

Figure 15.

Section 12

Pople, AR, Phinn, S, Grigg, GC, Possingham, HP, Menke, N, McAlpine, CA, Farroway, L, Payne, N, Lundie-Jenkins, G, Southwell, CJ, and Grice, D (submitted). Shifts in the pattern of distribution of the three kangaroo species in eastern Australia over the past 20 years towards the edge of their ranges. *Ecography*.

Shifts in the pattern of distribution of the three kangaroo species in eastern Australia over the past 20 years towards the edges of their ranges.

Anthony R. Pople, Stuart Phinn, Gordon C. Grigg, Norbert Menke, Clive McAlpine, Lisa Farroway, Nicole Payne, Geoff Lundie-Jenkins, Colin Southwell, David Grice and Hugh P. Possingham

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Abstract

Over the past 30 years, the eastern Australian populations of three species of kangaroos have been surveyed regularly from the air, enabling us to assess changes in the patterns of their distribution in an area greater than 1.2 million km^2. The changes were recorded as geographic variations in the rates of increase and include areas of local colonisation and extinction. Rates of increase were modelled as functions of latitude, longitude, standardised rainfall and, in some cases, land clearing, using regression analysis. The densities of all three species have undergone marked fluctuations over this time, punctuated by steep declines during major droughts in each of the last three decades. Eastern grey kangaroos have expanded their range westwards into more arid areas and their pattern of distribution behind this expanding front has also shifted westwards. Red kangaroos have expanded eastwards into more mesic areas in association with land clearing. In South Australia, western grey kangaroos have shifted their pattern of distribution northwards into more arid areas, perhaps being advantaged by the provision of artificial watering points. These changes in the geographic pattern of distribution were not uniform over time, with spatial variation in exponential rates of increase during drought being particularly pronounced. Rainfall could only partially explain these shifts in the pattern of distribution and then only in a small number of cases. Surprisingly, for all species, rates of increase during drought were either higher away from the range core (= areas of relatively high abundance) or unrelated to the range core. These patterns were often seen during periods of overall population increase as well. This study highlights the importance of having a long time series in assessing geographic patterns of distribution and cautions against using proximity to range core as an indicator of population resilience.

Introduction

The ability to monitor changes in wildlife distribution is needed to address questions about impacts of climate change and changes in land use. In Australia's rangelands, broad-scale monitoring of wildlife distribution is of particular interest as part of a recognised need for monitoring rangeland biodiversity (Smyth et al. 2004). Some of this occurs, almost inadvertently, as part of the management of several pest and commercially-harvested species. When the monitoring is extensive and long-term, these species may also be useful surrogates for other elements of biodiversity and as indicators of environmental change (Woinarski et al. 2000). This paper describes changes in the pattern of distribution of the three kangaroo species across the rangelands of eastern Australia over the past two decades by examining changes relative to the core of their respective ranges, changes relative to temporal fluctuations in overall population size and suggesting possible causes for these changes.

Two aspects of a species' distribution need to be distinguished, the range boundary and the distribution of density within that range. It is often considered that species tend to reach their highest densities towards the centre of their ranges and density declines towards the edge of the range as one or more environmental factors become less favourable (Brown 1984, Hengeveld and Haeck 1982, Brown et al. 1996, but see Sagarin and Gaines 2002). The actual geographic position of the abundance peak and the pattern of decline in density to the range edge will depend, almost by definition, on the factors limiting population size (Caughley et al. 1988, Krebs 2001). From this follows the prediction that, as environmental conditions deteriorate across the range, populations will decline at greater rates at the periphery than in the area of peak abundance. There is some empirical support for this prediction (Wilcove and Terborgh 1984, Mehlman 1997). However, there are contrary data and in fact numerous possible geographic patterns of rates of increase, including greater declines at the range core and declines distributed randomly through the range (Villard and Maurer 1996). Similarly, under improved environmental conditions, there are numerous scenarios of the geographic pattern of rates of increase. The actual pattern in these rates of increase will again depend on the spatial and temporal variation in the factors that limit populations (Sinclair 1989). What is of interest is how position within the range influences a population's response to variation in these limiting factors. For instance, the idea that populations are more resilient at the range core has raised further concern for many populations of endangered species that persist in low and variable densities at the edge of their former ranges (Channell and Lomolino 2000).

The geographic variation in the density of a species, its pattern of distribution, is therefore unlikely to be static. Changes in the pattern of distribution may be relatively permanent or temporary. A distributional change in a species may be an ongoing trend, triggered by events prior to a period of monitoring. Alternatively, it may be caused by events during a period of monitoring, increasing the chance that the causal agent can be identified. Spatial variation in weather, at least in arid environments, is likely to induce relatively short-term change in a species' distribution pattern, whereas longer-term changes are likely to result from the introduction or removal of other, interacting species. Data spanning a time period that is long relative to generation time and climatic cycles can therefore not only detect a long-term trend, but also help reveal a cause and timing.

Species' ranges are also not static (Brown et al. 1996). As a species' range expands, the density behind the expanding front is also likely to change. One simple model is logistic growth of the species in the new environment of the expanded range (Skellam 1951), which Caughley (1976) described for an invading herbivore. The factors that allowed a range expansion may also be operating within the original range, resulting in an increase in density. Overall, these responses will lead to a shift in the pattern of distribution of the species. There may also be a considerable lag between the original range expansion and the shift in distribution pattern behind the range boundary.

There is general agreement among Australian ecologists that the three species of kangaroos in Australia, the red kangaroo (*Macropus rufus*), eastern grey kangaroo (*M. giganteus*) and western grey kangaroo (*M. fuliginosus*), have increased in abundance in the semi-arid sheep rangelands since European settlement (Calaby and Grigg 1989, Pople and Grigg 1998). Land clearing (i.e. removal of woodland and forest), facilitative grazing by domestic stock, dingo control and provision of artificial water points have been offered as causal factors (Newsome 1975, Caughley et al. 1980, Hill 1981, Oliver 1986, Pople et al. 2000). The extent of this increase is hard to quantify because of the difficulty in assessing past densities from historical records. Changes in the range boundaries of these species are easier to assess, although it has been complicated by the difficulty in distinguishing the two grey kangaroo species within a large zone of overlap, predominantly in New South Wales. For eastern grey kangaroos, Caughley et al. (1984) reported a westward extension of its range into more arid areas since the early 1900s. In southern Queensland and northern New South Wales, they quantified this expansion at a rate of 4-5 km per year. An increase in the density of artificial watering points was suggested as a primary cause (Caughley et al. 1984), with both grey kangaroo species having higher water requirements than red kangaroos (Dawson 1995, Blaney et al. 2000). A change in arid-zone food supply has also been offered as a possible explanation (Dawson et al. 2004). Despite being similarly advantaged, there has been no strong evidence for changes in the range boundary of western grey kangaroos with the exception of some contractions in southern parts of the range due to land clearing for agriculture (Caughley et al. 1984, Barker and Caughley 1992). Similarly, the range of the red kangaroo is considered unchanged.

Since the late 1970s, and since most of the observations were made which generated these conclusions, there have been regular aerial surveys of the abundance of these three kangaroo species as part of their harvest management. This allows their pattern of distribution to be assessed over a period of >20 years. In most cases, these surveys occur within species' range boundaries, so the analysis concentrates on changes in the geographic variation in density. However, for all three species, these surveys map part of the limit of distribution, allowing changes in the range boundary to be examined. Rainfall and, in Queensland, land clearing were considered as possible explanatory variables for any distributional change.

Methods

Kangaroo surveys

The study area spans three states across a region where sheep grazing has been the predominant land use (Fig. 1). The relatively flat terrain and open vegetation makes the area suitable for aerial survey of large wildlife such as kangaroos. The vast size of the study area (>1.2 million km^2) makes aerial survey the only feasible monitoring method. Transects were flown at a ground speed of 185 km h^{-1} by a high-wing aircraft (Cessna) at 76 m above ground. An observer on either side of the aircraft counted kangaroos in 200 m wide strips along 5 km segments (i.e. 1 km^2), each separated by a seven second break (i.e. 0.2 km) in counting. Since 2001 in both New South Wales and Queensland, counts have been made in 100 m wide strips.

In South Australia, aerial surveys have been flown annually since 1978 along east-west transect lines that are 28 km apart (Caughley and Grigg 1981, Grigg et al. 1999). In New South Wales and Queensland, the survey transects are ~50 km apart (Caughley et al. 1977, Caughley and Grigg 1982). Surveys were flown across all of the western plains of New South Wales in 1975, 1976 and then annually from 1983 to 2003. Surveys were conducted in monitor blocks, representing a subset of the western plains, between 1977 and 1982 (Caughley et al. 1977, J. Caughley et al. 1984). Kangaroo densities for New South Wales from 1984 are presented in this study, although densities prior to 1993 were only available collated in one-degree blocks because of a fire that destroyed the raw data. In Queensland, surveys were flown in 1980, then annually from 1984 to 1992, then again in 2001. In 1991, the southern third of the Queensland study area was not flown. Density was therefore interpolated for this area using the 1990 and 1992 surveys. Since 1991, kangaroo managers in Queensland have used helicopters to survey kangaroo populations in non-contiguous monitor blocks and so these data were not used in these analyses (Lundie-Jenkins et al. 1999).

In South Australia, counts of red kangaroos were adjusted for visibility bias by a factor of 2.29 in open vegetation cover, 2.36 in light cover and 2.42 in medium cover (Caughley et al. 1976). Counts of western grey kangaroos were multiplied by 4.8 to account for visibility bias (Grigg and Pople 1999). Counts in 200 m strips were also adjusted if air temperatures (T) exceeded 15^o C at survey height by multiplying by $1/(1.474-0.0316 \times T)$ (Caughley 1989). Counts in Queensland were similarly adjusted, although a correction factor of 2.57 was used for red kangaroos in heavy cover. Correction factors had long been recognised as leading to underestimates of true density in many areas, but it was not until the use of helicopter surveys and line transect sampling (Clancy et al. 1987) that widely applicable revisions were possible (Pople 2004). In New South Wales, biogeographic correction factors were determined by Cairns and Gilroy (2001), ranging 2.21-6.05 for red kangaroos and 3.04-13.37 for the two species of grey kangaroos that are not readily distinguishable from the air. These revised correction factors were applied to counts in segments from 1993 to 2003. Average correction factors for densities of each species in each one-degree block were then applied to data for 1984 to 1992. In Queensland, similar correction factors have been identified (Pople et al. 1998, Pople 1999). Concurrent helicopter and fixed-wing surveys in Queensland in 1992, suggested the latter counts needed to be further adjusted by 1.4 for red kangaroos and 1.14 for grey kangaroos.

These adjustments were applied to counts over 1980-1992. The assessment of the accuracy of fixed-wing surveys in New South Wales and Queensland (Cairns and Gilroy 2001) suggested counts in 100 m strips were more repeatable, so these were adopted in 2001. Biogeographic correction factors were applied to 100 m counts in New South Wales, ranging 1.67-2.97 for red kangaroos and 2.98-5.55 for grey kangaroos, and applied to 100 m counts in Queensland, ranging 1.92-2.16 for red kangaroos and 2.98-3.79 for grey kangaroos. South Australian densities also needed adjustment to make them comparable to the other states. Comparing averages of the old and new correction factors from New South Wales suggested multiplying the South Australian densities of red kangaroos by 1.58 and grey kangaroos by 1.27 would be appropriate, albeit rough.

To provide a context for an analysis of distribution patterns, population densities of all species in each state were determined for all available years. Helicopter survey estimates of kangaroo density in Queensland were compiled for 1993-2003. Monitor block densities in New South Wales in 1978-83 (J. Caughley et al. 1984) were extrapolated to the entire study area by the ratio of these densities to densities for the whole study area in 1975-6 (Caughley et al. 1977). Estimates were further adjusted to account for the revision of correction factors described above. Where raw data were available, standard errors of density estimates based on fixed-wing surveys were calculated using ratio estimation (Cochran 1977). Standard errors for the helicopter survey estimates were calculated by treating the monitor block estimates as stratified random samples.

Within a broad zone of overlap, ground surveys are required to separate counts of grey kangaroos into the two species. Vehicle surveys were conducted throughout the zone in 1982 (Caughley et al. 1984), in the overlap zone in New South Wales in 2000 (Cairns and Gilroy 2001) and in the zone in Queensland in 2003 (Graham 2003). In New South Wales, the 1982 ratios of the two species were used to separate counts over 1976-1992 and the 2000 ratios were used for subsequent counts. In the Queensland study area, where ≤ 2% of grey kangaroos are western greys (Graham 2003), the 1982 ratios were applied to the 1980-1992 counts and the 2003 ratios were applied to the 2001 survey counts.

Map production

Densities in aerial survey segments were available across all three states most recently in 2001. The earliest data available at this scale across all three states was for 1993 in New South Wales and South Australia and 1992 in Queensland. Each 5 km long aerial survey segment was first georeferenced to its midpoint. Universal, anisotropic kriging was then used to create interpolated density surfaces for the entire study area in 1992-3 and 2001 by estimating densities within 5 km × 5 km cells. Rather than calculate rates of increase from two interpolated density surfaces (Villard and Maurer 1996), annual exponential rates of increase (the differences between the logarithms of density+0.001) were calculated between 1992-3 and 2001 in half-degree blocks (~2,500 km^2), then interpolated. Kriging was implemented with the Geostatistical Analyst extension to ArcGIS (ESRI 2004), using a spherical correlation structure and a search neighbourhood of five survey segments for the density surface and two half-degree blocks for the rate of increase surface.

Analysis

Shifts in the pattern of distribution were assessed by comparing the average rates of increase of each species across their ranges within each state. Simple linear regressions were fitted for $\log_e$(density+0.001) against time in each half-degree block in Queensland and South Australia and each one degree block (~10,000 km^2) in New South Wales. While the slopes of these relationships provide in each block estimates of *r*, the average annual exponential rate of increase (Caughley and Sinclair 1994), they assume the only error is sampling error, but there is clearly considerable process error in these data as well (McCallum 2000). However, in this case, the focus is not an estimate of trend over time, but a comparison of trends across space. For this, comparisons of the slopes determined by simple linear regression were considered adequate. Rates of increase were calculated over the entire study period for each species in each state. Patterns of distribution were expected to show an expansion of areas of higher density during wet periods and overall population increase, while dry periods would show a contraction and overall population decrease. Therefore, the study period was also split into periods of decline or increase in kangaroo numbers throughout the entire study areas in each state to identify the timing of shifts in distribution patterns and possible causes. For these shorter time periods, rates of increase were again calculated using linear regression, although the difference between logged density estimates was used when there were only two years.

Rates of increase were then regressed against latitude, longitude and annual (financial year) rainfall standardised over time within each block, using the long-term (~100 year) mean and standard deviation, then averaged over relevant time periods plus the previous year. In each state and for all three species, rain that falls two years prior to the second of two winter aerial surveys correlates with kangaroo rate of increase between the surveys (Bayliss 1985, Cairns and Grigg 1993, McCarthy 1996, A. R. Pople et al. unpublished data). Monthly rainfall surfaces were interpolated using inverse distance weighting from Bureau of Meteorology data recorded at stations throughout the study areas. Regression models were simplified using backwards elimination (Crawley 2002) and included curvilinear terms for, and interactions between, latitude and longitude. Spatial autocorrelation was assessed using a semivariogram (Isaaks and Srivastava 1989) and, if present, the correlation structure was incorporated into the regression models using R version 1.9.1 (R Development Core Team 2003). The significance of the spatial correlation parameters was tested using a likelihood ratio (Crawley 2002).

Shifts in the pattern of distribution were expected along a gradient of increasing aridity, being a longitudinal gradient in Queensland and New South Wales and a latitudinal gradient in South Australia. For each time period, predicted (using models excluding rainfall and land clearing) rates of increase were plotted against longitude or latitude. Comparisons of the relationship between rates of increase and longitude and latitude (plus interaction and curvilinear terms) among time periods were made using an analysis of covariance. This method essentially compares a regression model common to all time periods with separate relationships for each period. For these analyses, rates of increase were standardised within time periods to eliminate obvious differences in average rates of increase over time. For each species in each state, the peak in density along each gradient was determined from plots of density, standardised over the study area, and averaged over the study period.

In Queensland, land clearing was also included as a potential explanatory variable for the latter half of the time series. The percentage of the landscape within 10 km of the transect line that was 'open' (woody foliage projective cover < 12%) within each half-degree block was calculated from the Statewide Landcover and Trees Study (SLATS) (Department of Natural Resources and Mines 2003) using FRAGSTATS (McGarigal and Marks 1994) and arcsine transformed to improve normality. The change in woody cover was determined as the difference between 1991 and 1999 values expressed as a percentage of the 1991 value, and transformed to $\log(x+10)$ to improve normality.

Results

Distribution and abundance of kangaroos in eastern Australia

Numbers of kangaroos in the sheep rangelands of eastern Australia have fluctuated from an estimated low of 14.5 million in 1984 to a high of almost 32 million in 2002 (Fig.2). These numbers are important to management, as annual harvest quotas have been set as a proportion of population size. The time series contains major droughts in 1981-83, 1991-3 and 2001-03. There were other periods of drought during the study period, but these three droughts were particularly widespread and extended over >20 months. Droughts brought about dramatic declines in the populations of all three species (e.g. Caughley et al. 1985). Also notable are extended periods of general decline and increase in the time series for each species and these are explored in the analyses below.

The overall patterns of densities for each of the three species in 2001 (Fig. 3) are similar to those described by Caughley (1987) for the 1980-82 surveys. There is a notable peak in density synonymous with the range core for each species, although there are subsidiary peaks and more modes would have been present with less smoothing. Figure 4 identifies notable shifts in the patterns over the past decade. This was a period of general increase for all three species in eastern Australia (Fig. 2). Red kangaroo rate of increase tended to be higher in the east of their range and in the northern half of the Queensland study area, while eastern grey kangaroo densities tended to increase most at the western edge of their range. Western greys tended to have higher rates of increase at the north-western and south-eastern periphery of their range in New South Wales and in the north of their range in South Australia. These results include zeros (+0.001) in half-degree blocks in either 1992-3 or 2001, resulting respectively in local 'colonisation' or 'extinction' in the block, producing extreme rates of increase (i.e. $r < -0.29$ or $r > 0.29$). Nevertheless, this is consistent with a shift in the pattern of distribution and many nearby blocks with non-zero density in both years also had relatively high rates of increase, supportive of an overall trend. It also has the advantage of distinguishing large and small increases from or decreases to zero; information that is lost when treating the data as simply presence or absence. These changes in the pattern of distribution are examined over a longer time period and in more temporal detail along latitudinal and longitudinal gradients within each state in the regression analyses described below.

Queensland

Annual rainfall over 1978-2000 was slightly above average (0.05 SD units) and variable (coefficient of variation (CV) = 0.34). Between 1991 and 1999, most land clearing occurred in the southeast of the study area between146.5^o and 149.5^{o}E, with more isolated declines in woody cover further north, but again at the eastern edge of the study area (Department of Natural Resources and Mines 2003). Within this band, the percentage increase in open areas averaged 18.7 ± 3.4 %. To the east of this band, clearing averaged 3.3 ± 0.7 %. To the west, clearing averaged 2.2 ± 0.6 %.

Over the entire study period (1980-2001), red kangaroo rate of increase was related linearly and positively to longitude (Table 1), being higher in the east of the study area (Fig. 5a). This pattern was seen during a period of decline and a period of increase. The study period was subdivided into four periods of increase or decrease and an analysis of covariance indicated that the geographic pattern in rate of increase differed amongst the four periods (four relationships *vs* one relationship: $F_{18,680} = 4.34$, $p<0.001$). Combining periods of increase (1984-90 and 1991-2001) and decrease (1980-84 and 1990-91) was also not preferred over separate relationships for each period (four relationships *vs* two relationships: $F_{12,680} = 3.86$, $p<0.001$). Nevertheless, the pattern in the periods covering drought was strikingly different to periods of overall population increase (Fig. 5a), with relatively steep declines in the west, although the absolute size of these declines was partly a result of extinctions in some cells as discussed above. Notably, rainfall was not included in the regression models for any period. For 1991-2001, rate of increase in red kangaroos was positively related to land clearing (Table 1).

Eastern grey kangaroos showed a contrasting geographic pattern to red kangaroos (Fig. 5b), with a negative relationship between rate of increase and longitude over the study period (Table 1). This shift became apparent only after 1986 and was recorded during periods of overall population increase and decline. Neither rainfall nor land clearing was a significant predictor. The geographic pattern in rate of increase differed among the four periods identified for this species ($F_{18,692} = 4.40$, $p<0.001$) and could not be simplified by combining periods of increase and periods of decrease ($F_{12,692} = 5.07$, $p<0.001$). There were also latitudinal shifts over 1980-2001, with declines restricted to the northern and southern regions of the study area; the pattern similar to that for the last decade (Fig. 4b).

New South Wales

Annual rainfall over 1983-2002 was above average (0.13 SD units) and highly variable (CV = 0.40). Red kangaroos also showed a relative increase in the northeast of the study area over 1984-2003 (Table 2, Fig. 6a) and this occurred mainly during a period of increase over 1996-98. The geographic pattern in rate of increase differed among four time periods ($F_{18,160} = 2.18$, $p<0.01$). Combining periods of increase and periods of decrease was not a warranted simplification ($F_{12,160} = 3.06$, $p<0.001$). Again, rainfall was not a significant predictor in the regression models for any period.

Eastern grey kangaroos shifted their pattern of distribution to the west over the study period, consistent with the Queensland data (Fig. 6b). This change was largely manifest during the decline in density over 1993-96. Rainfall influenced this change, but did not account for the longitudinal shift (Table 2). The geographic pattern in rate of increase differed among four time periods ($F_{18,160} = 14.40$, $p<0.001$) and could not be simplified by combining periods of increase and periods of decrease ($F_{12,160} = 10.65$, $p<0.001$).

Western grey kangaroos did not show a shift in their pattern of distribution over 1984-2003 (Table 2, Fig. 6c), although the pattern differed among the three time periods ($F_{12,99} = 7.00$, $p<0.001$). In particular, the 2002-03 drought saw a shift in the pattern of relative density towards the west (Fig 6c), but this was influenced by rainfall that was furthest below average in the east (Table 2).

South Australia

Annual rainfall over 1977-2002 was slightly above average (0.08 SD units) and again highly variable (CV = 0.43). There were only slight changes in the pattern of distribution of red kangaroos along a latitudinal gradient over the entire study period, although there were no increases at the northern and southern extremities (Table 3, Fig. 7a). However, there was a shift westwards. Again, the geographic pattern in rate of increase differed among four time periods ($F_{18,338} = 4.24$, $p<0.001$) and could not be simplified by combining periods of increase and periods of decrease ($F_{12,338} = 5.45$, $p<0.001$). The first twelve years saw a shift in the distribution pattern to the south, but this was reversed in the following 13 years (Fig. 7a). Rainfall was not incorporated in any models for red kangaroos.

Western grey kangaroos showed highest rates of increase in the northeast of their range over the 25-year study period (Table 3, Fig. 7b), tending to decline in the southeast. This shift in the pattern of distribution occurred during the population decline in the drought of the early 1980s (Fig. 7b), which was particularly pronounced in the southeast. Once more, the geographic pattern in rate of increase differed among four time periods ($F_{24,345} = 3.45$, $p<0.001$) and could not be simplified by combining periods of increase and periods of decrease ($F_{18,345} = 2.43$, $p<0.01$). Rainfall was related to the change in distribution pattern during the population decline over 1995-2003 (Table 3), but the effect was negative, counter to what was expected.

For all states, semivariograms showed no strong evidence of spatial autocorrelation at the scale examined here. Likelihood ratio tests gave little support for the inclusion of spatial correlation parameters in the regression models.

Discussion

Over the past 20 years, the eastern Australian kangaroo population has undergone marked population fluctuations (Fig. 2) that have been associated with changes in the pattern of distribution (Figs 4-7). These changes were not uniform over time, and were often but not always triggered by drought, which is the major perturbation for these populations. Against predictions, declines during drought were either less severe away from the range core or unrelated to the range core. This result was seen across species, states and droughts.

The most likely explanation for the apparent greater resilience away from the range core is that rates of increase were simply a function of the severity of drought.

Standardised rainfall entered into only a few of the regression models, but it may have been too crude a measure of spatial variability in food supply. The fact that these species showed contrasting patterns suggests rainfall will not provide a simple explanation for the change in distribution patterns. For red kangaroos, a possible alternative explanation is that declines were most pronounced in the more arid parts of the study area and that absolute rather than relative rainfall is the determining factor. However, this does not apply to the two grey kangaroo species. Assessment of the spatial variation in the numerical response of these species to rainfall (e.g. Cairns and Grigg 1993), or some other surrogate for food supply, should shed light on this.

Eastern grey kangaroos appear to have continued the westward extension of their range, particularly in Queensland. There is a concomitant shift in the pattern of distribution behind this expanding front as well. The shift is not solely along a longitudinal gradient, with a movement in density towards the mid-latitudes of the study area. However, this would match a gradient of aridity that is directed roughly towards the centre of the continent. Land clearing in Queensland does not appear to have altered the pattern of distribution of eastern grey kangaroos, despite their recorded variation in density along a gradient from open to forested areas and a preference for partially cleared areas (Hill 1981, McAlpine et al. 1999). The analysis here may have been on too coarse a spatial resolution and too large a geographic area to detect changes in eastern grey kangaroo density in response to clearing.

The data suggest red kangaroos and western grey kangaroos have also expanded their ranges over the study period, but in different directions. Red kangaroos have become more common in the east of their range and this is associated with land clearing, at least in Queensland. A more sparsely forested landscape is in line with their habitat preferences (Pople 1989). Western grey kangaroos have become more common in the northern parts of their range in South Australia. This parallels the range expansion shown by eastern grey kangaroos into more arid areas, and would be explained by both species being advantaged by the provision of artificial watering points.

The shifts observed for western grey kangaroos over 1992-2001 (Fig. 4c), are partly the result of changes in the ratio of the two species grey kangaroos recorded in ground surveys by Caughley et al. (1984) and Cairns and Gilroy (2001). This study extends the analysis of the latter by calculating densities, enabling a shift in density rather than ratio of the two species to be determined.

Given that these three species have expanded their ranges, it is difficult to generalise the results to wildlife species whose abundance and distribution have not changed or are in decline. Nevertheless, this study highlights how the observed changes in distribution pattern will vary depending on the length of the time series as well as how distribution patterns will obviously wax and wane within a time series. It also cautions against using geographic position within a range (e.g. edge *vs* core) solely as an indicator of resilience. The spatial pattern of environmental fluctuation and habitat change must also be considered.

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Table 1. Regression coefficients and adjusted R^2 for the most parsimonious models predicting annual rates of increase of kangaroos in half-degree blocks in the Queensland study area over various periods between 1980 and 2001. %Δopen, percentage change in the percentage of the landscape that is open.

Period	Latitude	Longitude	Lat×Long	Latitude^2	Longitude^2	[1]%Δopen	Adj. R^2
(a) Red kangaroos							
1980-2001		0.03					0.21
1980-1984	-31.11	68.82	0.21		-0.25		0.08
1984-1990	0.05						0.11
1990-1991	10.12	2.82	-0.09	0.07			0.13
1991-2001	0.67	-4.85		-0.01	0.02	0.15	0.16
(b) Eastern grey kangaroos							
1980-2001	-0.53	-0.21	-0.01	-0.01			0.27
1980-1984	-0.28						0.04
1984-1986	Intercept only						-
1986-1991	0.12	-7.18			0.02		0.16
1991-2001	0.78	-0.07		-0.01			0.23

[1] Examined only for 1991-2001

Table 2. Regression coefficients and adjusted R^2 for the most parsimonious models predicting annual rates of increase of kangaroos in one-degree blocks in the New South Wales study area over various periods between 1984 and 2003. zRain, standardised financial year rainfall.

Period	Latitude	Longitude	Lat×Long	Latitude^2	Longitude^2	zRain	Adj. R^2
(a) Red kangaroos							
1984-2003		-1.13			0.004		0.44
1984-1991	-1.18			0.02			0.19
1991-1996	Intercept only						-
1996-1998	-0.11	0.12					0.23
1998-2003	Intercept only						-
(b) Eastern grey kangaroos							
1984-2003	0.03	-2.59			0.01	0.52	0.27
1984-1991		2.49			-0.01		0.07
1993-1996	-3.41	-0.81	-0.02				0.40
1996-2002		0.04					0.43
2002-2003		-21.95			0.08		0.24
(b) Western grey kangaroos							
1984-2003	Intercept only						-
1984-1991	1.49	3.79		-0.02	-0.01		0.30
1993-2002	-1.90	-0.39	-0.01				0.39
2002-2003	0.21					2.48	0.17

Table 3. Regression coefficients and adjusted R^2 for the most parsimonious models predicting annual rates of increase of kangaroos in half-degree blocks in the South Australian study area over various periods between 1978 and 2003. zRain, standardised financial year rainfall.

Period	Latitude	Longitude	Lat×Long	Latitude^2	Longitude^2	zRain	Adj. R^2
(a) Red kangaroos							
1978-2003	0.62	-0.78	0.004		0.003		0.15
1978-1981	6.48	2.55	0.08	0.08			0.20
1981-1984	0.07						0.06
1984-1990	-2.32	-4.90		0.04	0.02		0.22
1990-2003	1.62	-0.01		-0.03			0.18
(b) Western grey kangaroos							
1978-2003	2.81	0.03		-0.04			0.36
1978-1980	Intercept only						-
1980-1981	Intercept only						-
1981-1984	-0.28	-0.21					0.27
1984-1995	3.39	0.07		-0.05			0.37
1995-2003	-3.71	9.09		0.06	-0.03	-0.47	0.19

Figure legends

Figure 1. The survey area within the sheep rangelands of eastern Australia. In New South Wales and South Australia, the survey area has been broken up into regions in which kangaroo harvests are managed. Biogeographic boundaries (Environment Australia 2000) adjusted to coincide with possible future administrative (shire) boundaries, are shown in the Queensland survey area. Transect lines flown in the 2001 aerial survey are shown as east-west lines.

Figure 2. Trends in the numbers (± s.e.) of kangaroos in the sheep rangelands of a) Queensland, b) and c) New South Wales and d) South Australia over 1975-2003. Solid lines connect solid symbols that are numbers estimated using fixed-wing surveys across the entire study area of a state. Dashed lines connect open symbols representing estimates from monitor blocks and were not used to assess changes in patterns of distribution here. The thin line connecting grey kangaroo population estimates in New South Wales for 1993-4 reflects a change in the ratio, based on ground surveys, used to separate aerial counts of the two species. ■, red kangaroos; ●, eastern grey kangaroos; ▲, western grey kangaroos.

Figure 3. Density (km^{-2}) of a) red kangaroos, b) eastern grey kangaroos and c) western grey kangaroos in 2001 within the sheep rangelands of eastern Australia. Densities in 5 km × 5 km cells were interpolated from densities in aerial survey segments (Fig. 1) using universal kriging.

Figure 4. Annual exponential rate of increase of a) red kangaroos, b) eastern grey kangaroos and c) western grey kangaroos over 1992-2001 within the sheep rangelands of eastern Australia. Rates of increase were first calculated in half-degree blocks (~50km × 50km) then interpolated using universal kriging. In South Australia, all grey kangaroos recorded during aerial survey were assumed to be western grey kangaroos.

Figure 5. Relationship between longitude and predicted annual exponential rates of increase of kangaroos for a) red kangaroos and b) eastern grey kangaroos, in the Queensland study area for periods of increase and decrease over 1980-2001. The longitude where density has consistently been highest is indicated with an arrow.

Figure 6. Relationship between longitude and predicted annual exponential rate of increase of a) red kangaroos, b) eastern grey kangaroos and c) western grey kangaroos, in the New South Wales study area for periods of increase and decrease over 1984-2003. The longitude where density has consistently been highest is indicated with an arrow.

Figure 7. Relationship between latitude and annual exponential rate of increase of a) red kangaroos and b) western grey kangaroos in the South Australian study area for periods of increase and decrease over 1978-2003. The latitude where density has consistently been highest is indicated with an arrow.

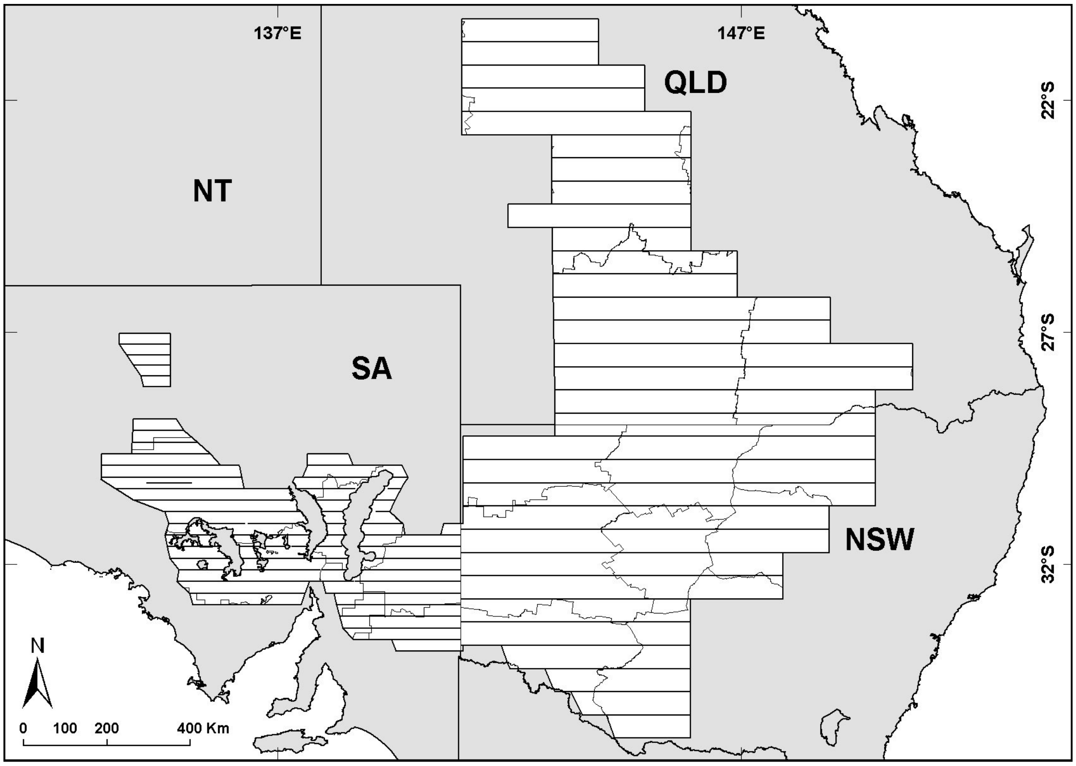


Figure 1.

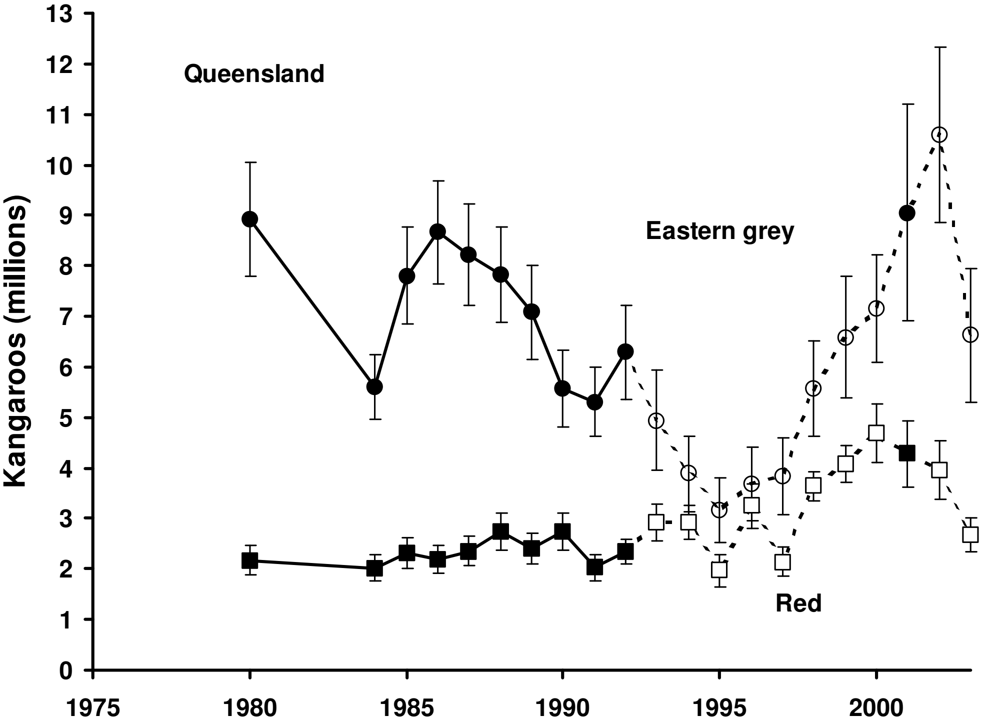
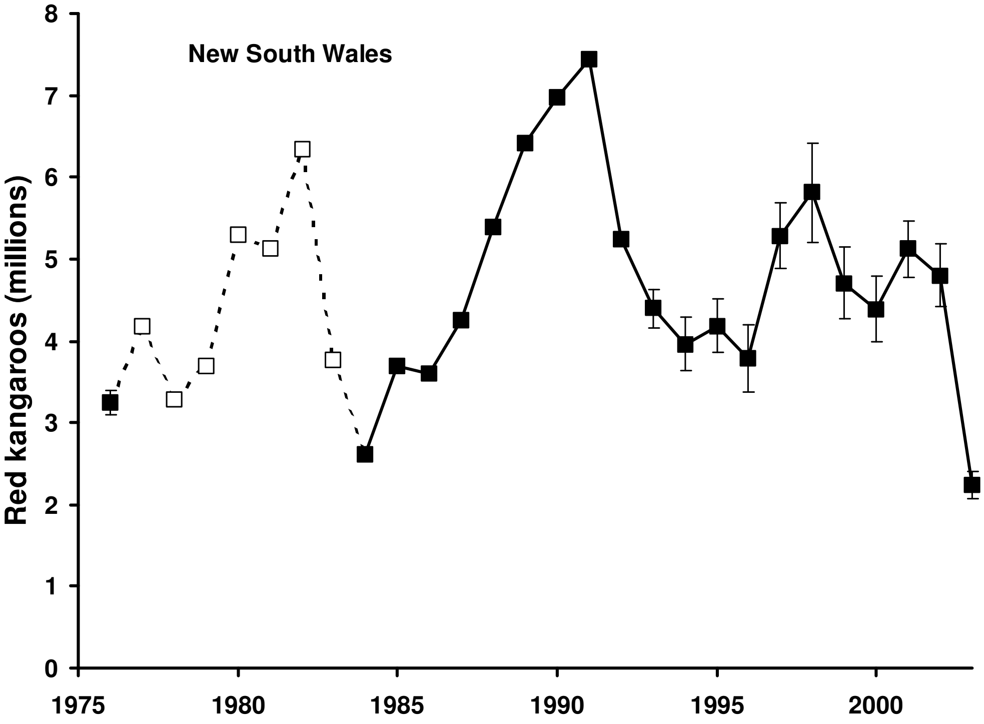


Figure 2 (a)



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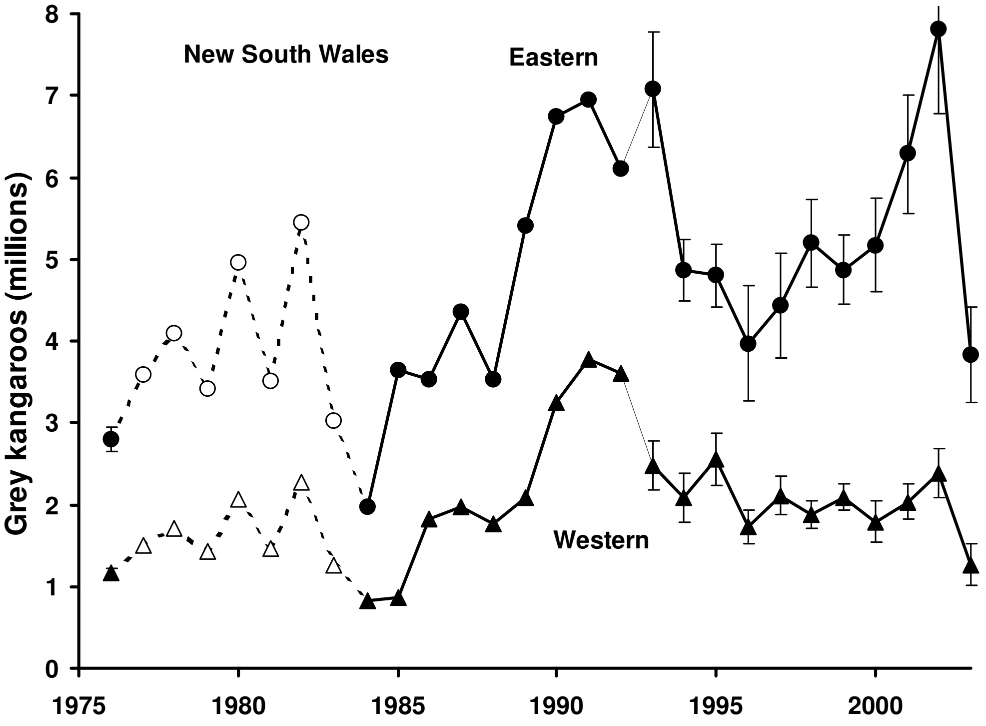

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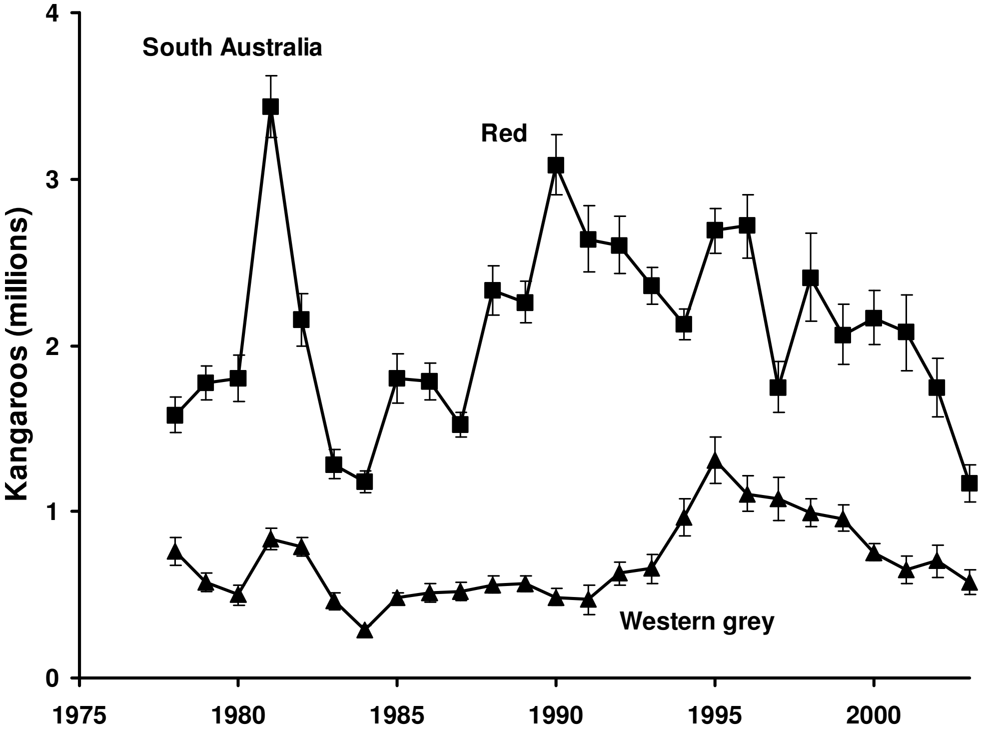

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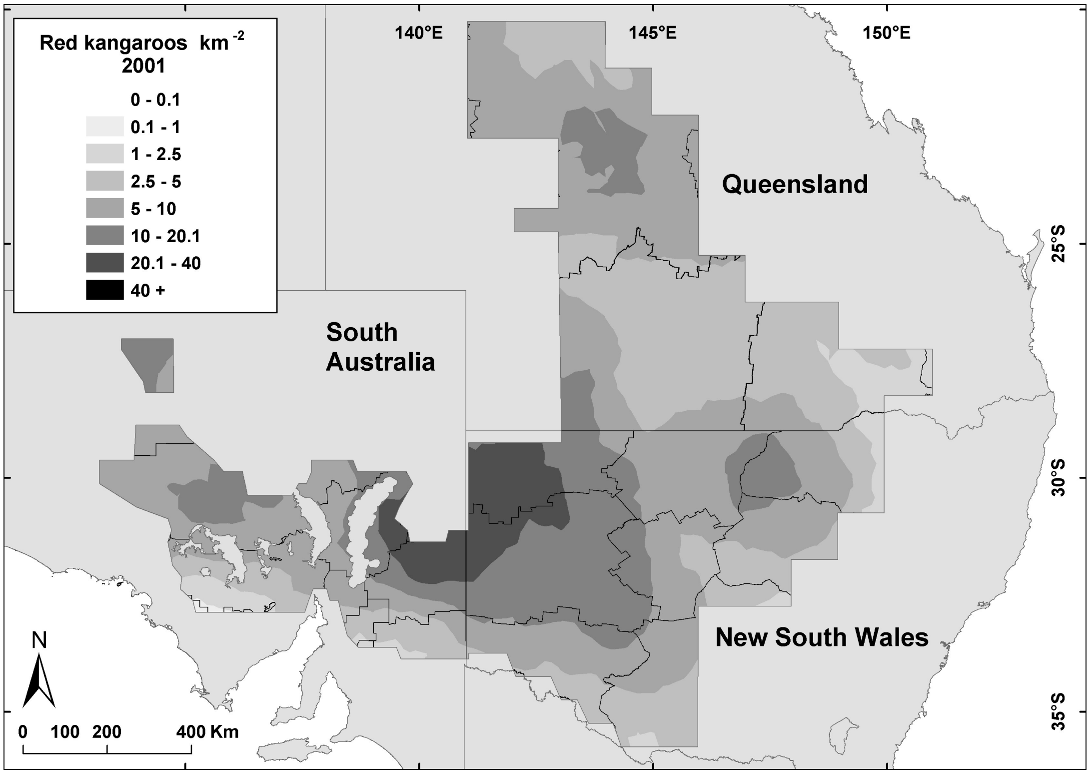


Figure 3 (a)

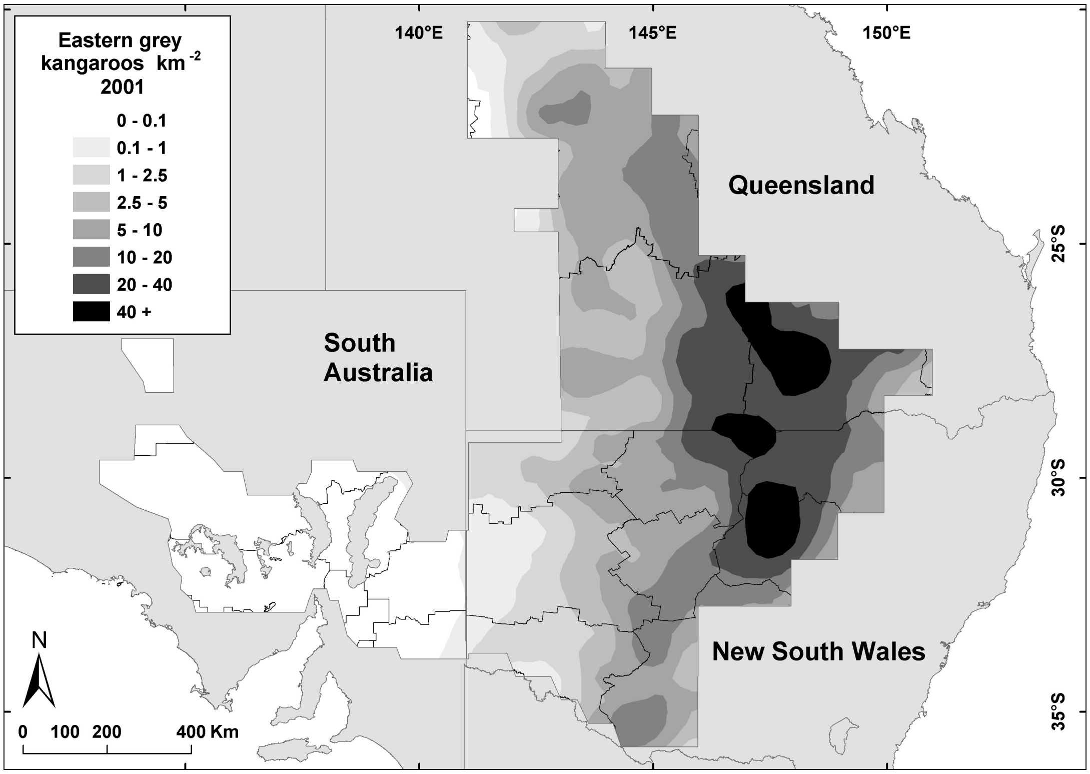


Figure 3 (b)

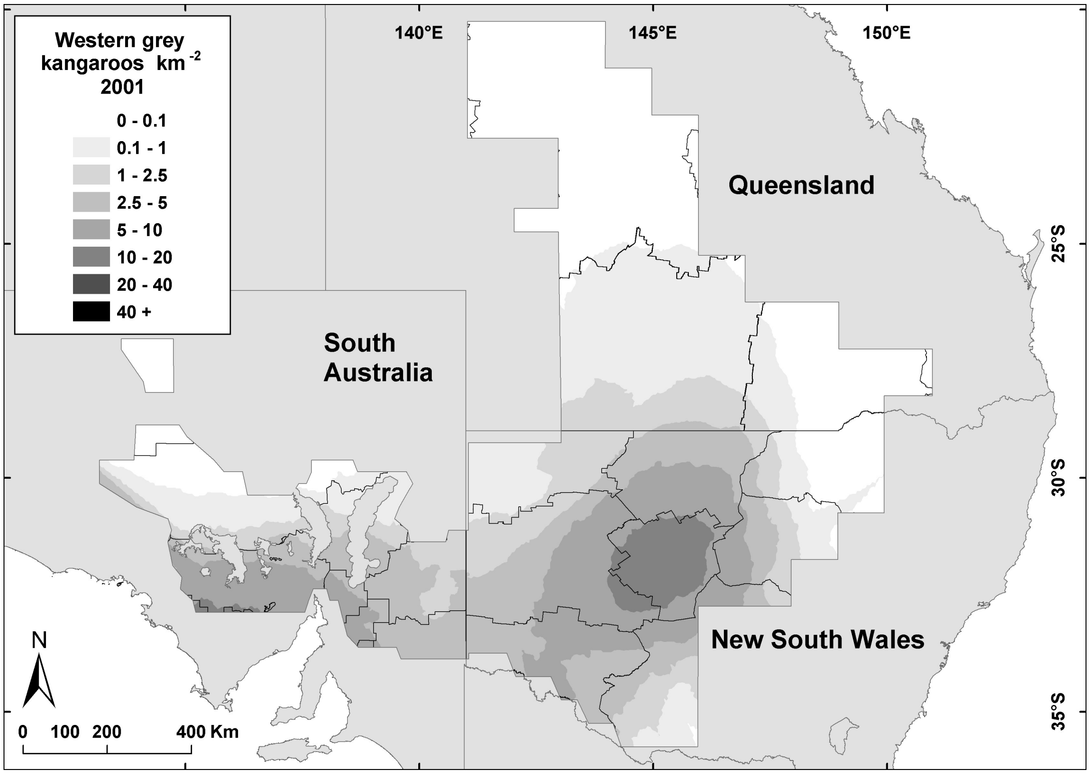

Western grey kangaroos km $^{-2}$ 2001
0 - 0.1
0.1 - 1
1 - 2.5
2.5 - 5
5 - 10
10 - 20
20 - 40
40 +
140°E
145°E
150°E
25°S
30°S
35°S
Queensland
South Australia
New South Wales
N
0 100 200 400 Km

Figure 3 (c)

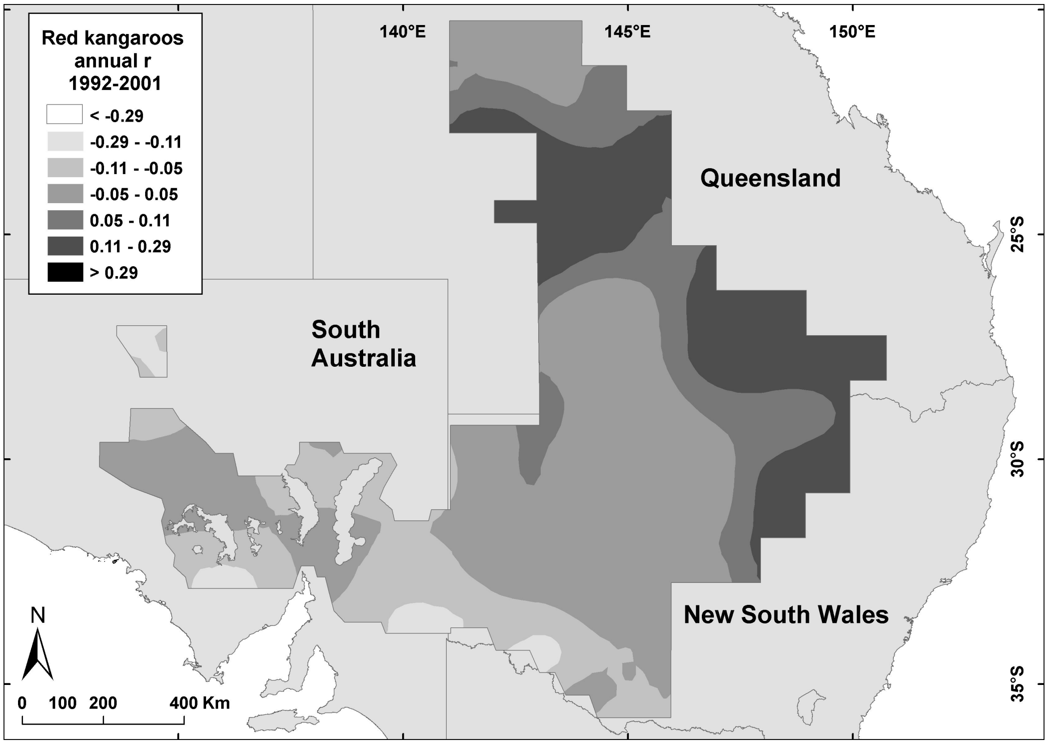


Figure 4 (a)

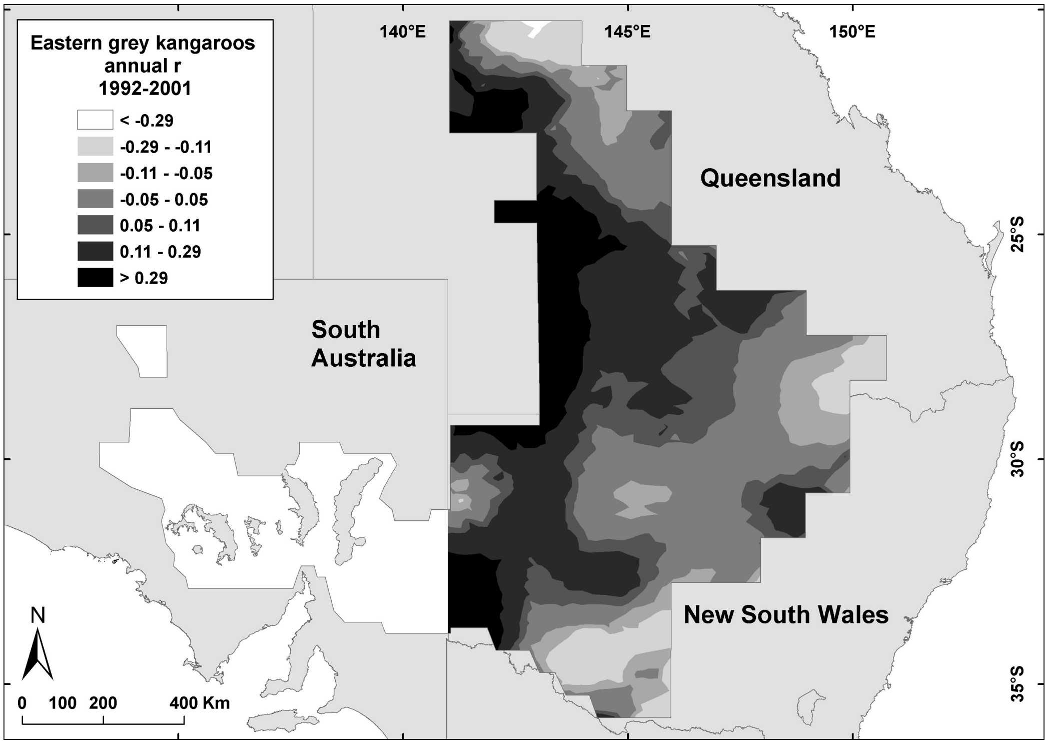


Figure 4 (b)

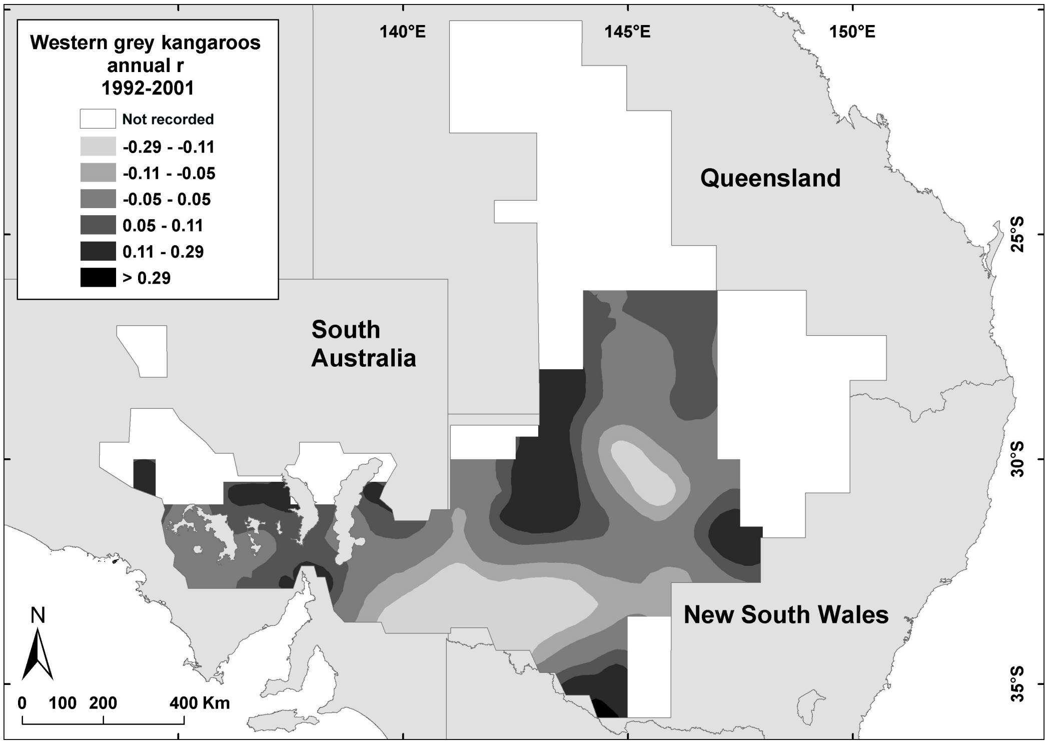

Western grey kangaroos
annual r
1992-2001
Not recorded
-0.29 - -0.11
-0.11 - -0.05
-0.05 - 0.05
0.05 - 0.11
0.11 - 0.29
> 0.29
140°E
145°E
150°E
Queensland
South
Australia
New South Wales
25°S
30°S
35°S
N
0 100 200 400 Km

Figure 4 (c)

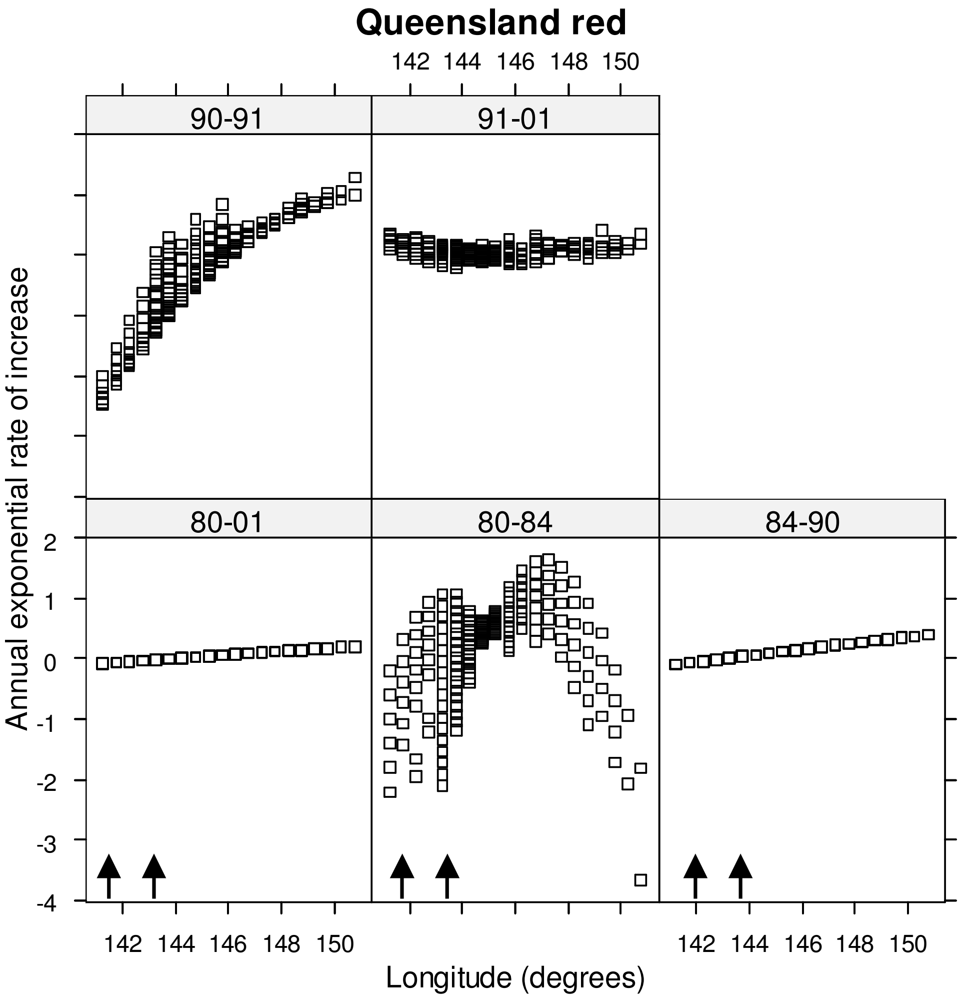

Queensland red
90-91
91-01
80-01
80-84
84-90
Annual exponential rate of increase
2
1
0
-1
-2
-3
-4
142
144
146
148
150
Longitude (degrees)

Figure 5 (a)

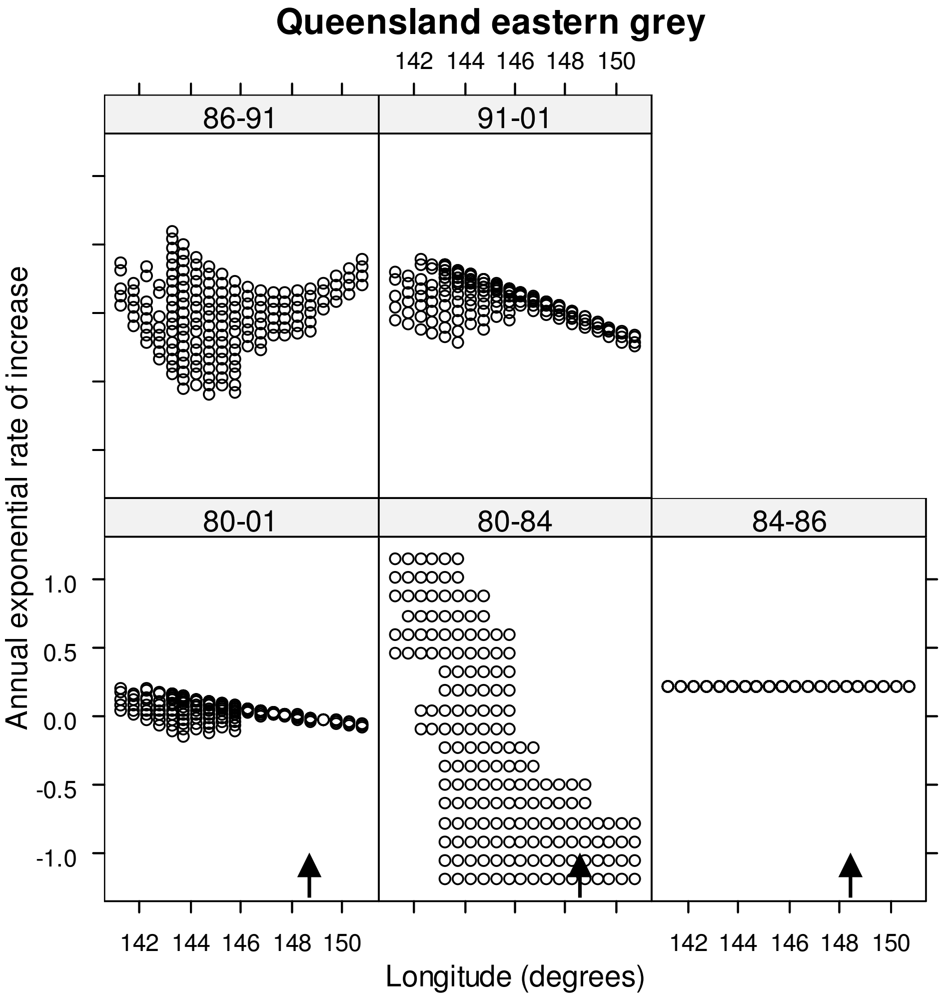

Queensland eastern grey
86-91
91-01
80-01
80-84
84-86
Annual exponential rate of increase
1.0
0.5
0.0
-0.5
-1.0
142
144
146
148
150
Longitude (degrees)

Figure 5 (b)

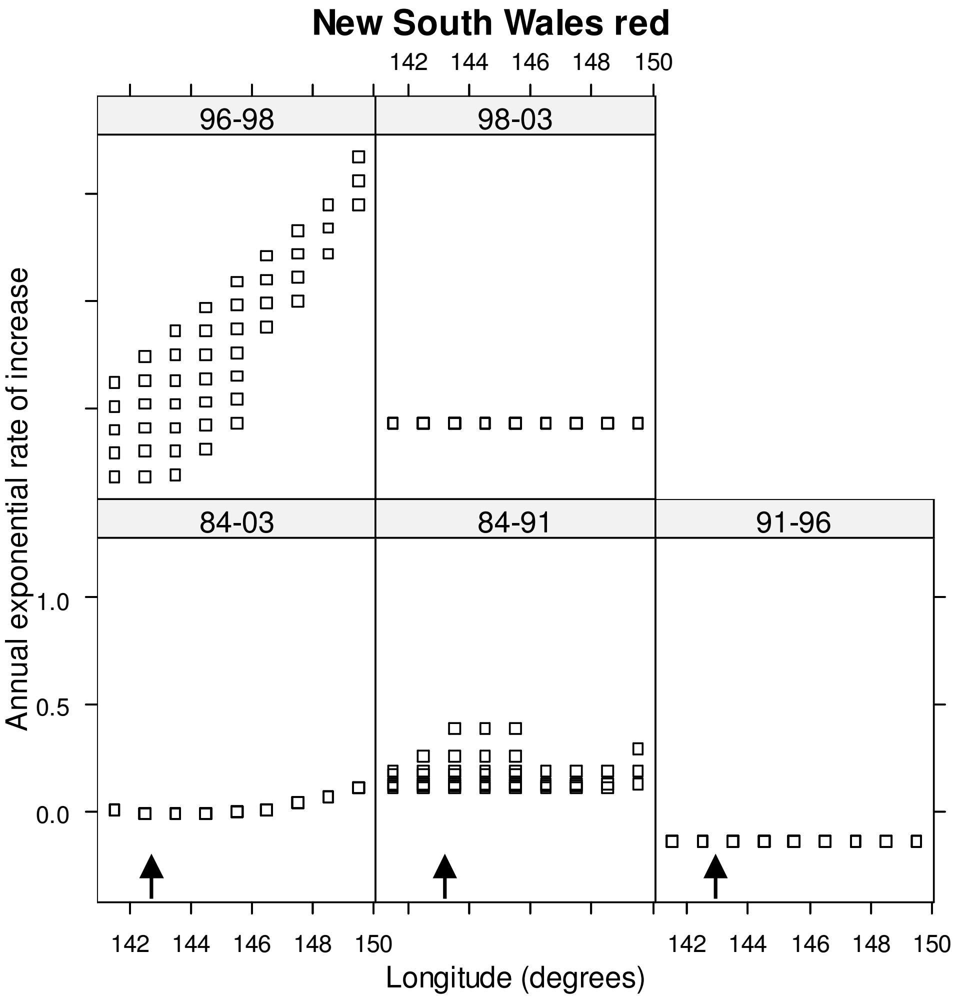

New South Wales red
96-98
98-03
84-03
84-91
91-96
142
144
146
148
150
1.0
0.5
0.0
Annual exponential rate of increase
Longitude (degrees)

Figure 6 (a)

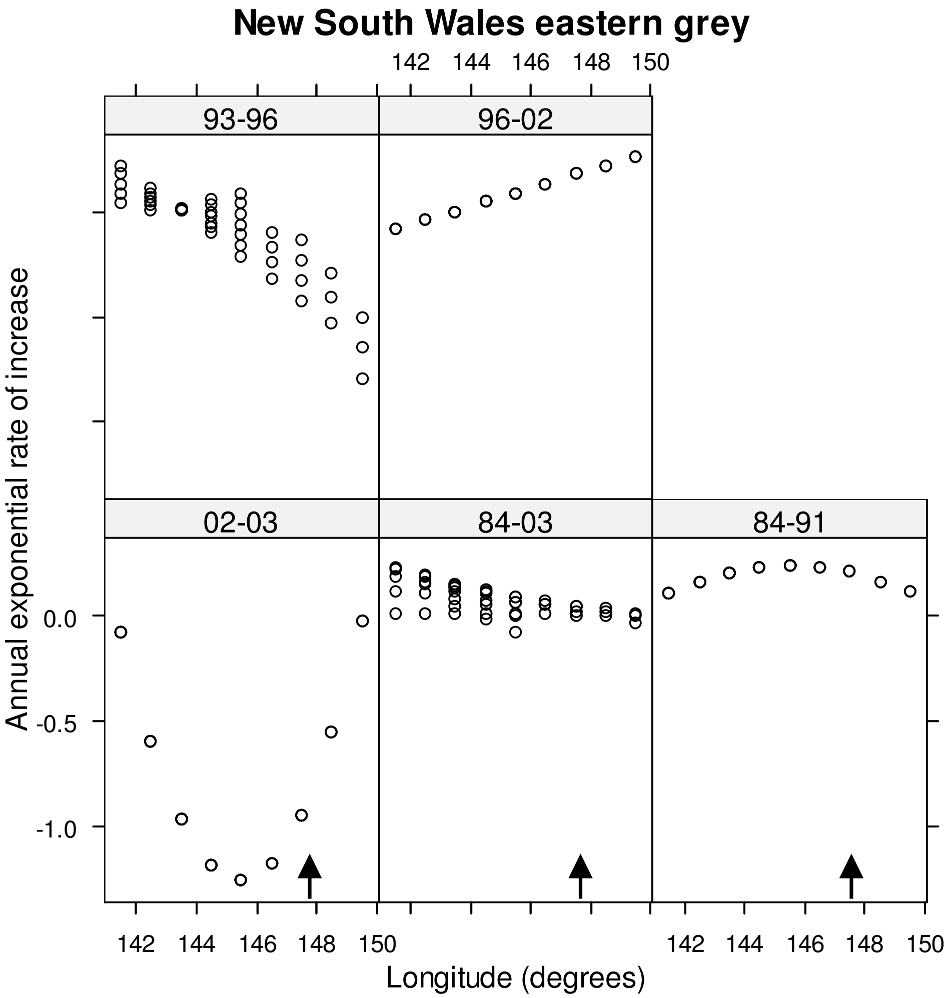

New South Wales eastern grey
93-96
96-02
02-03
84-03
84-91
Annual exponential rate of increase
0.0
-0.5
-1.0
142
144
146
148
150
Longitude (degrees)

Figure 6 (b)

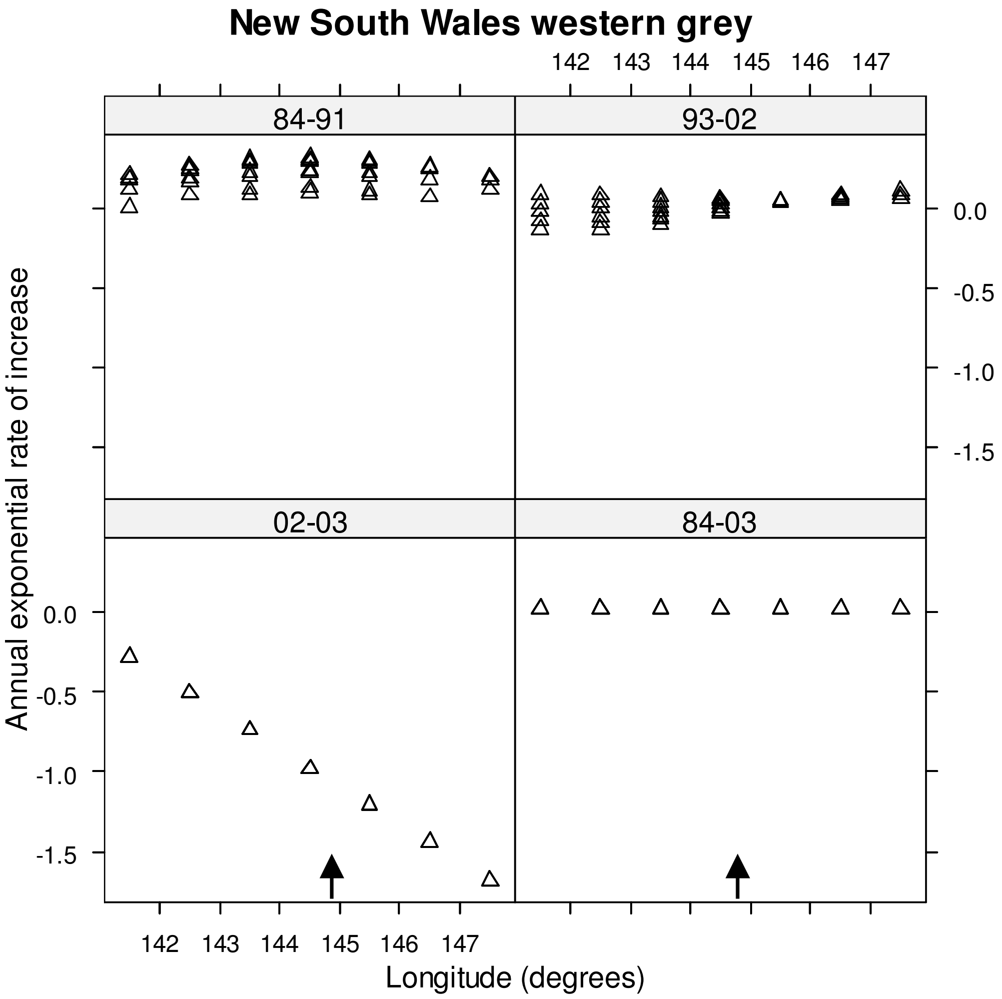

New South Wales western grey
84-91
93-02
02-03
84-03
Annual exponential rate of increase
0.0
-0.5
-1.0
-1.5
142
143
144
145
146
147
Longitude (degrees)

Figure 6 (c)

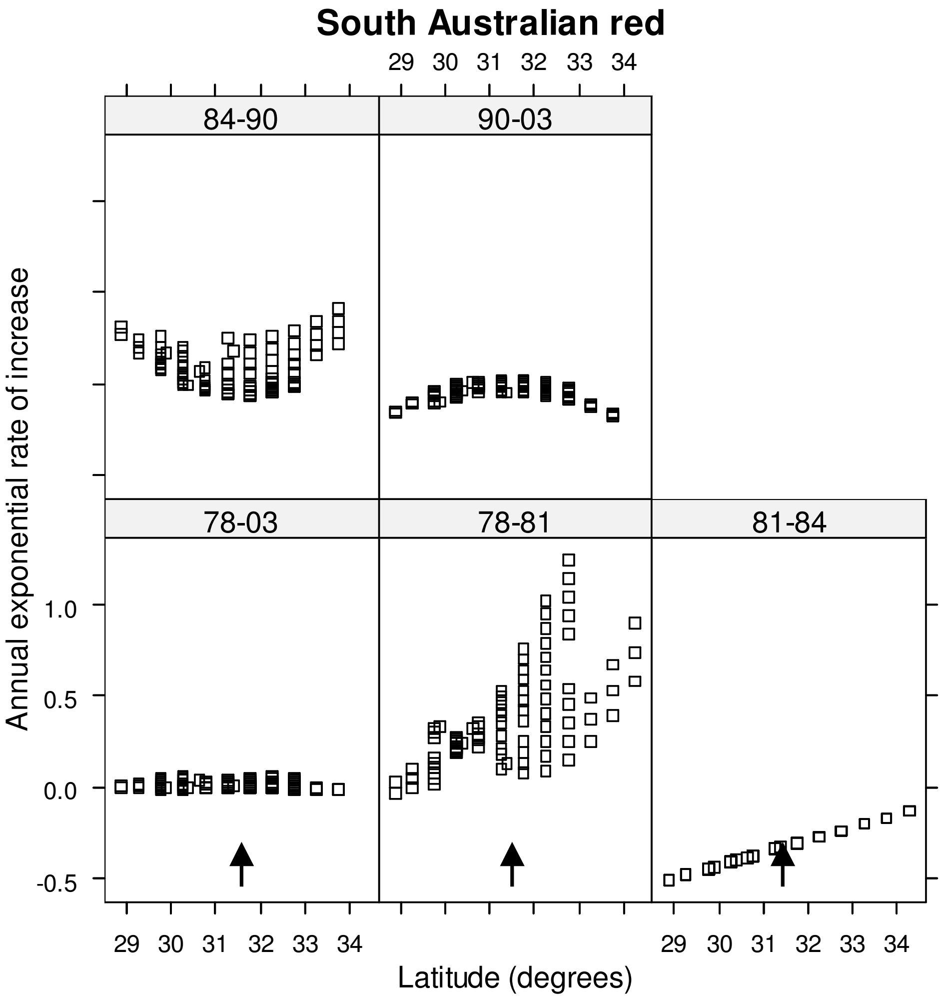

South Australian red
84-90
90-03
78-03
78-81
81-84
Annual exponential rate of increase
1.0
0.5
0.0
-0.5
29
30
31
32
33
34
Latitude (degrees)

Figure 7 (a)

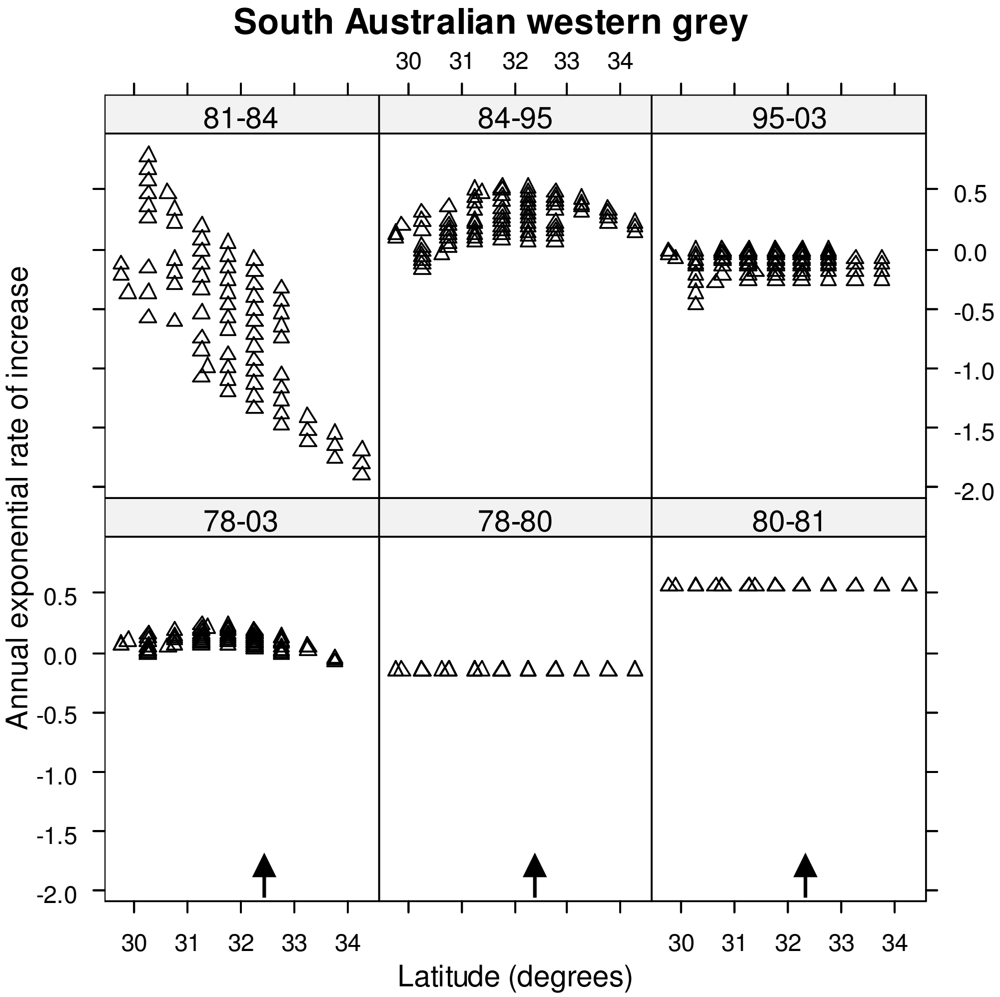

South Australian western grey
81-84
84-95
95-03
78-03
78-80
80-81
Annual exponential rate of increase
0.5
0.0
-0.5
-1.0
-1.5
-2.0
30
31
32
33
34
Latitude (degrees)

Figure 7 (b)

13. Using harvest statistics to monitor temporal variation in kangaroo density and harvest rate

13.1 Introduction

Throughout Australia, government agencies responsible for kangaroo harvest management have routinely collected a number of harvest statistics. These data may provide information on population abundance (and therefore trend) and status (i.e. under- or overharvest), offering a cost-effective means of indirectly monitoring kangaroo populations. Status includes the desired harvest rate as well as deleterious effects of harvesting, such as reduced body size (see Section 15). From a harvester's point of view, harvest data indicate the quality of the product (e.g. average size or range of sizes). These data provide a more extensive coverage of harvest areas than direct monitoring methods such as aerial survey and the data are collected continuously as opposed to the infrequent, snapshot survey estimates of density. Harvest data include sex ratio, carcass weight, skin size and animals shot per unit time (i.e. catch-per-unit-effort, *CPUE*) and these are generally recorded for each property where kangaroos are harvested. In the larger states of Western Australia and Queensland, because aerial surveys are expensive and logistically difficult, a greater emphasis has been placed on harvest data to monitor populations (Anon. 1984; Southwell 1989). However, as pointed out by Southwell (1989), there has been no empirical investigation to validate the use of harvest parameters as a monitoring tool.

The use of harvest data to monitor populations is commonplace in wildlife management, particularly in fisheries and small, fledgling operations where direct monitoring is either not feasible or not affordable. In fisheries management, *CPUE* is a notoriously poor index of population size for a variety of reasons including improved catching efficiency and 'targeting' of fish stock (Hilborn and Walters 1992). Kangaroo harvesting is less prone to some of these problems and so the potential of *CPUE* and other harvest statistics to indirectly monitor kangaroo populations is worth exploring. Harvest statistics are used in the management of waterfowl and deer in North America, which are some of the most sophisticated management programs for harvested wildlife in the world. The ideal appears to be combining harvest and direct survey data into models of population dynamics (White and Lubow 2002; Williams *et al.* 2002). For duck management, new data each year have provided an opportunity to compare and weight models and therefore learn about the system. In this sense the management is adaptive. Such a system of management is not proposed here for kangaroos, but should be considered as a logical extension. The first step is outlined in this study, which involves describing the regional and temporal variation in harvest statistics and identifying their likely determinants. The next step involves integrating this information with rainfall-driven population models (see Sections 9 and 10), and direct monitoring and the harvest strategy (see Sections 2 and 5) in the management program.

13.1.1 Theoretical considerations

Catch-per-unit-effort

An index I is only useful if the 'proportionality constant' β connecting it to actual population size X (i.e. $I = \beta X$) does indeed remain constant between locations or over time (Lancia *et al.* 1996; McCallum 2000). For *CPUE* to effectively monitor population abundance or harvest rate, a number of assumptions must therefore be satisfied (Caughley 1977). Southwell (1989) identified several potential violations of these assumptions when monitoring kangaroo populations. These assumptions are discussed in turn below.

1. *Harvesting equipment must be standardised*

   Unlike fisheries, kangaroo harvesting equipment (e.g. vehicles, rifles, spotlight) has changed little over the past 30 years.

2. *Harvesting efficiency must be standardised*

   There is variation between shooters (e.g. part-time versus full-time shooters) in the speed in which they can shoot and process animals. As shooters change in areas, *CPUE* will therefore change. This factor will be less pronounced as data are pooled over larger areas.

3. *Harvesting conditions (e.g. weather, access to animals and market prices) must be standardised*

   As with any index of population size, *CPUE* is likely to be more useful in comparing estimates of population abundance over time rather than between areas (McCallum 2000). Regional differences in vegetation, road network and distance between towns will invariably lead to regional differences in *CPUE.* However, shooter success also varies with weather conditions. It is generally accepted that shooting is difficult in wet conditions when the ground is boggy (Prince 1984a) or under windy conditions when animals seek cover and are restless, making them difficult targets. Shooting is considered easier during dry times when access is easier, ground cover is low and kangaroos tend to concentrate at watering points and on remaining food patches (Kirkpatrick and Amos 1985).

4. *Harvesting of each animal is independent*

   The relationship between *CPUE* and population abundance is unlikely to be linear, because of time saturation (Caughley 1977), whereby *CPUE* eventually reaches a plateau at some level of population density. Changes in abundance in this zone of saturation will not be reflected in the *CPUE.* If the density of interest is below this zone of saturation, which may be the case in drought, then the index could obviously still be useful.

5. *Kangaroos do not learn to avoid shooters.*

   This is possible in the longer term of > 10 years, but is unlikely to be a problem for monitoring year-to-year changes in abundance.

Harvest composition

These assumptions must also hold if aspects of harvest composition (e.g. sex ratio, carcass weight) are to be useful indices of population size or status. Harvest composition will change in quite different ways to *CPUE* and so it warrants separate discussion. Changes in the composition of the harvest will reflect one or more of three factors:

1. Changes in shooter selectivity due to the environment, prices or population density
2. Changes in population composition due to harvesting and
3. Changes in population composition due to the environment.

Kangaroos show considerable sexual size dimorphism, with males growing to 2-3 times the maximum size of females (Jarman 1989). Growth, particularly for males, extends well into adulthood and beyond the age at sexual maturity. Shooters are generally paid by carcass weight (although some human consumption shooting will be selective for intermediate sizes) or skin size so, not surprisingly, there is selection for larger, older, predominantly male kangaroos (Pople 1996). As population density declines, the rationale is that shooters will not be able to maintain this selectivity, and will therefore take fewer males, smaller animals and, overall, fewer animals per unit time. Similarly, as harvest rate increases, the age structure and sex ratio of the population will change. The sex ratio of the harvest should therefore shift towards females and average carcass weight should decline.

However, the composition of the population (i.e. size structure and therefore age structure and sex ratio) will also vary in response to the environment regardless of the rate that it is being harvested. In arid areas, it is well documented that kangaroo populations have unstable age distributions, resulting from pulses of recruitment during good seasons and no recruitment during drought (Frith and Sharman 1964; Kirkpatrick and McEvoy 1966; Newsome 1966, 1977). This is compounded by male-biased mortality during drought (Pople 1996); a mortality that may be also biased towards older animals (Robertson 1986). Assuming shooter selectivity remains constant, a surge in recruitment may lead to an increase in population size, but a decline in the size of harvested animals. Similarly, a shift in the sex ratio towards females during drought would see a decline in the size of harvested animals. Fluctuations in the adult sex ratio of an unharvested red kangaroo population in southern Queensland have been recorded over a ten-year period and are shown in Figure 13.1 (A. R. Pople and G. Lundie Jenkins unpublished data). The sex ratio became strongly female-biased (>80% female) during drought in the early 1990s (see Sections 16 and 17), returning slowly towards parity over the ensuing years.

Regional variation in population composition is only one factor that will lead to differences in harvest composition between areas. Adult sex ratios have been determined in a number of harvested red kangaroo populations throughout eastern Australia (Pople and Cairns 1995; A. R. Pople and S. C. Cairns unpublished data) and these can be compared with the sex ratio of the harvest from the same population (Fig. 13.2). The population sex ratio is restricted to animals > 2 years, which is the age when red kangaroos are large enough to be harvested. The comparison shows considerable variation in the strength of selection for males, indicated by departures from the line of no selection shown in Figure 13.2.

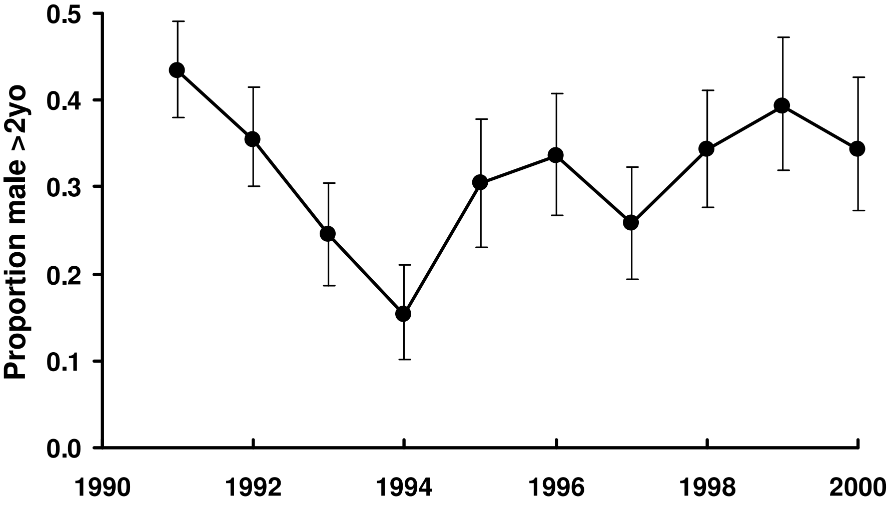


Fig. 13.1. Adult (> 2 years old) sex ratio (± 95% bootstrapped confidence intervals) for the unharvested red kangaroo population at Currawinya National Park in southern Queensland (A. R. Pople and G. Lundie Jenkins unpublished data). The population declined markedly during drought in the early 1990s. The sex ratio was determined from random shot samples of 200-400 animals taken annually (Pople 1996).

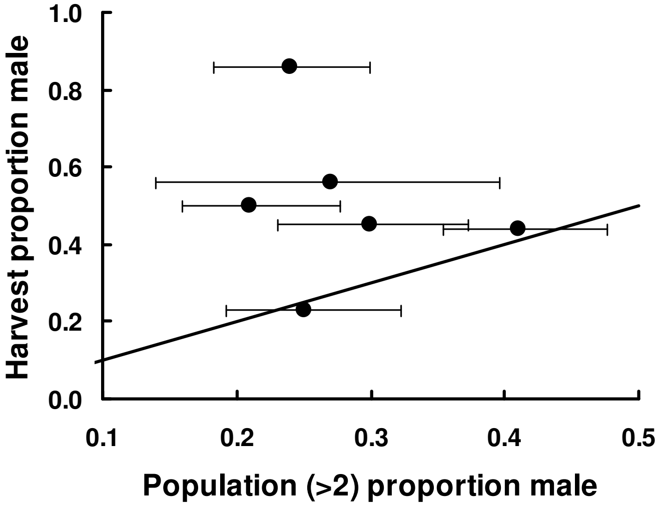


Fig. 13.2. Relationship between adult (> 2 years old) sex ratio (± 95% bootstrapped confidence intervals) and harvest sex ratio in six populations of red kangaroos (Pople and Cairns 1995; A. R. Pople and S. C. Cairns unpublished data). Populations were located in far northern Queensland, central Queensland, southern Queensland, eastern South Australia and western South Australia.

Regional variation in other factors such as environmental differences affecting shooter access, population density of red kangaroos and other kangaroo species, harvesting costs and market prices, are influencing shooter selectivity. These data come from the scale of a single property, so individual variation amongst shooters may well be a factor too.

In addition, there are regional differences in kangaroo morphology, particularly body weight and overall size (Pople 1996), which will be reflected in the composition of the harvest. Variation in the growth of male red kangaroos is shown in Figure 13.3, highlighting the latitudinal gradient in body size synonymous with Bergmann's rule and observed in a number of Australian mammalian species including macropods (Yom and Nix 1986). It is interesting to note that the most northerly population sampled in Figure 13.3 at Julia Creek in Queensland, recorded a relatively large asymptotic weight, reversing the trend. An explanation for the pattern is not straightforward. Harvest statistics will therefore be more useful in monitoring abundance or status over time rather than between areas.

13.1.2 Empirical support

Until recently, there has been limited analysis of kangaroo harvest data. Analyses of historical data, prior to the imposition or influence of harvest quotas, focussed on the factors determining harvest offtake. Kirkpatrick and Amos (1985) argued that both market demand and prevailing weather conditions determined the size of the harvest offtake of kangaroos in Queensland. Prince (1984b) found that a large component of the variation in the historical offtake of kangaroos in Western Australia could be explained by previous rainfall, whereas market fluctuations accounted for only a minor component. (Prince 1984a, b) suggested that offtake was impaired by rainfall in the short-term and increased with rainfall in the long-term because of resultant increases in population size.

Regional differences and temporal variation in harvest sex ratio and carcass weight in Western Australia were reported by Prince (1984a), who speculated on the factors responsible. Population modelling by Nance (1985) suggested that harvest sex ratio could effectively monitor the status of an eastern grey kangaroo population. This modelling, supplemented by samples of population composition from harvested and unharvested samples, supported the management program for kangaroos in Queensland prior to the 1990s (Kirkpatrick and Amos 1985). Under this program, harvest statistics were used to monitor the status of kangaroo populations and determine the size of harvest quotas (Anon. 1984; Queensland National Parks and Wildlife Service 1989). Nance's (1985) model made a number of unsupported assumptions about regulation in kangaroo populations and shooter behaviour. Nevertheless, the work provides the hypothesis that sex ratio can monitor harvest rate, which can be assessed in studies such as the present one. Notably, these previous studies lacked data on population abundance.

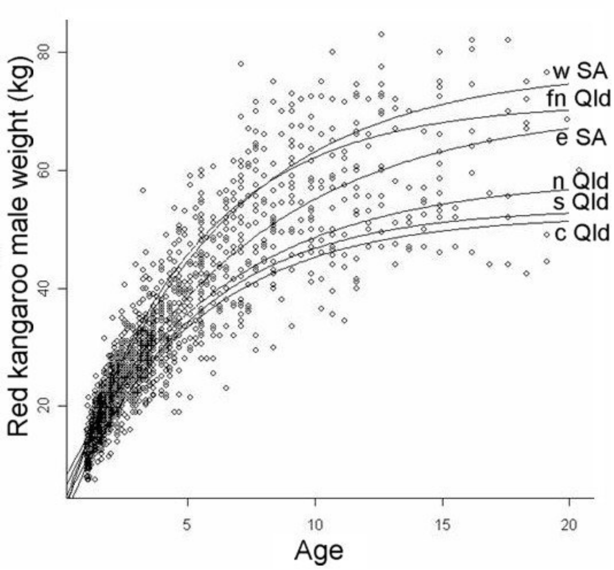


Fig. 13.3. Fitted generalised von Bertalanffy growth curves for male red kangaroos sampled from a number of locations in eastern Australia (A. R. Pople and S. C. Cairns, unpublished data). The concentration of points at low values reflects the age structure of populations, which is dominated by young animals. w SA, western South Australia; fn Qld, far northern Queensland; e SA, eastern South Australia; n Qld, northern Queensland; s Qld, southern Queensland; c Qld, central Queensland.

With the benefit of estimates of population size, Pople (1996) examined the relationship between harvest statistics and harvest rate across several regions in Queensland for two years in the early 1990s. For red kangaroos, the effect of harvesting appeared to be detected in the size of male skins. However, the effect of drought in on the population sex ratio was thought to have overshadowed any relationship between harvest sex ratio and harvest rate. For eastern grey kangaroos, carcass weight, skin size and harvest sex ratio all appeared to be potential indicators of harvest rate. The results supported Nance's (1985) modelling and also refuted the argument of de la Mare (1988) that the selectivity of shooters when taking skins would be too weak to adequately monitor the population's status. However, the suggestion that Nance's (1985) model could be extended to other species (Kirkpatrick and Nance 1985; Queensland National Parks and Wildlife Service 1989), particularly red kangaroos, was not supported.

13.2 Methods

13.2.1 Study area

The study area encompasses the sheep rangelands of eastern Australia in which kangaroo density has been estimated by annual aerial survey since the late 1970s (see Section 9, Figs 9.1 and 9.2). This coincides with the main harvest areas in each of the three states covered by this area. The separate management regions within each state were again the units of analysis as they were in Section 9. In Queensland, the ten helicopter survey blocks (see Section 9, Fig. 9.2) were the units of analysis, rather than the three broader regions as the latter did not provide a longer time series as it did in Section 9 with harvest statistics only available from 1991. Variation in harvest statistics between regions was expected and is examined in Section 14. The primary interest in this section was temporal variation within each region.

13.2.2 Analysis

Two approaches were taken in the analysis. Firstly, harvest statistics were used response variables and modelled as a function of a number of explanatory variables including kangaroo density, harvest rate and rainfall. This follows current management practice involving monitoring harvest statistics to infer changes in kangaroo density or harvest rate (e.g. Queensland Parks and Wildlife Service 2003). This approach should also be useful to the kangaroo industry as it provides an understanding of product quality and quantity, such as carcass weight and catch rates. The second approach was to use density and harvest rate as response variables and use harvest statistics as the explanatory variables. This would allow managers to predict density or harvest rate to set harvest quotas, in years when direct monitoring such as aerial survey is not conducted (see Section 5). The first approach allows greatest use of the monthly harvest data, while the second approach is restricted to the smaller sample size of annual estimates of population size and harvest rate and density.

Monthly harvest data were available for South Australia over 1980-2001, for New South Wales over 1993-2003 and for Queensland over 1991-2003 (see Section 1). Three harvest statistics were used in the analyses: the percentage of the harvest comprising males (*%male*), *CPUE* and male carcass weight (*male wt*). Skin size was not examined, because skin-only shooting is currently restricted to Queensland within the study area and it is declining there as a proportion of the overall harvest. In Queensland, harvest sex ratio was restricted to carcasses. *CPUE* was calculated as the harvest in a region divided by the number of shooter nights. The structure of the harvest database for South Australia meant that effort was calculated as the number of shooter nights when males were harvested. This was determined separately for each species. In New South Wales, *CPUE* was only available quarterly and only from 1997 and so was not incorporated into analyses here. In Queensland, effort was calculated as the number of shooter nights regardless of species harvested. Male rather than female weight was considered a more sensitive indicator of changes in density and harvest rate as it spans a greater range, asymptotes at an older age and males are generally targeted by shooters.

Explanatory variables used to predict harvest statistics included kangaroo density and density squared to allow for a saturation effect, instantaneous harvest rate, effort (but not with *CPUE*), seasonality [comprising $sin(2\times\pi\times time)$ and $cos(2\times\pi\times time)$ terms], dummy variables to account for harvest seasons and regulatory changes, and a number of rainfall terms. Harvest rate was calculated as the annual harvest divided by the winter density estimate. Density and harvest rate were only estimated once a year and so were interpolated, assuming exponential growth, to provide monthly values. Rain that fell in the month of collection of harvest data was expected to reduce access and selectivity, thereby resulting in a drop in the value of all harvest statistics. Rain falling in the three months prior to collection was also expected to have a negative effect on *CPUE* and *%male* by increasing food supply resulting in a more even dispersion of kangaroos that make less use of open, accessible areas (see Section 11). Rain falling in the 12 months lagged one month prior to collection was expected to improve kangaroo body condition, thereby increasing *male wt*. Shooters appear to be less size selective when taking only skins (Pople 1996) can potentially harvest more animals per night. In Queensland, the proportion of the harvest comprising skins was included as a variable as this may have a knock-on effect to the composition of the carcass harvest and *CPUE.* In New South Wales, a dummy variable was included to account for skin-only shooting, which occurred up to mid-1996. The harvest of each species is likely to be influenced by availability of other species to harvest (Pople 1996). This is manifest as spatial variation in the harvest and will be explored in detail in Section 14. However, temporal variation in the harvest is likely to be influenced by season closures for other species and so the closure of the red kangaroo season in Queensland over the study period was included as a dummy variable in the analysis for eastern greys kangaroos and wallaroos. In South Australia, carcasses were dressed to a smaller weight prior to 1997. Furthermore, an initial examination of the data revealed no differences between male and female carcass weights up to 1987. Dummy variables were therefore included to account for these changes. A likely influence that was not incorporated in these models was economics, such as prices paid for carcasses.

Serial correlation in the data was expected and a correlated regression structure (first order autoregressive, AR1) was included in the regression models using generalised least squares (gls) in R 1.9.1 (R Development Core Team 2003). Models were simplified by stepwise removal of non-significant ($P > 0.05$) terms from the full model (Crawley 2002). Finally the most parsimonious model was compared with the equivalent model without the correlated error structure using a likelihood ratio test (Maindonald and Braun 2003). *%male* could have been modelled using logistic regression, but was instead arcsine transformed and analysed in a linear regression to take advantage of the correlated error structure in gls. Only monthly harvests of > 50 animals of both sexes combined were used in analyses.

Explanatory variables used to predict population statistics (i.e. density and harvest rate) were restricted to *CPUE*, *%male* and *male wt*, because sample size was limited to annual estimates of density and harvest rate, unlike the monthly harvest statistics. Harvest statistics were smoothed using a three point moving average centred on the winter aerial survey estimate of density. Data were also analysed using multiple regression with a correlated error structure if needed. Kangaroo density was log transformed to improve linearity. The purpose of the analyses with harvest statistics as response variables was to identify their likely determinants. For the analyses with population statistics as response variables, the purpose was prediction. 95% prediction intervals were therefore determined for fitted values.

13.3 Results

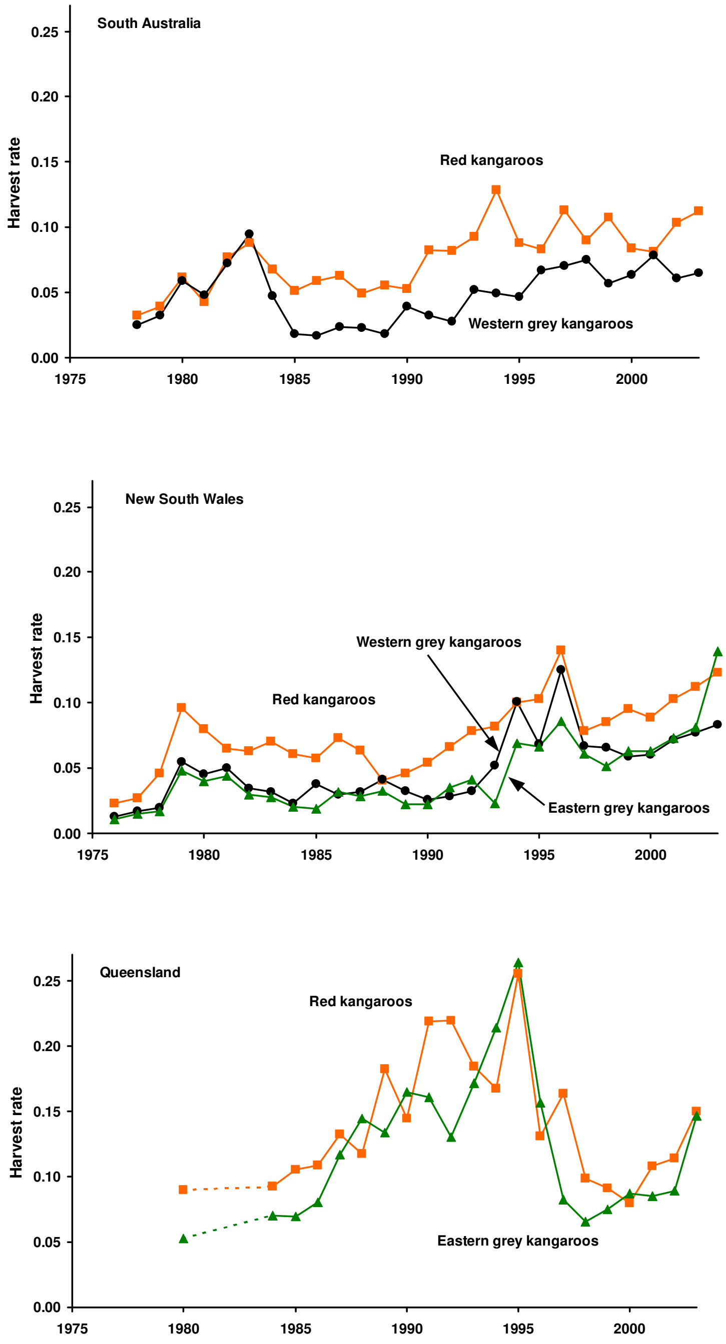
13.3.1 Harvest rate across all states

Variation in density of the three kangaroo species across the study area was described in Section 12. Wallaroo density in Queensland is described in Section 4. Harvest rate of the three kangaroo species over the study period in each state is shown in Figure 13.4. Harvest rate in South Australia (Fig. 13.4*a*) was multiplied by 0.63 for red kangaroos and 0.79 for western grey kangaroos to account for the likely underestimate of densities in that state and make them comparable to harvest rates in New South Wales and Queensland (see Section 12). There are four points worth noting from these plots. Firstly, harvest rates have been consistently higher in Queensland. Secondly, red kangaroos have generally been harvested at higher rates than either of the grey kangaroo species, although the pattern is less marked in Queensland. Thirdly, harvest rates declined steeply in Queensland after 1995 following a loss of markets. Finally, harvest rates have generally been increasing in New South Wales and South Australia since the mid-1980s.

13.3.2 South Australia

Standardised parameter estimates for models predicting harvest and population statistics in South Australia are shown in Table 13.1. The ability to model fluctuations in harvest statistics varied greatly among soil conservation boards (SCBs). The apparent good fit for *male wt* is largely influenced by the change in carcass dressing being explained by the dummy variable. Often the model with the lower R^2 provided the more impressive and useful fit to the data, particularly if it captured declines in harvest statistics during drought and large increases. Adjusted R^2 cannot be compared directly between regions as the range of explanatory variables differs. Examples of model fits are shown in Figures 13.5 and 13.6. In the Northeast Pastoral SCB, trends in all three harvest statistics have been tracked reasonably well by the fitted models. In particular, the decline in red kangaroo numbers during the 1982-83 drought was accompanied by a sharp decline in the proportion of males in the harvest. For western grey kangaroos in Gawler SCB, the relationships are poorer with much greater scatter and lack of trend in all three statistics.

Kangaroo density and harvest rate were generally important influences on harvest statistics for both species. As expected, higher densities were usually associated with a higher proportion of males, higher catch rates and greater weights. Where the coefficient for density was negative, there was a curvilinear term indicating an inverted parabola. Density had a saturating effect in a number of cases. Higher harvest rates were generally associated with lower values of *%male* and *male wt* and higher catch rates, again in line with expectations. Rainfall had a smaller influence on harvest statistics as gauged by the size of the standardised coefficients and the few models where terms were included. Three months rainfall was not incorporated in any of the models. The effect of recent rainfall was negative while 12 months rainfall had a positive effect on male carcass weight. Effort also had a minor, positive influence on red kangaroo *%male* in Northeast Pastoral SCB and male red kangaroo carcass weight in Kingoonya SCB. The dummy variable for the change in carcass dressing was incorporated in many models for *%male* and *CPUE*, but the sign was not always consistent.



(*a*)

(*b*)

(c)

Fig. 13.4. Harvest rate of the red kangaroos (orange squares), western grey kangaroos (black circles) and eastern grey kangaroos (green triangles) in the main harvest areas (see Section 9, Fig. 9.1) of (a) South Australia, (b) New South Wales and (c) Queensland. Harvest rates in South Australia have been multiplied by 0.63 for red kangaroos and 0.79 for western grey kangaroos to make them comparable to other states.

Table 13.1. Standardised parameter estimates with standard errors (in brackets) and adjusted R^2 for the most parsimonious (according to backwards elimination) regression models (see Equation 4) predicting (a) red kangaroo harvest statistics, (b) western grey kangaroo harvest statistics, (c) red kangaroo population statistics, and (d) western grey kangaroo population statistics. The average 95% prediction interval (*95%PI*) is also shown for models predicting population statistics. Models are shown for soil conservation boards (SCBs) in the South Australian pastoral zone (see Section 9, Fig. 9.1). Population statistics are log transformed kangaroo density (log*D*) and harvest rate expressed as a percentage (*HR%*). Harvest statistics are catch-per-unit-effort (*CPUE*), the percentage of the harvest comprising males (*%male*, arcsine transformed) and average male carcass weight (*male wt*). Explanatory variables include untransformed density (*D*), harvest rate expressed as a proportion (*HR*), *CPUE*, *male wt*, the proportion of the harvest comprising males (*pmale*, arcsine transformed), rain falling in the same month of collection of the harvest statistic (*rn*.1.0), 3 months rain lagged 1 month prior to collection (*rn*.3.1) , 12 months rain lagged 1 month prior to collection (*rn*.12.1), the number of shooter-nights (*effort*), seasonal *cycle* comprising *sin*(2×π×*time*) and *cos*(2×π×*time*) terms, and 2-3 dummy variables (c*arcass*) representing periods when carcasses were dressed differently (*male wt* and *CPUE*) and when carcass weight was not distinguished between the sexes (*male wt*). The parameter for *sin*(2×π×*time*) is given above the parameter for *cos*(2×π×*time*). K, Kingoonya; M, Marree; NF, North Flinders Ranges; NP, Northeast Pastoral; ED, Eastern Districts; G, Gawler

(*a*) *Red kangaroos (South Australia)*

SCB	Response	Intercept	Explanatory variables								*Adj.* R^2
			D	D^2	*HR*	*rn*.1.0	*rn*.12.1	*effort*	*carcass*	*cycle*	
NP	*%male*	91.64 (1.60)	5.19 (1.57)		-4.86 (1.52)			1.07 (0.52)			0.49
	CPUE	28.01 (081)	2.94 (0.75)		2.80 (0.81)	-1.00 (0.22)			4.72 (1.87)	0.07 (0.46) 0.94 (0.46)	0.52
	male wt	17.71 (0.40)	-2.93 (1.28)	3.12 (1.22)	1.02 (0.23)		0.54 (0.14)		1.05 (0.58) 7.19 (0.66)	-0.06 (0.12) 0.32 (0.12)	0.77
NF	*%male*	83.60 (0.53)	2.07 (0.55)		-2.36 (0.55)						0.32
	CPUE	23.97 (0.42)	8.20 (1.99)	-6.11 (1.97)	3.23 (0.39)				3.40 (0.96)		0.51
	male wt	18.04 (0.34)			-0.82 (0.21)				0.73 (0.45) 7.77 (0.54)		0.83
M	*%male*	78.29 (1.46)			-4.99 (1.34)	-1.24 (0.45)					0.14
	CPUE	35.05 (1.59)				-1.17 (0.41)					0.00
	male wt	17.73 (0.50)	0.74 (0.29)						1.38 (0.64) 13.28 (0.80)		0.82
K	*%male*	80.61 (0.92)									-
	CPUE	30.86 (0.82)	18.20 (5.59)	-13.59 (5.51)							0.41
	male wt	18.07 (0.32)					0.33 (0.13)	0.13 (0.07)	0.42 (0.42) 8.19 (0.53)	-0.28 (0.11) 0.21 (0.11)	0.87
G	*%male*	86.86 (0.97)	17.89 (7.45)	-17.86 (7.45)						-2.50 (0.76) 0.55 (0.75)	0.10
	CPUE	25.01 (0.88)	21.51 (6.18)	-17.43 (6.14)	6.85 (0.87)				-9.49 (2.07)		0.51
	male wt	17.84 (0.22)							0.41 (0.29) 8.11 (0.35)	-0.35 (0.11) 0.21 (0.11)	0.85
ED	*%male*	91.50 (1.28)							-17.87 (2.79)		0.24
	CPUE	15.83 (0.34)	5.40 (1.73)	-4.20 (1.73)						0.97 (0.33) -0.06 (0.33)	0.13
	male wt	19.05 (0.54)	3.99 (1.09)	-3.33 (0.94)	-1.00 (0.23)	-0.24 (0.12)			-0.97 (0.85) 5.03 (0.73)	-0.30 (0.15) 0.02 (0.15)	0.54

(*b*) *Western grey kangaroos (South Australia)*

SCB	Response	Intercept	Explanatory variables								*Adj.* R^2
			D	D^2	*HR*	*rn*.1.0	*rn*.12.1	*effort*	*carcass*	*cycle*	
NP	*%male*	107.1 (1.50)	-5.29 (1.48)		-6.50 (1.38)				14.03 (3.53)		0.34
	CPUE	8.09 (0.25)	1.30 (0.23)						2.31 (0.57)		0.37
	male wt	19.33 (0.42)			-1.39 (0.26)				0.43 (0.58) 3.42 (0.66)	-0.38 (0.19) 0.08 (0.18)	0.46
NF	*%male*	101.9 (1.70)								-4.12 (1.63) -0.24 (1.63)	0.03
	CPUE	7.14 (0.21)	3.27 (0.92)	-2.12 (0.89)	0.71 (0.25)					0.46 (0.20) 0.58 (0.20)	0.22
	male wt	18.72 (0.34)					0.47 (0.18)		0.81 (0.44) 4.85 (0.48)	-0.78 (0.18) 0.25 (0.17)	0.52
K	*%male*	101.2 (3.65)									-
	CPUE	9.12 (1.21)	2.39 (1.13)						-6.02 (2.35)	-1.61 (0.69) 1.53 (0.71)	0.13
	male wt	17.26 (0.81)	-1.59 (1.36)	2.75 (1.24)			0.78 (0.34)		2.05 (0.95) 7.02 (1.29)		0.59
G	*%male*	89.91 (0.77)							-5.38 (1.69)	-3.65 (0.56) 1.26 (0.56)	0.30
	CPUE	19.83 (0.63)			-1.73 (0.60)					-1.17 (0.52) -0.86 (0.52)	0.12
	male wt	17.77 (0.31)			-0.55 (0.19)				0.47 (0.44) 6.40 (0.49)	-0.52 (0.13) 0.33 (0.13)	0.78
ED	*%male*	95.69 (1.81)			-5.99 (1.80)						0.12
	CPUE	13.42 (0.36)	0.99 (0.36)		3.18 (0.36)					-0.41 (0.35) 0.71 (0.34)	0.37
	male wt	18.33 (0.48)	2.93 (1.06)	-2.71 (1.04)	-0.85 (0.32)				1.18 (0.57) 5.18 (0.92)		0.44

Table 13.1 cont.

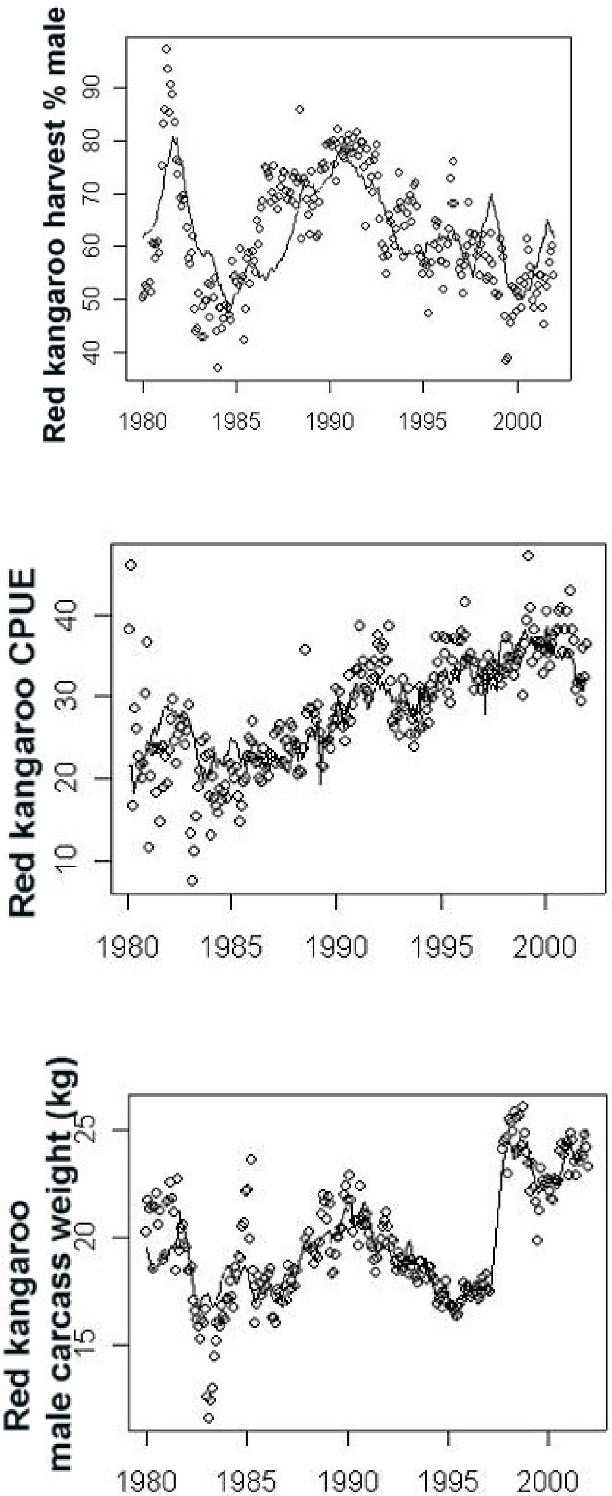
(*c*) *Red kangaroos (South Australia)*

SCB	Response	Intercept	Explanatory variables *CPUE*	*pmale*	*Adj.* R^2	*95%PI*
NP	log*D*	2.50 (0.05)	0.15 (0.05)	0.21 (0.05)	0.55	2.54
	HR%	12.82 (0.70)	2.41 (0.70)	-2.21 (0.70)	0.49	14.8
NF	log*D*	2.13 (0.05)	0.13 (0.06)	0.21 (0.06)	0.36	2.26
	HR%	12.36 (0.87)	2.96 (0.89)		0.33	17.6
M	log*D*	1.58 (0.10)		0.32 (0.11)	0.28	2.57
	HR%	19.46 (2.15)		-4.76 (2.20)	0.15	40.9
K	log*D*	1.65 (0.07)			-	-
	HR%	11.23 (0.71)	1.71 (0.73)		0.17	14.6
G	log*D*	1.03 (0.06)			-	-
	HR%	11.41 (0.89)	2.04 (0.91)		0.16	18.1
ED	log*D*	0.76 (0.13)			-	-
	HR%	13.32 (0.19)			-	-

Table 13.1 cont.

(*d*) *Western grey kangaroos (South Australia)*

SCB	Response	Intercept	Explanatory variables *CPUE*	 *pmale*	*Adj.* R^2	*95%PI*
NP	log*D*	0.23 (0.22)			-	-
	HR%	16.09 (3.92)	-14.05 (5.53)	-13.73 (5.53)	0.21	57.1
NF	log*D*	-1.14 (0.33)			-	-
	HR%	51.8 (30.1)			-	-
K	log*D*	-2.65 (0.37)			-	-
	HR%	8.89 (3.41)			-	-
G	log*D*	1.83 (0.08)			-	-
	HR%	4.45 (0.38)	-0.93 (0.39)		0.18	7.6
ED	log*D*	-1.91 (0.39)	0.03 (0.01)	3.08 (0.34)	0.81	0.79
	HR%	8.05 (1.05)	3.91 (1.08)		0.40	17.5



(*a*)

(*b*)

(*c*)

Fig. 13.5. Monthly (a) *%male*, (b) *CPUE* and (c) average male carcass weight for harvested red kangaroos in Northeast Pastoral SCB in South Australia. Fitted models (Table 13.1*a*) are shown as solid lines.

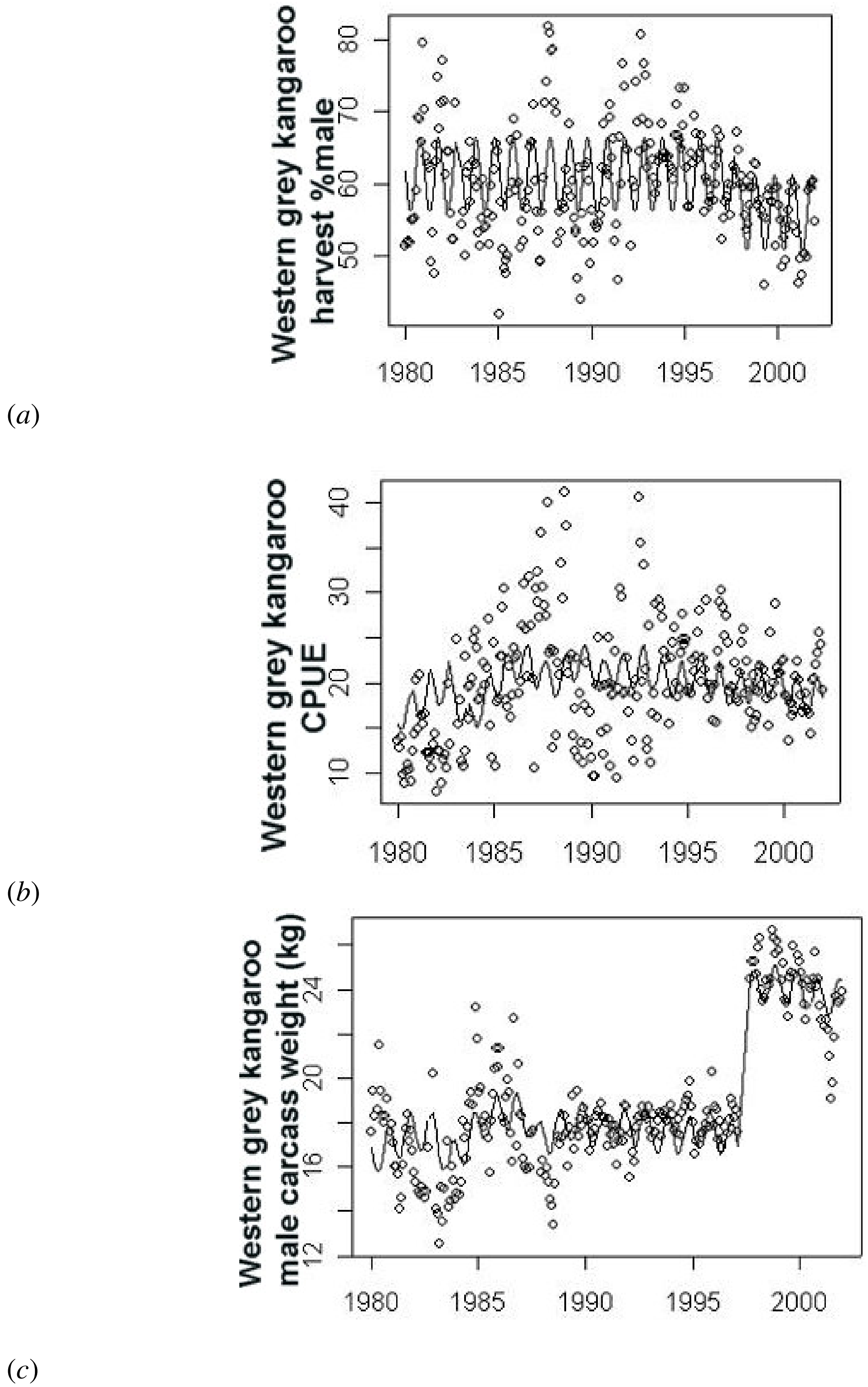


Fig. 13.6. Monthly (a) *%male*, (b) *CPUE* and (c) average male carcass weight for harvested western grey kangaroos in Gawler SCB in South Australia. Fitted models (Table 13.1*b*) are shown as solid lines.

Seasonal cycles were also incorporated into many models, but these were not strong. Likelihood ratio tests supported a correlated error structure for all models.

Predictions of population statistics were best in the higher density SCBs, which are in the northeast for red kangaroos and the south for western grey kangaroos. Correlated error structures did not improve any models predicting population statistics. Approximate precision (SE/mean) of predictions of density and harvest rate using these relationships can be calculated as the intercept divided by a quarter of the prediction interval (*95%PI*). For red kangaroos these estimates range 0.25-0.53 and for western grey kangaroos they range 0.43-0.89. Examples of fitted models are shown in Figure 13.7.

13.3.3 New South Wales

Standardised parameter estimates for models predicting harvest and population statistics in South Australia are shown in Table 13.2. Striking features of the data are the decline in male weight during the recent 2002-3 drought and drops in *%male* at different times during the time series depending on the zone and species. Trends in the two harvest statistics were tracked reasonably well by the fitted models in the examples shown in Figures 13.8, 13.9 and 13.10. The decline in average carcass weight in the recent drought was tracked by the models for red kangaroos in Figures 13.8*b* and 13.8*c*, but not western grey kangaroos in Figure 13.10*b* and only partly in Figure 13.10*c*.

As with South Australia, kangaroo density and harvest rate were generally important influences on harvest statistics for all three species. Recent rainfall entered into the models in some zones, but only as a minor influence. Inclusion of 12 months rainfall as an explanatory variable allowed the decline in carcass weight during the recent drought to be modelled. However, it was only included in 7 of 23 cases. The dummy variable for skin shooting was incorporated in many models for *%male*, but not always as an expected negative effect. Seasonal cycles were also incorporated into many models and, while more marked than in South Australia, their overall effect was small. Likelihood ratio tests supported a correlated error structure for all models.

Predictions of red kangaroo population statistics were only possible for density and only in three zones. Models could be fitted for both statistics for eastern grey kangaroos, but again only in three zones. Western grey kangaroos faired better, with models fitted in five of seven zones. Correlated error structures did not improve any models predicting population statistics. Approximate precision of predictions of density and harvest rate ranged 0.27-0.28 for red kangaroos, 0.18-0.43 for eastern grey kangaroos and 0.24-0.86 for western grey kangaroos. Examples of fitted models are shown in Figure 13.11.

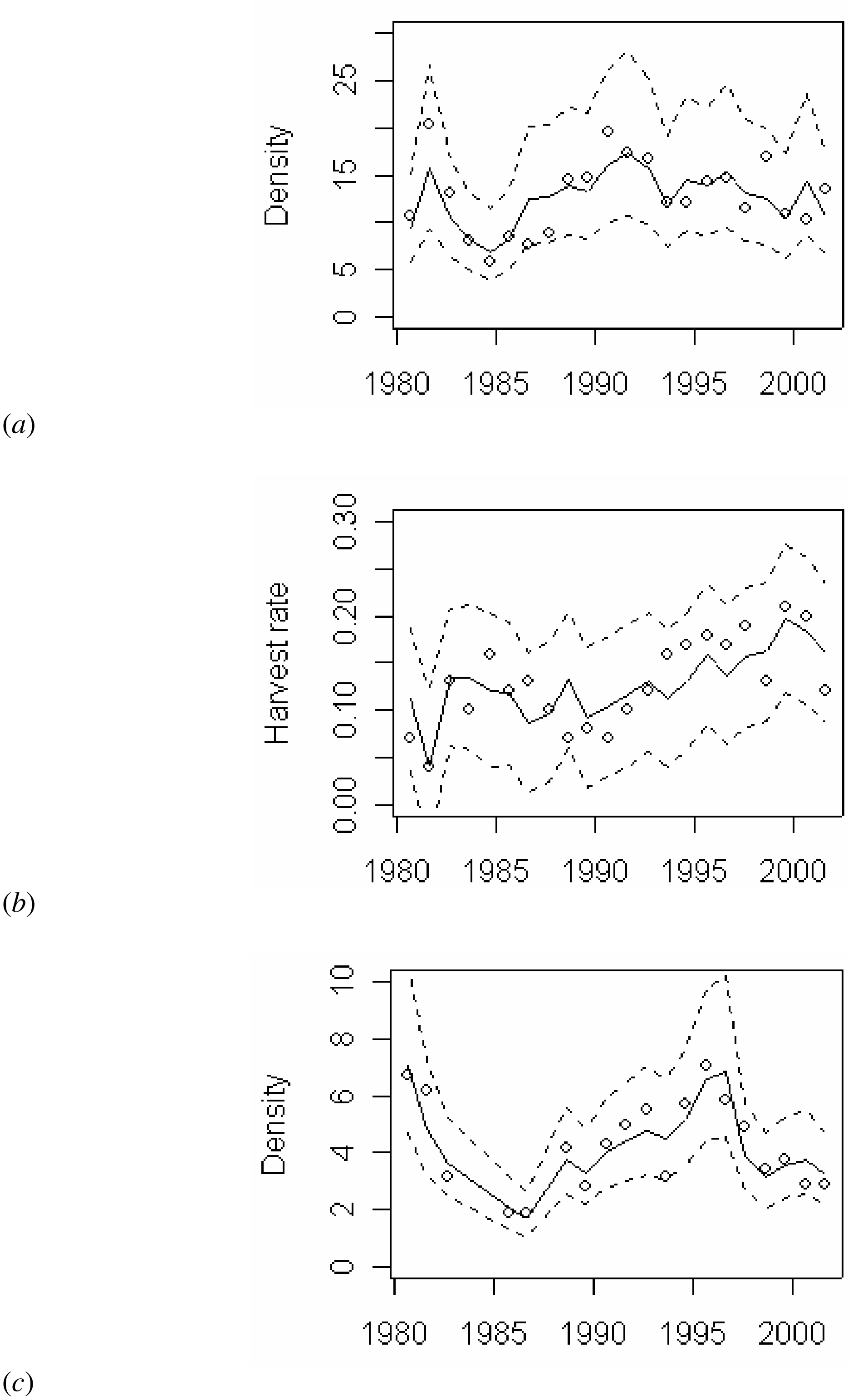


Fig. 13.7. Fitted models (solid line, Table 13.1*c* and *d*) and 95% prediction intervals (dashed lines) for (a) red kangaroo density (km^{-2}) in Northeast Pastoral SCB, (b) harvest rate of red kangaroos in Northeast Pastoral SCB and (c) western grey kangaroo density (km^{-2}) in Gawler SCB in South Australia.

Table 13.2. Standardised parameter estimates with standard errors (in brackets) and adjusted R^2 for the most parsimonious (according to backwards elimination) regression models (see Equation 4) predicting (a) red kangaroo harvest statistics, (b) eastern grey kangaroo harvest statistics, (c) western grey kangaroo harvest statistics, (d) red kangaroo population statistics, (e) eastern grey kangaroo population statistics, and (f) western grey kangaroo population statistics. The average 95% prediction interval (*95%PI*) is also shown for models predicting population statistics. Models are shown for kangaroo management zones (KMZs) in New South Wales (see Section 9, Fig. 9.1). Population statistics are log transformed kangaroo density (log*D*) and harvest rate expressed as a percentage (*HR%*). Harvest statistics are the percentage of the harvest comprising males (*%male*, arcsine transformed) and average male carcass weight (*male wt*). Explanatory variables include untransformed density (*D*), harvest rate expressed as a proportion (*HR*), *male wt*, the proportion of the harvest comprising males (*pmale*, arcsine transformed), rain falling in the same month of collection of the harvest statistic (*rn*.1.0), 3 months rain lagged 1 month prior to collection (*rn*.3.1), 12 months rain lagged 1 month prior to collection (*rn*.12.1), seasonal *cycle* comprising *sin*(2×π×*time*) and *cos*(2×π×*time*) terms, and a dummy variables (*skin*) representing the period when there was skin-only shooting. The parameter for *sin*(2×π×*time*) is given above the parameter for *cos*(2×π×*time*).

Table 13.2 cont.

(*a*) *Red kangaroos (New South Wales)*

KMZ	Response	Intercept	Explanatory variables								*Adj.* R^2
			D	D^2	*HR*	*rn*.1.0	*rn*.3.1	*rn*.12.1	*skin*	*cycle*	
1	*%male*	92.40 (0.73)	10.61 (3.16)	-10.49 (3.16)					-8.46 (1.38)	-0.87 (0.55) -1.38 (0.56)	0.33
	male wt	22.65 (0.27)	1.19 (0.27)								0.32
2	*%male*	98.45 (0.75)	2.63 (0.61)						-7.36 (1.30)		0.45
	male wt	21.50 (0.17)	0.54 (0.17)								0.25
4	*%male*	86.18 (0.90)							3.24 (1.48)		0.13
	male wt	21.24 (0.17)	-0.32 (0.20)		-0.49 (0.19)			0.55 (0.16)			0.45
6	*%male*	110.01 (2.2)									-
	male wt	21.44 (0.11)	2.21 (0.82)	-1.83 (0.82)		-0.18 (0.06)					0.29
7	*%male*	115.88 (1.0)	11.64 (3.82)	-9.17 (3.79)		-1.87 (0.50)	-1.71 (0.67)		-18.75 (1.75)		0.75
	male wt	22.17 (0.25)						0.66 (0.18)	-1.07 (0.42)	-0.15 (0.14) -0.45 (0.15)	0.45
8	*%male*	108.75 (1.4)	17.12 (4.87)	-14.30 (4.66)					6.47 (2.59)	-0.80 (0.72) -1.83 (0.80)	0.35
	male wt	23.47 (0.49)								-0.32 (0.15) -0.36 (0.17)	0.02
10	*%male*	117.85 (0.9)	14.53 (4.34)	-9.19 (4.29)	5.98 (1.08)						0.45
	male wt	22.49 (0.40)									-
11	*%male*	84.20 (0.73)							5.31 (1.23)		0.35
	male wt	24.00 (0.10)						0.60 (0.10)			0.41

Table 13.2 cont.

(*b*) *Eastern grey kangaroos (New South Wales)*

KMZ	Response	Intercept	Explanatory variables								*Adj.* R^2
			D	D^2	*HR*	*rn*.1.0	*rn*.3.1	*rn*.12.1	*skin*	*cycle*	
1	*%male*	100.09 (1.9)									-
	male wt	22.47 (0.20)	0.96 (0.20)						3.15 (0.73)		0.31
2	*%male*	97.75 (1.60)			-4.45 (1.56)				-9.17 (3.40)		0.08
	male wt	21.48 (0.17)	0.39 (0.17)							-0.42 (0.17) 0.19 (0.17)	0.08
4	*%male*	83.09 (0.46)	-15.96 (3.48)	17.51 (3.43)	2.88 (0.93)		-0.88 (0.41)				0.37
	male wt	23.20 (0.14)	-4.35 (1.05)	4.61 (1.07)				0.63 (0.15)		-0.22 (0.12) -0.31 (0.12)	0.52
6	*%male*	109.64 (1.9)	3.42 (1.68)						8.58 (3.52)		0.12
	male wt	20.56 (0.14)	0.46 (0.14)			-0.13 (0.06)				-0.08 (0.10) -0.22 (0.11)	0.29
7	*%male*	122.36 (1.0)			-2.81 (0.77)				-11.46 (1.64)		0.43
	male wt	21.56 (0.21)	2.50 (1.10)	-2.44 (1.07)	-0.58 (0.20)	-0.18 (0.08)			-1.09 (0.37)	-0.16 (0.13) -0.34 (0.14)	0.50
8	*%male*	98.15 (0.73)	2.16 (0.81)		-3.01 (0.78)					-0.39 (0.53) -1.17 (0.57)	0.50
	male wt	22.40 (0.10)	-1.67 (0.49)	1.73 (0.48)	-0.33 (0.10)				-1.21 (0.18)	-0.15 (0.08) -0.52 (0.08)	0.60
10	*%male*	112.24 (0.8)	1.59 (0.75)								0.11
	male wt	21.28 (0.29)			-0.44 (0.22)					-0.12 (0.09) 0.38 (0.10)	0.19
11	*%male*	88.08 (0.64)	-13.87 (5.92)	14.07 (5.80)	2.51 (0.68)	-0.55 (0.21)			2.91 (1.12)		0.47
	male wt	24.19 (0.18)	3.75 (1.74)	-3.42 (1.73)				0.32 (0.14)		-0.16 (0.09) -0.25 (0.10)	0.47

Table 13.2 cont.

(*c*) *Western grey kangaroos (New South Wales)*

KMZ	Response	Intercept	Explanatory variables								*Adj.* R^2
			D	D^2	*HR*	*rn*.1.0	*rn*.3.1	*rn*.12.1	*skin*	*cycle*	
1	*%male*	102.5 (1.57)								-0.78 (1.50) -3.44 (1.50)	0.04
	male wt	20.96 (0.97)			-0.78 (0.26)						0.15
2	*%male*	95.01 (0.72)	1.69 (0.66)						-6.85 (1.39)		0.19
	male wt	21.53 (0.16)	0.98 (0.18)		0.50 (0.15)			0.34 (0.11)		-0.22 (0.10) 0.17 (0.10)	0.41
4	*%male*	86.80 (0.63)	2.91 (0.62)								0.35
	male wt	20.63 (0.18)	-2.90 (1.17)	3.71 (1.17)							0.51
6	*%male*	109.10 (1.3)	-33.71 (13.2)	33.53 (13.19)		1.35 (0.68)					0.10
	male wt	20.65 (0.11)	0.55 (0.11)			-0.21 (0.06)				-0.23 (0.09) -0.18 (0.10)	0.40
7	*%male*	107.73 (1.7)	-25.80 (6.41)	27.91 (6.60)					-7.64 (3.20)		0.47
	male wt	21.26 (0.20)	0.63 (0.20)								0.17
10	*%male*	130.66 (1.6)									-
	male wt	21.89 (1.73)							-7.34 (1.21)		0.05
11	*%male*	92.70 (0.79)	24.08 (10.21)	-24.03 (10.07)	2.32 (1.09)						0.20
	male wt	22.05 (0.06)	-3.39 (0.92)	3.71 (0.91)	0.59 (0.09)			0.71 (0.07)			0.71

Table 13.2 cont.

(d) Red kangaroos (New South Wales)

KMZ	Response	Intercept	Explanatory variables		*Adj. R^2*	*95%PI*
			Male wt	*pmale*		
1	log*D*	2.94 (0.08)	0.30 (0.08)		0.56	3.27
	HR%	9.55 (0.76)			-	-
2	log*D*	2.57 (0.07)	0.21 (0.07)		0.42	2.76
	HR%	13.09 (1.17)			-	-
4	log*D*	1.80 (0.10)			-	-
	HR%	13.91 (1.18)			-	-
6	log*D*	1.55 (0.07)	0.20 (0.07)		0.41	1.72
	HR%	11.09 (1.46)			-	-
7	log*D*	1.70 (0.14)			-	-
	HR%	9.36 (0.94)			-	-
8	log*D*	1.81 (0.20)			-	-
	HR%	7.36 (1.35)			-	-
10	log*D*	1.50 (0.14)			-	-
	HR%	8.91 (1.63)			-	-
11	log*D*	1.40 (0.08)			-	-
	HR%	10.18 (1.14)			-	-

Table 13.2 cont.

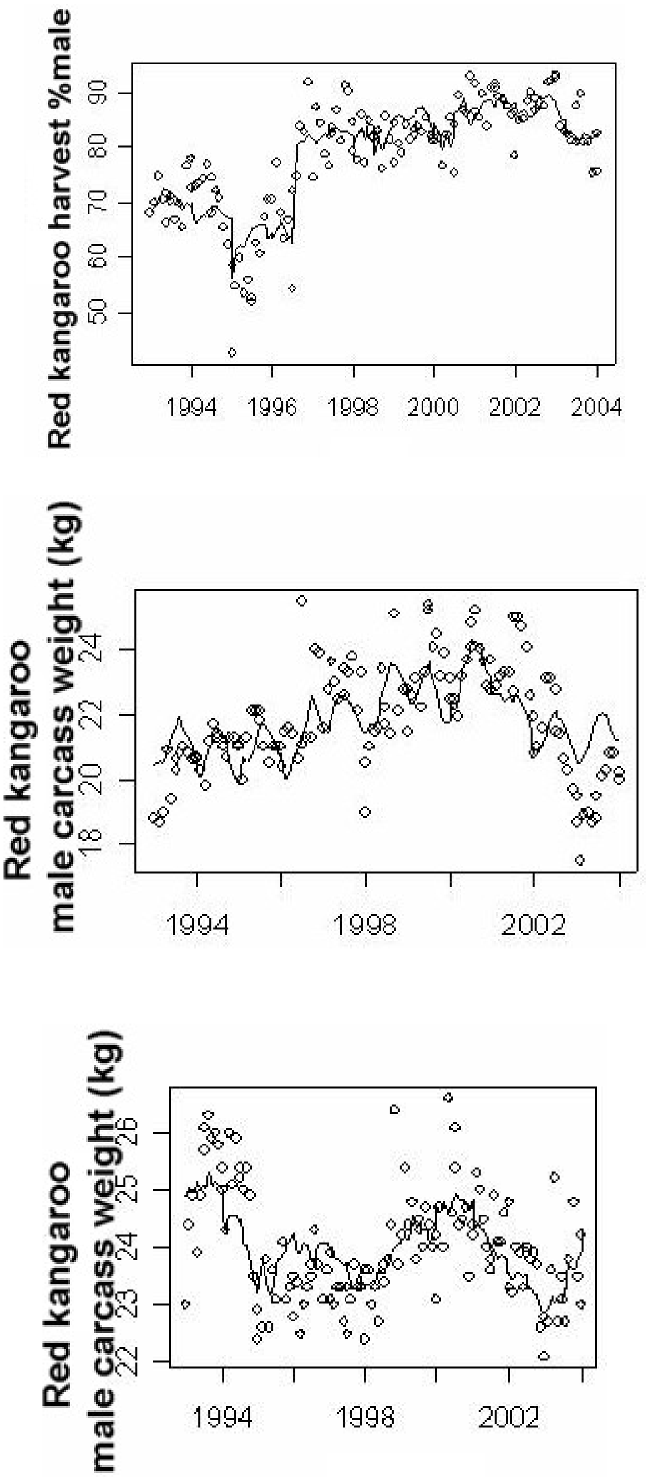
(*e*) *Eastern grey kangaroos (New South Wales)*

KMZ	Response	Intercept	Explanatory variables *Male wt*	 *pmale*	*Adj.* R^2	*95%PI*
1	log*D*	0.94 (0.10)	0.32 (0.12)	0.32 (0.12)	0.46	1.61
	HR%	3.40 (0.47)	-2.97 (1.19)	3.45 (1.19)	0.42	4.6
2	log*D*	1.15 (0.12)			-	-
	HR%	6.36 (0.10)			-	-
4	log*D*	1.09 (0.09)		-0.25 (0.09)	0.37	1.59
	HR%	9.18 (0.41)		1.31 (0.43)	0.46	6.7
6	log*D*	1.99 (0.07)			-	-
	HR%	5.90 (1.22)			-	-
7	log*D*	2.21 (0.13)			-	-
	HR%	5.36 (0.64)			-	-
8	log*D*	2.78 (0.12)		0.34 (0.12)	0.41	3.60
	HR%	9.64 (0.94)		-3.45 (0.99)	0.53	14.9
10	log*D*	3.27 (0.07)			-	-
	HR%	6.27 (0.86)			-	-
11	log*D*	2.29 (0.06)			-	-
	HR%	8.78 (0.72)			-	-

Table 13.2 cont.

(f) Western grey kangaroos (New South Wales)

KMZ	Response	Intercept	Explanatory variables		*Adj.* R^2	*95%PI*
			Male wt	*pmale*		
1	log*D*	-0.14 (0.12)	0.33 (0.13)		0.42	0.48
	HR%	9.33 (1.73)			-	-
2	log*D*	1.59 (0.07)	0.34 (0.08)		0.65	1.85
	HR%	12.36 (1.97)			-	-
4	log*D*	2.03 (0.12)			-	-
	HR%	10.27 (0.78)			-	-
6	log*D*	2.37 (0.05)	0.17 (0.06)		0.45	2.30
	HR%	4.30 (0.56)			-	-
7	log*D*	1.24 (0.09)	0.35 (0.10)		0.54	1.79
	HR%	5.36 (0.87)			-	-
10	log*D*	1.05 (0.11)			-	-
	HR%	1.55 (0.17)		0.44 (0.18)	0.34	2.6
11	log*D*	0.70 (0.08)			-	-
	HR%	11.10 (1.44)			-	-

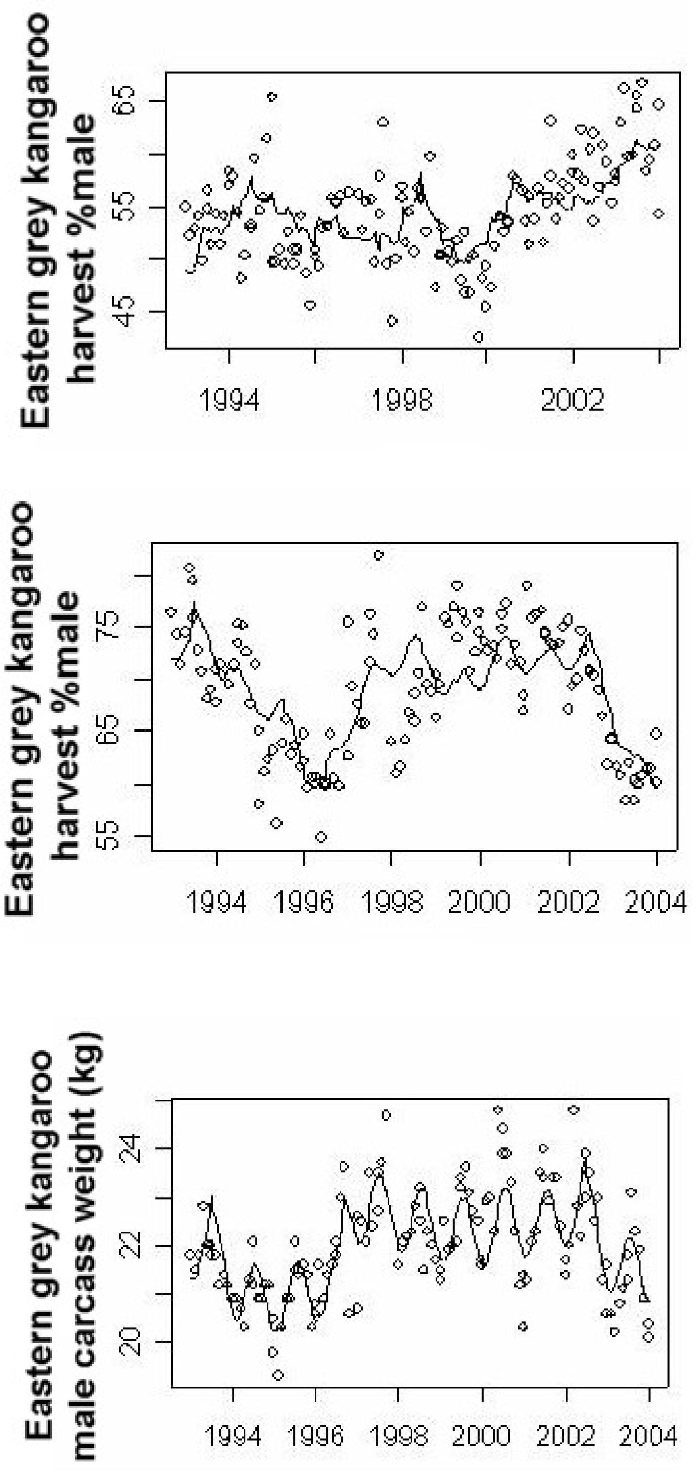


(*a*)

(*b*)

(*c*)

Fig. 13.8. Monthly (a) *%male* and (b) average male carcass weight in KMZ4 and (c) average male carcass weight in KMZ11 for harvested red kangaroos in New South Wales. Fitted models (Table 13.2*a*) are shown as solid lines.



(*a*)

(*b*)

(*c*)

Fig. 13.9. Monthly (a) *%male* in KMZ4 and (b) *%male* and (c) average male carcass weight in KMZ8 for harvested eastern grey kangaroos in New South Wales. Fitted models (Table 13.2*b*) are shown as solid lines.

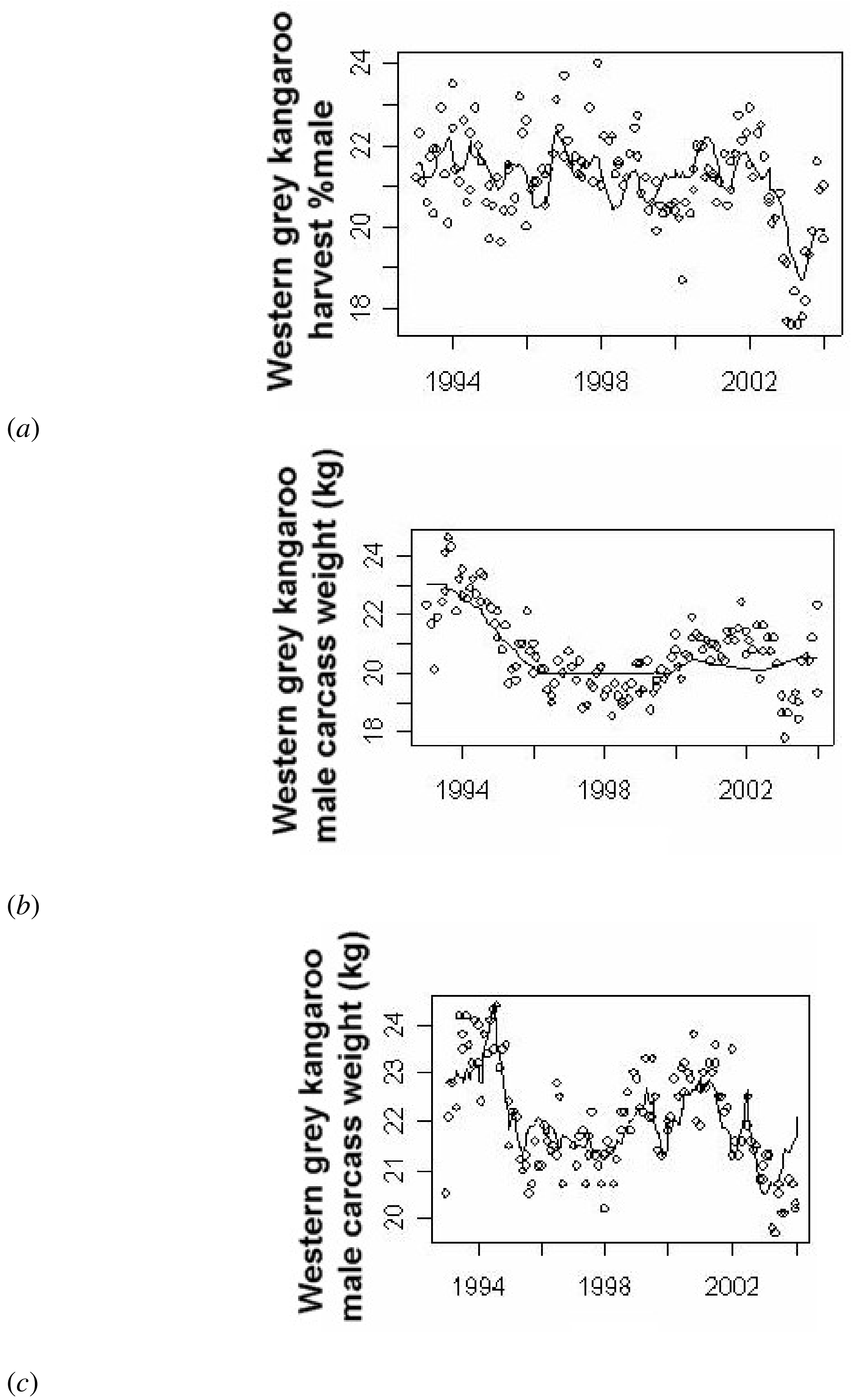


Fig. 13.10. Monthly (a) *%male* in KMZ2, (b) average male carcass weight in KMZ4 and (c) average male carcass weight in KMZ11 for harvested western grey kangaroos in New South Wales. Fitted models (Table 13.2*c*) are shown as solid lines.

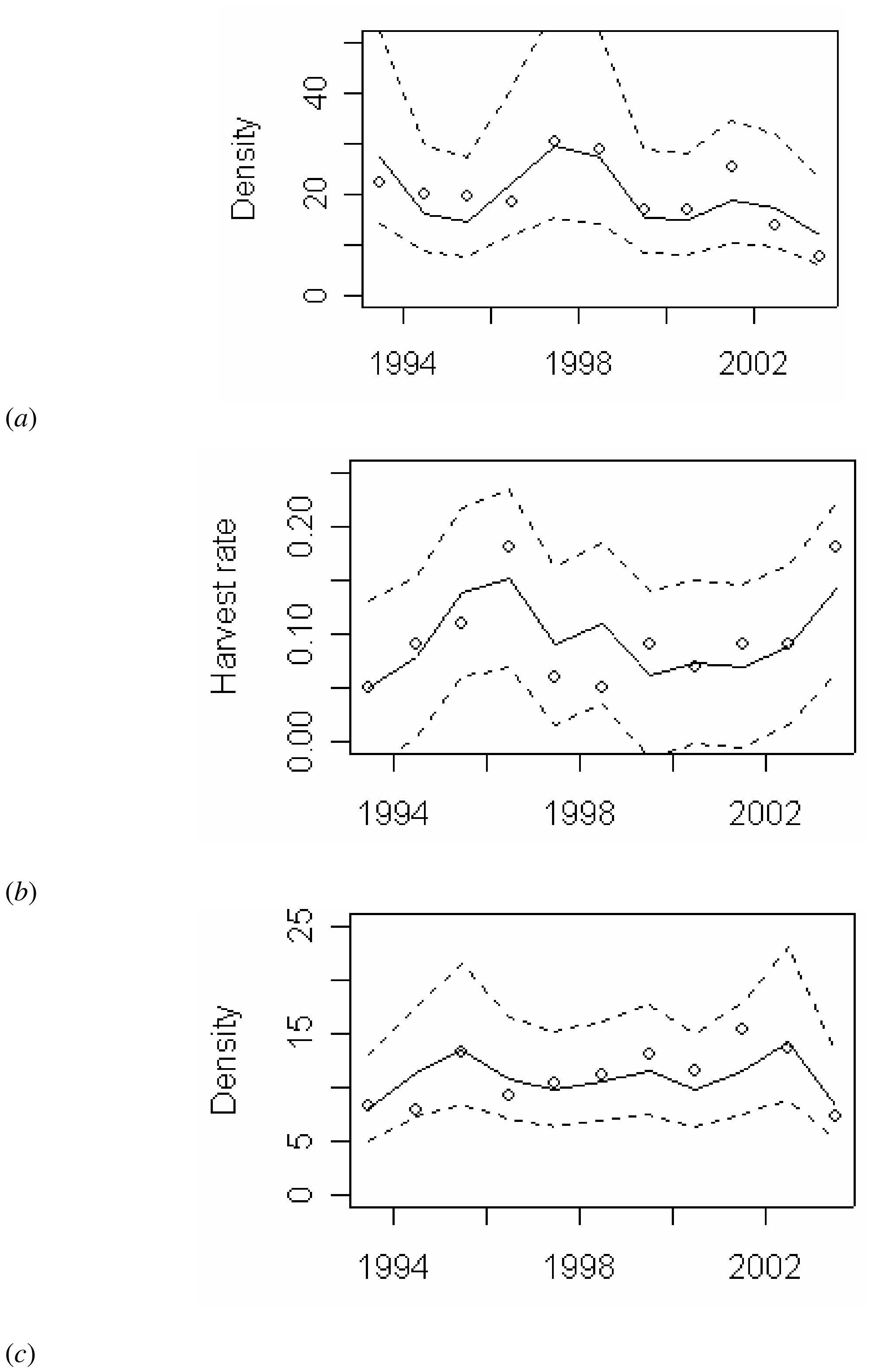


Fig. 13.11. Fitted models (solid line, Table 13.2*d*, *e* and *f*) and 95% prediction intervals (dashed lines) for (a) red kangaroo density (km^{-2}) in KMZ1, (b) harvest rate of eastern grey kangaroos in KMZ8 and (c) western grey kangaroo density (km^{-2}) in KMZ6 in New South Wales.

13.3.4 Queensland

While the harvest of all species and harvest effort in Queensland dropped substantially after 1995 (Figs 13.12 and 13.13*a*), there was a recovery in the offtake for eastern grey kangaroos and wallaroos but not red kangaroos. There is a marked seasonal cycle in the harvest, with greater effort (Fig. 13.13*a*) and offtake (Fig. 13.12) in the winter months. The closures of the harvest season for red kangaroos and wallaroos were met with sharp increases in *CPUE* for eastern grey kangaroos (Fig. 13.13*b*). On a regional scale, declines in the densities of red and eastern grey kangaroos during the drought of the early 1990s and their subsequent recovery (see Section 12) were mirrored by declines in the proportion of males in the harvest for each species (Fig. 13.14). Figure 13.14 also highlights the higher proportion of males in the carcass harvest than in the skin-only harvest. The wallaroo harvest has been comprised almost entirely of males (Fig. 13.14*c*). An exception was a brief period in the mid-1990s, just prior to the industry's collapse, when very small skins were accepted into the industry and high prices were paid for small carcasses providing a market for female wallaroos. The percentage of the harvest that is skin-only has declined to less than 20% in recent years, although there continues to be considerable monthly variation in this percentage (Fig. 13.15).

Standardised parameter estimates for models predicting harvest and population statistics in South Australia are shown in Table 13.3. There have been considerable fluctuations in all three harvest statistics over the 13-year study period in Queensland, coinciding with a period of drought in the early 1990s, good rainfall in the late 1990s followed by dry seasons. Examples of good model fits are shown for the three harvest statistics for the three species in Figures 13.16, 13.17 and 13.18.

Kangaroo density and harvest rate were again important influences on harvest statistics for all three species. Recent rainfall entered into the models for eastern grey kangaroos and wallaroos as minor negative influences in some blocks, but not for red kangaroos. Twelve months rainfall was a predictor for red kangaroo carcass weight in half of the blocks, but only in three cases for the other species. The number of shooter nights (i.e. effort) influenced harvest composition in some cases, but the sign of the coefficient varied. This is likely to reflect variation in selectivity among shooters. Skin-only harvesting generally had a positive influence on *%male* and *male wt*, indicating that smaller and often female animals were being taken for skins. There are likely to be economic reasons for this that are not explored here. *pskin* also had a positive effect on *CPUE* indicating that skin-only shooting allows higher catch rates. The dummy variable for the harvest season for red kangaroos (*red.hs*) had a strong negative coefficient for *CPUE* for eastern grey kangaroos and wallaroos in most blocks as expected from inspection of Fig.13.13*b*. The dummy variable generally had a positive coefficient for *%male* and *male wt*, suggesting that shooters were more selective when three rather than two species could be shot. The blocks where *red.hs* was not important had low densities of eastern grey kangaroos or wallaroos. Seasonal cycles were again incorporated into many models, being more marked than in the southern states. Likelihood ratio tests supported a correlated error structure for all models.

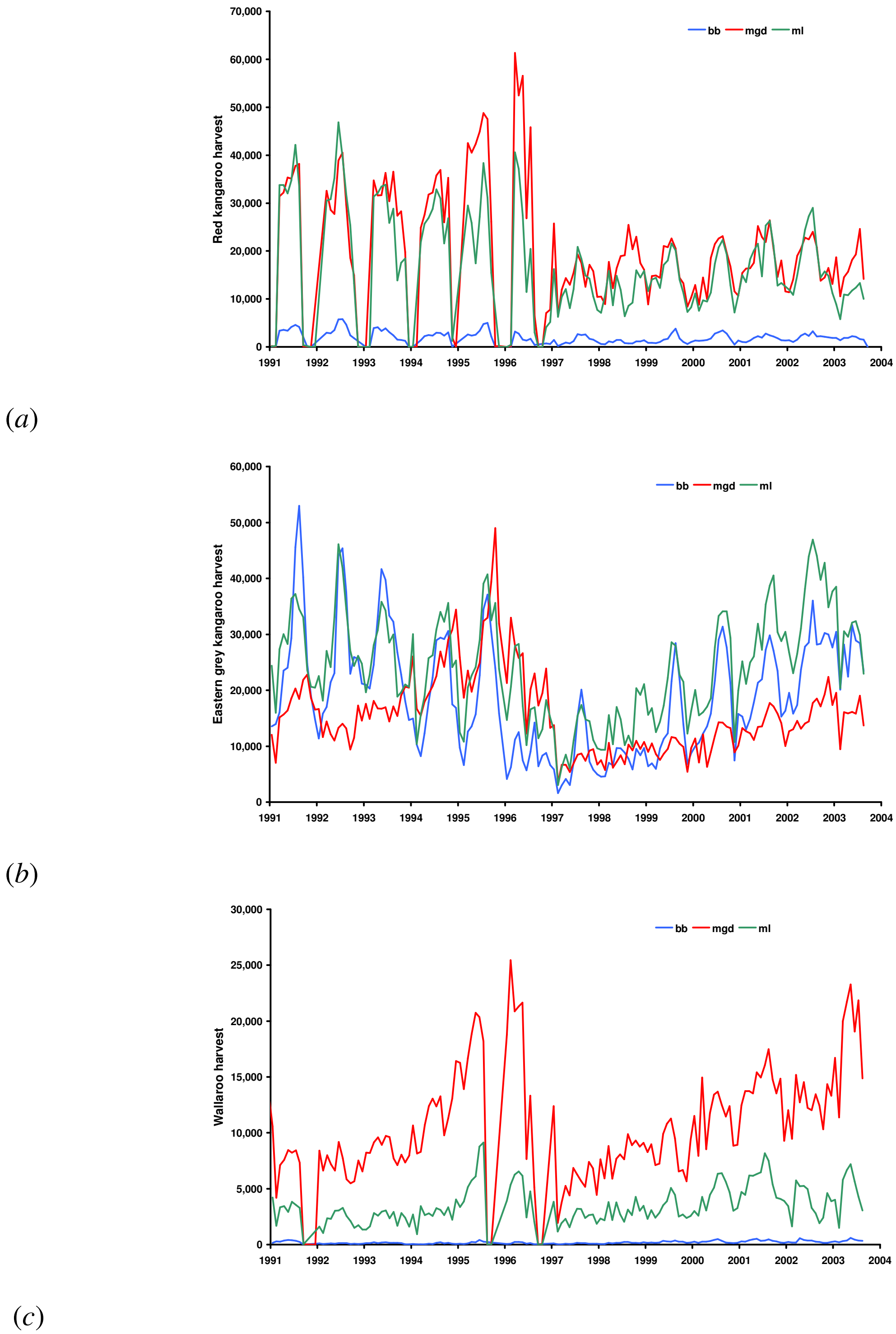
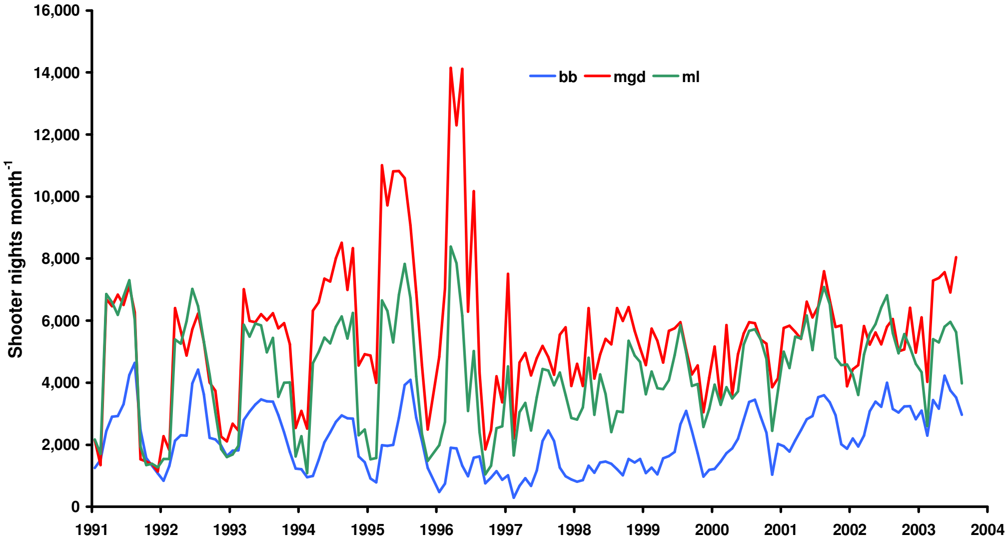
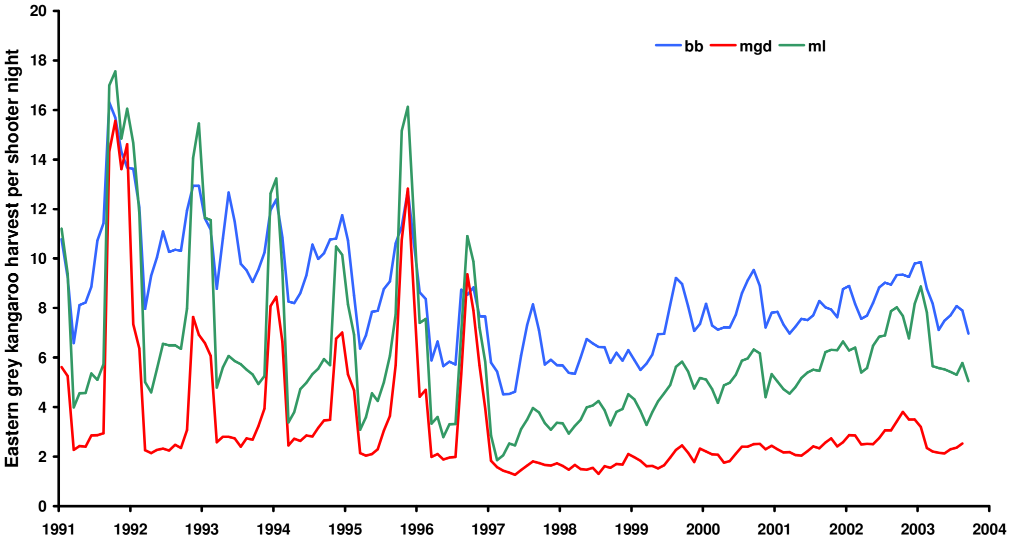


Fig. 13.12. Monthly harvest of (a) red kangaroos, (b) eastern grey kangaroos and (c) wallaroos in Queensland in the brigalow belt (bb, blue), mulga lands (ml, green) and Mitchell grass downs (mgd, red) regions (see Section 9, Fig. 9.1).

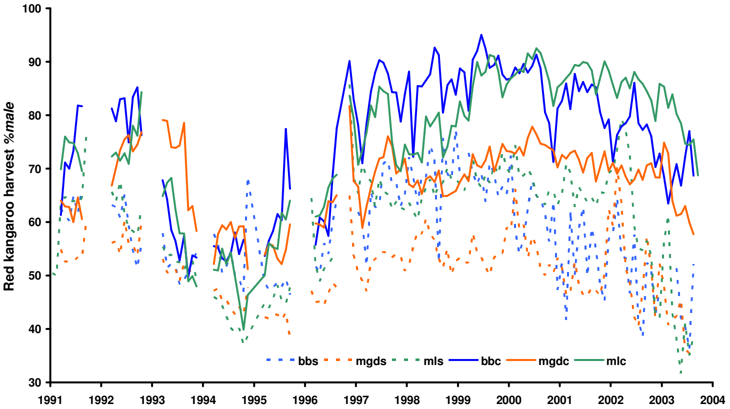


(*a*)

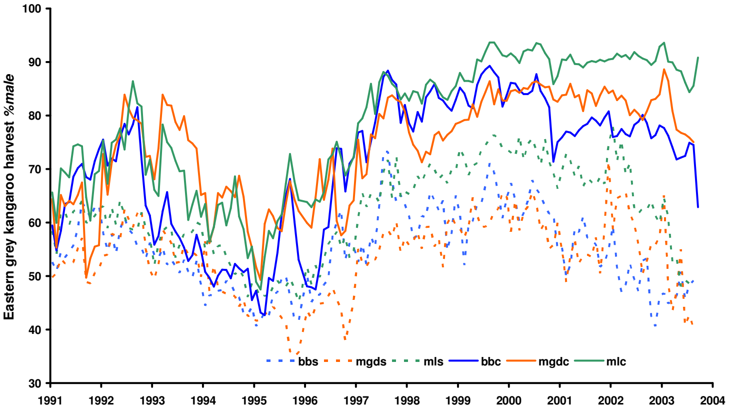


(*b*)

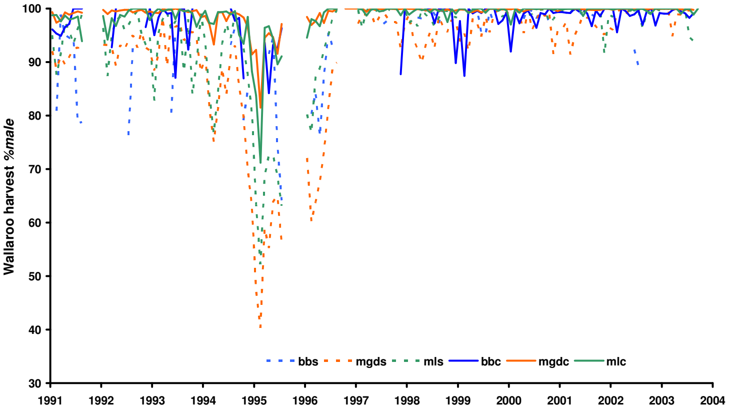
Fig. 13.13. Monthly (a) shooter nights (i.e. effort) and (b) *CPUE* of eastern grey kangaroos in the brigalow belt (bb, blue), mulga lands (ml, green) and Mitchell grass downs (mgd, red) regions in Queensland (see Section 9, Fig. 9.1).



(*a*)



(*b*)



(*c*)

Fig. 13.14. Monthly %male in the skin-only (dashed lines) and carcass (solid lines) harvest of (a) red kangaroos, (b) eastern grey kangaroos and (c) wallaroos in Queensland in the brigalow belt (bb, blue), mulga lands (ml, green) and Mitchell grass downs (mgd, red) regions (see Section 9, Fig. 9.1).

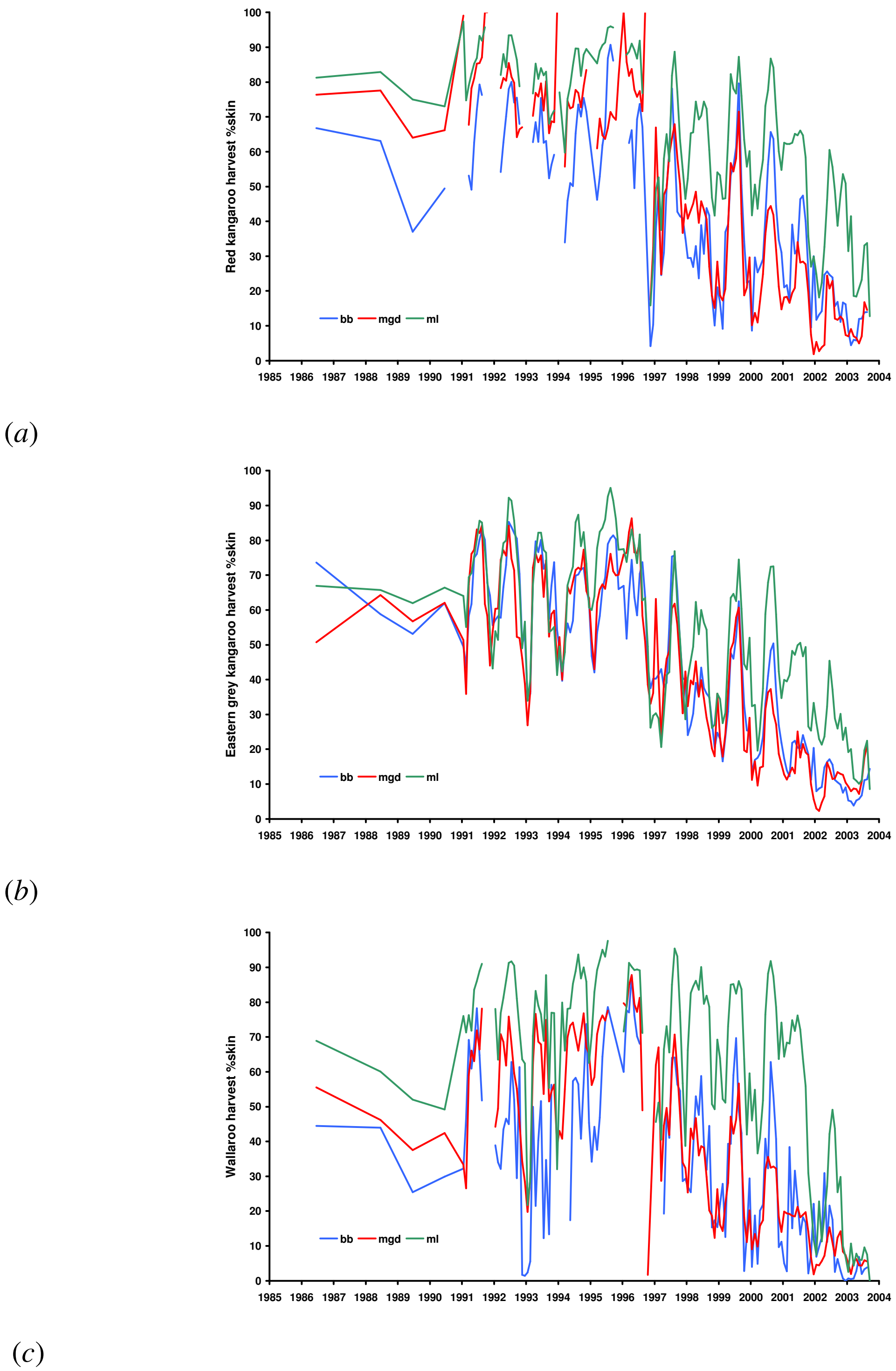


Fig. 13.15. Monthly (>1991) or annual (<1991) percentage of the harvest that is skin-only for (a) red kangaroos, (b) eastern grey kangaroos and (c) wallaroos in Queensland in the brigalow belt (bb, blue), mulga lands (ml, green) and Mitchell grass downs (mgd, red) regions (see Section 9, Fig. 9.1).

Table 13.3. Standardised parameter estimates with standard errors (in brackets) and adjusted R^2 for the most parsimonious (according to backwards elimination) regression models (see Equation 4) predicting (a) red kangaroo harvest statistics, (b) eastern grey kangaroo harvest statistics, (c) wallaroo harvest statistics, (d) red kangaroo population statistics, (e) eastern grey kangaroo population statistics, and (f) wallaroo population statistics. The average 95% prediction interval (*95%PI*) is also shown for models predicting population statistics. Models are shown for survey blocks in the Queensland core harvest area (see Section 9, Fig. 9.1). Population statistics are log transformed kangaroo density (log*D*) and harvest rate expressed as a percentage (*HR%*). Harvest statistics are catch-per-unit-effort (*CPUE*), the percentage of the carcass harvest comprising males (*%male*, arcsine transformed) and average male carcass weight (*male wt*). Explanatory variables include untransformed density (*D*), harvest rate expressed as a proportion (*HR*), *CPUE*, *male wt*, the proportion of the carcass harvest comprising males (*pmale*, arcsine transformed), rain falling in the same month of collection of the harvest statistic (*rn*.1.0), 3 months rain lagged 1 month prior to collection (*rn*.3.1) , 12 months rain lagged 1 month prior to collection (*rn*.12.1), the number of shooter-nights (*effort*), seasonal *cycle* comprising *sin*(2×π×*time*) and *cos*(2×π×*time*) terms, the proportion of the harvest that was skin-only (*pskin*), and a dummy variable (*red.hs*) for months when the harvest season for red kangaroos was open. The parameter for *sin*(2×π×*time*) is given above the parameter for *cos*(2×π×*time*). J, Julia Creek; Wt, Winton; L, Longreach; Wd, Windorah; Bk, Blackall; Cv, Charleville; H, Hungerford; Bo, Bollon; R, Roma; Wm, Westmar.

Table 13.3 cont.

(*a*) *Red kangaroos (Queensland)*

SCB	Response	Intercept	Explanatory variables									*Adj.* R^2
			D	D^2	*HR*	*rn*.1.0	*rn*.3.1	*rn*.12.1	*effort*	*pskin*	*cycle*	
J	*%male*	90.08 (1.60)	5.09 (1.61)									0.25
	CPUE	11.64 (0.40)								2.37 (0.40)		0.25
	male wt	26.14 (0.20)	1.74 (0.35)		1.63 (0.45)						-0.20 (0.22) -0.75 (0.21)	0.24
Wt	*%male*	93.18 (1.11)										-
	CPUE	4.72 (0.15)	0.94 (0.25)		1.13 (0.25)							0.29
	male wt	25.83 (0.25)	3.86 (1.63)	-3.43 (1.59)						0.80 (0.26)		0.20
L	*%male*	104.52 (2.5)			-6.86 (2.11)					2.32 (1.08)		0.35
	CPUE	2.94 (0.12)								0.40 (0.10)	0.07 (0.09) -0.23 (0.11)	0.37
	male wt	24.77 (0.32)								0.70 (0.26)	-0.50 (0.25) 0.08 (0.28)	0.18
Wd	*%male*	111.93 (2.7)			-13.70 (2.65)							0.53
	CPUE	6.65 (0.29)	0.69 (0.31)							1.36 (0.30)		0.20
	male wt	24.83 (0.26)	-13.89 (2.2)	13.79 (2.18)				2.24 (0.28)		1.22 (0.29)	-0.30 (0.27) 0.66 (0.26)	0.72
Bk	*%male*	98.51 (1.22)	-16.07 (8.7)	19.23 (8.58)	-8.03 (1.37)							0.62
	CPUE	2.76 (0.12)	2.57 (0.81)	-2.18 (0.80)	0.42 (0.15)					0.77 (0.10)		0.74
	male wt	21.59 (0.16)	-3.91 (1.35)	3.01 (1.32)	-1.08 (0.28)			0.37 (0.18)		1.37 (0.24)	-0.05 (0.15) -0.03 (0.17)	0.40
Cv	*%male*	115.41 (2.4)	14.68 (2.31)						-1.92 (0.91)			0.67
	CPUE	2.45 (0.04)	0.14 (0.07)		0.45 (0.07)						-0.00 (0.04) -0.10 (0.04)	0.73
	male wt	22.04 (0.23)	0.59 (0.27)					0.57 (0.23)		0.71 (0.22)		0.32
H	*%male*	106.94 (2.1)	6.15 (2.04)									0.18
	CPUE	7.16 (0.43)	-4.82 (2.23)	5.88 (2.17)	1.43 (0.49)					0.69 (0.30)		0.30
	male wt	23.86 (0.37)				0.57 (0.24)				1.23 (0.30)		0.18

Table 13.3 cont.

(*a*) *Red kangaroos (Queensland)*

SCB	Response	Intercept	Explanatory variables									Adj. R^2
			D	D^2	*HR*	*rn*.1.0	*rn*.3.1	*rn*.12.1	*effort*	*pskin*	*cycle*	
Bo	*%male*	119.08 (2.7)	60.74 (13.8)	-41.97 (14.0)						8.15 (2.61)		0.51
	CPUE	2.35 (0.09)			0.27 (0.09)						0.17 (0.07) -0.12 (0.08)	0.20
	male wt	21.96 (0.24)	0.57 (0.24)					0.97 (0.23)				0.28
R	*%male*	110.4 (3.7)	-5.45 (2.37)									0.16
	CPUE	0.56 (0.02)	0.42 (0.11)	-0.30 (0.10)	0.19 (0.03)					0.17 (0.02)		0.63
	male wt	22.12 (0.22)	-0.64 (0.24)							-1.01 (0.23)		0.18
Wm	*%male*	107.47 (3.2)										-
	CPUE	0.46 (0.03)								0.14 (0.03)	0.10 (0.03) 0.04 (0.03	0.22
	male wt	24.18 (0.33)						0.90 (0.33)		0.70 (0.32)		0.13

Table 13.3 cont.

(b) Eastern grey kangaroos (Queensland)

SCB	Response	Intercept	Explanatory variables										*Adj. R^2*
			D	*D^2*	*HR*	*rn*.1.0	*rn*.3.1	*rn*.12.1	*effort*	*pskin*	*cycle*	*red.hs*	
J	*%male*	115.59 (4.91)								-4.44 (1.89)			-0.03
	CPUE	50.76 (7.05)	-81.17 (25)	47.50 (23.6)	-29.25 (7.19)						-11.48 (4.02) -5.25 (4.55)		0.40
	male wt	25.62 (0.17)									-0.40 (0.18) -1.04 (0.18)		0.22
Wt	*%male*	90.62 (4.31)	21.33 (7.36)	-20.26 (7.3)			-3.47 (1.23)		2.48 (1.04)			10.57 (4.30)	0.30
	CPUE	18.93 (2.75)										-10.01 (2.66)	0.08
	male wt	23.59 (0.59)	-2.34 (0.82)	3.21 (0.83)	0.64 (0.20)						-0.22 (0.16) -0.58 (0.17)	1.73 (0.62)	0.45
L	*%male*	102.49 (2.82)	-34.03 (9.8)	29.77 (9.64)	-5.28 (2.00)							-9.69 (2.52)	0.40
	CPUE	30.75 (2.23)	-32.84 (5.5)	26.05 (5.38)						-2.19 (0.91)		-20.74 (2.35)	0.67
	male wt	23.05 (0.42)	-3.73 (0.90)	3.13 (0.89)	-1.03 (0.22)					0.59 (0.18)	-0.63 (0.14) -0.55 (0.15)	1.39 (0.45)	0.54
Wd	*%male*	126.76 (0.94)	10.02 (1.16)			-4.32 (1.52)	-4.66 (1.76)				0.39 (1.82) 4.57 (1.33)		0.71
	CPUE	80.78 (7.69)	-154.9 (46)	136.7 (46.1)	-20.87 (9.25)								0.27
	male wt	26.22 (0.44)			-2.46 (0.44)								0.38
Bk	*%male*	101.90 (4.54)			-46.37 (11.98)					16.88 (4.69)		6.42 (2.21)	0.50
	CPUE	4.84 (0.32)			0.42 (0.17)	-0.29 (0.09)					-0.55 (0.13) 0.16 (0.14)	-2.73 (0.33)	0.60
	male wt	19.80 (0.25)									-0.13 (0.09) -0.32 (0.10)	0.76 (0.27)	0.26
Cv	*%male*	112.51 (1.40)	8.17 (2.08)		-14.31 (2.06)					2.23 (0.82)			0.87
	CPUE	7.47 (0.39)			1.27 (0.19)							-4.70 (0.40)	0.77
	male wt	19.88 (0.31)	0.73 (0.23)		-1.17 (0.23)					0.79 (0.12)		0.72 (0.31)	0.78
H	*%male*	107.61 (4.25)	13.59 (3.20)	-9.71 (3.09)								15.13 (4.52)	0.38
	CPUE	59.10 (7.66)	-29.10 (6.5)	23.22 (6.38)						-4.59 (1.82)		-34.45 (7.65)	0.40
	male wt	21.46 (0.58)	4.84 (1.32)	-4.67 (1.34)				0.81 (0.26)		0.55 (0.19)		2.66 (0.60)	0.45

Table 13.3 cont.

(b) Eastern grey kangaroos (Queensland)

SCB	Response	Intercept	Explanatory variables									*Adj. R^2*
			D	*D^2*	*HR*	*rn*.1.0	*rn*.3.1	*rn*.12.1	*effort*	*pskin*	*cycle*	*red.hs*	
Bo	*%male*	110.82 (3.04)	79.27 (8.27)	-61.12 (7.55)	4.41 (1.98)							8.84 (3.19)	0.80
	CPUE	34.40 (2.06)	-15.61 (4.7)	12.90 (4.31)	2.38 (1.13)						0.27 (0.68) 3.31 (0.74)	-20.97 (2.2)	0.76
	male wt	20.75 (0.16)	0.69 (0.23)		-0.76 (0.26)			0.46 (0.19)	0.34 (0.15)				0.56
R	*%male*	93.67 (2.07)	-4.82 (1.93)		-10.10 (1.87)	-0.66 (0.30)	-1.47 (0.53)					2.71 (1.21)	0.73
	CPUE	8.37 (0.57)			1.02 (0.35)	-0.41 (0.14)					0.01 (0.24) 0.69 (0.27)	-4.07 (0.58)	0.62
	male wt	20.48 (0.30)			-0.34 (0.15)			0.45 (0.12)		-0.49 (0.14)	-0.32 (0.11) -0.32 (0.12)	1.26 (0.32)	0.62
Wm	*%male*	103.09 (1.82)	5.30 (1.97)		-10.21 (1.85)	-1.54 (0.77)	-3.48 (1.13)			3.69 (1.49)			0.48
	CPUE	19.80 (2.11)	-2.87 (0.98)							2.33 (1.04)	2.33 (0.83) 3.84 (0.95)	-759 (2.29)	0.48
	male wt	21.66 (0.16)	6.63 (1.05)	-5.87 (1.06)	-1.33 (0.18)				0.43 (0.18)	0.48 (0.18)			0.57

Table 13.3 cont.

(*c*) *Wallaroos (Queensland)*

SCB	Response	Intercept	Explanatory variables										Adj. R^2
			D	D^2	*HR*	*rn*.1.0	*rn*.3.1	*rn*.12.1	*effort*	*pskin*	*cycle*	*red.hs*	
Wt	*%male*	151.65 (1.15)											-
	CPUE	1.66 (0.33)										-0.82 (0.33)	0.03
	male wt	23.40 (0.20)	-1.37 (0.57)	1.21 (0.58)					0.62 (0.19)				0.26
L	*%male*	149.83 (1.35)							-2.63 (0.45)			4.51 (1.45)	0.17
	CPUE	3.61 (0.29)	-2.14 (0.91)	2.73 (0.90)								-1.36 (0.29)	0.38
	male wt	23.10 (0.27)				-0.28 (0.13)							0.04
Bk	*%male*	146.13 (1.74)			-4.84 (1.00)				-3.02 (0.69)	2.05 (0.77)		6.30 (1.87)	0.64
	CPUE	7.26 (0.22)	1.08 (0.15)		0.34 (0.15)		-0.22 (0.08)					-3.47 (0.22)	0.74
	male wt	19.94 (0.12)			-0.74 (0.16)					0.81 (0.15)			0.27
Cv	*%male*	146.82 (2.54)	3.90 (0.99)							3.31 (0.98)	-0.79 (0.95) 2.11 (0.93)	7.00 (2.73)	0.29
	CPUE	1.31 (0.07)	0.64 (0.12)	-0.40 (0.12)			-0.06 (0.03)				0.05 (0.03) 0.01 (0.02)	-0.44 (0.08)	0.59
	male wt	20.88 (0.16)	3.80 (0.74)	-2.84 (0.74)		-0.40 (0.11)							0.47
R	*%male*	150.60 (0.95)											-
	CPUE	0.12 (0.02)								-0.03 (0.01)		0.06 (0.02)	0.37
	male wt	21.83 (0.12)	0.69 (0.46)	-0.90 (0.45)					-0.36 (0.16)	-1.09 (0.21)	-0.23 (0.13) -0.56 (0.14)		0.30

Table 13.3 cont.

(*d*) *Red kangaroos (Queensland)*

SCB	Response	Intercept	Explanatory variables *CPUE*	 *pmale*	 *male wt*	*Adj. R*^{2}	*95%PI*
J	log*D*	1.88 (0.23)				-	-
	HR%	14.00 (2.14)				-	-
Wt	log*D*	1.67 (0.16)				-	-
	HR%	16.33 (1.74)	6.68 (1.85)			0.60	26.3
L	log*D*	2.55 (0.10)				-	-
	HR%	10.30 (0.88)	2.99 (1.07)	-4.01 (1.07)		0.60	14.5
Wd	log*D*	2.14 (0.12)				-	-
	HR%	8.43 (0.90)	16.01 (5.64)	-21.35 (5.6)		0.87	8.8
Bk	log*D*	2.24 (0.09)		0.25 (0.09)		0.39	2.67
	HR%	33.36 (4.88)		-19.39 (5.1)		0.57	68.6
Cv	log*D*	1.67 (0.09)		0.41 (0.10)		0.61	2.26
	HR%	34.92 (2.94)	15.74 (3.08)		-8.46 (3.08)	0.75	48.6
H	log*D*	1.56 (0.10)		0.35 (0.10)		0.50	2.18
	HR%	13.10 (3.13)				-	-
Bo	log*D*	1.46 (0.16)		0.50 (0.17)		0.44	2.61
	HR%	23.36 (5.79)	15.17 (6.07)			0.34	69.6
R	log*D*	0.08 (0.18)				-	-
	HR%	25.70 (7.61)				-	-
Wm	log*D*	-1.07 (0.16)				-	-
	HR%	57.11 (12.2)				-	-

Table 13.3 cont.

(*e*) *Eastern grey kangaroos (Queensland)*

SCB	Response	Intercept	Explanatory variables			*Adj. R^2*	*95%PI*
			CPUE	*pmale*	*male wt*		
J	log*D*	0.58 (0.27)				-	-
	HR%	7.33 (0.95)		-4.97 (1.04)		0.81	12.9
Wt	log*D*	1.40 (0.13)				-	-
	HR%	11.38 (3.17)				-	-
L	log*D*	2.32 (0.10)	-0.32 90.11)			0.45	3.06
	HR%	10.18 (0.89)	4.61 (1.00)	-3.69 (1.00)		0.71	18.0
Wd	log*D*	1.55 (0.11)				-	-
	HR%	3.43 (0.96)		-2.68 (1.04)		0.48	10.8
Bk	log*D*	2.21 (0.09)	0.34 (0.10)	0.37 (0.10)		0.64	2.81
	HR%	31.58 (4.63)	-18.80 (4.8)			0.56	65.7
Cv	log*D*	2.67 (0.10)		0.51 (0.11)		0.68	3.41
	HR%	23.36 (1.60)		-13.53 (1.7)		0.86	25.2
H	log*D*	1.57 (0.19)				-	-
	HR%	8.09 (2.07)				-	-
Bo	log*D*	3.18 (0.08)		0.45 (0.09)		0.70	3.68
	HR%	12.75 (2.08)			-6.25 (2.17)	0.40	26.9
R	log*D*	3.03 (0.14)				-	-
	HR%	17.33 (2.47)		-9.69 (2.58)		0.54	35.4
Wm	log*D*	3.26 (0.10)				-	-
	HR%	16.09 (1.45)		-5.51 (1.52)		0.55	21.7

Table 13.3 cont.

(*f*) *Wallaroos (Queensland)*

SCB	Response	Intercept	Explanatory variables			*Adj.* R^2	*95%PI*
			CPUE	*pmale*	*male wt*		
Wt	log*D*	-0.20 (0.22)				-	-
	HR%	12.44 (2.99)				-	-
L	log*D*	2.09 (0.22)				-	-
	HR%	16.91 (3.13)		-9.11 (3.29)		0.40	39.4
Bk	log*D*	2.93 (0.11)	0.53 (0.11)	0.48 (0.11)		0.76	3.92
	HR%	33.00 (5.30)		-21.94 (5.5)		0.57	73.4
Cv	log*D*	1.11 (0.17)	0.73 (0.18)			0.61	2.60
	HR%	22.00 (3.19)	-7.80 (3.35)			0.31	46.1
R	log*D*	-0.41 (0.57)				-	-
	HR%	9.67 (1.89)				-	-

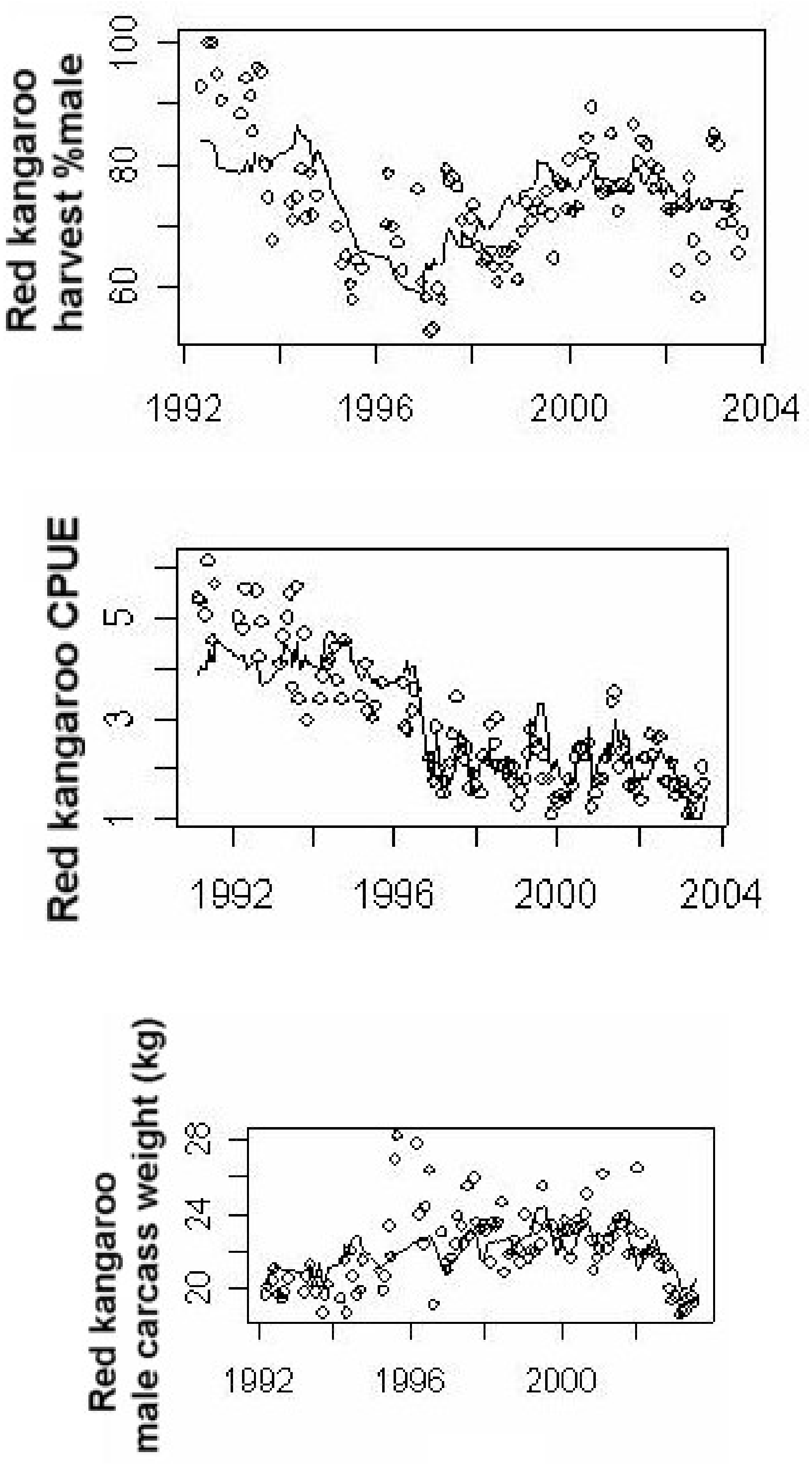
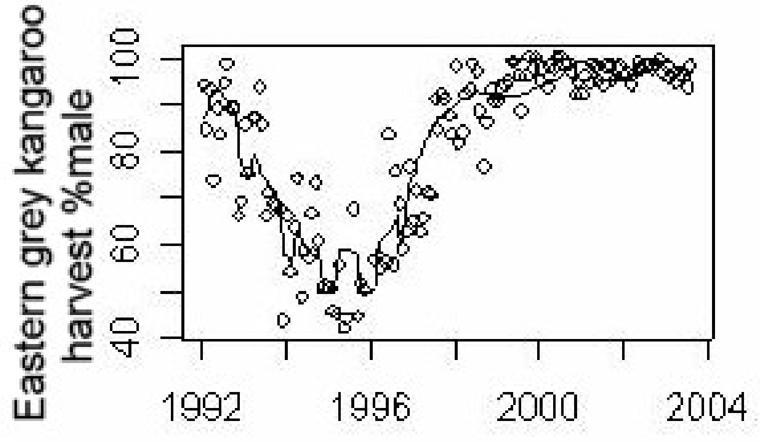
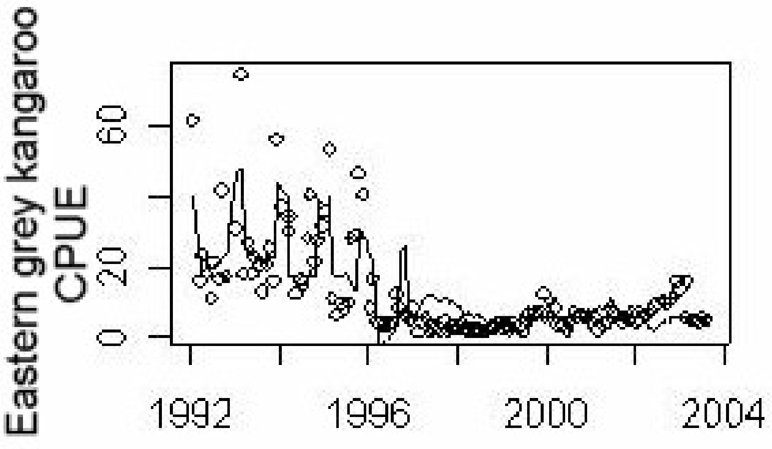


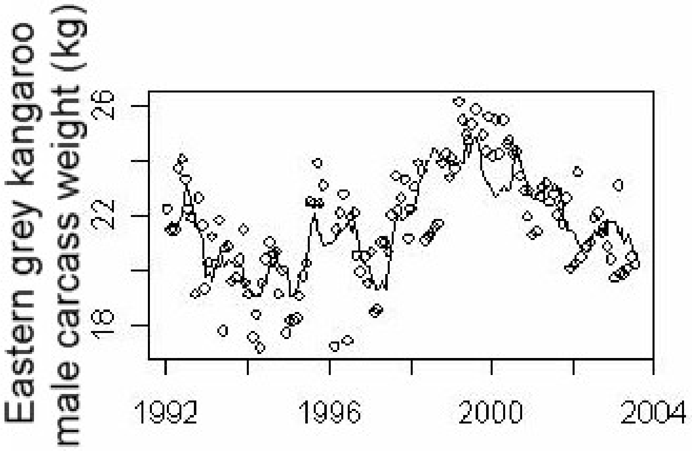
Fig. 13.16. Monthly (a) *%male* at Longreach and (b) *CPUE*at Blackall and (c) average male carcass weight at Charleville for harvested red kangaroos in Queensland. Fitted models (Table 13.3*a*) are shown as solid lines.



(*a*)



(*b*)



(*c*)

Fig. 13.17. Monthly (a) *%male* at Bollon, (b) *CPUE* at Longreach and (c) average male carcass weight at Westmar for harvested eastern grey kangaroos in Queensland. Fitted models (Table 13.3*b*) are shown as solid lines.

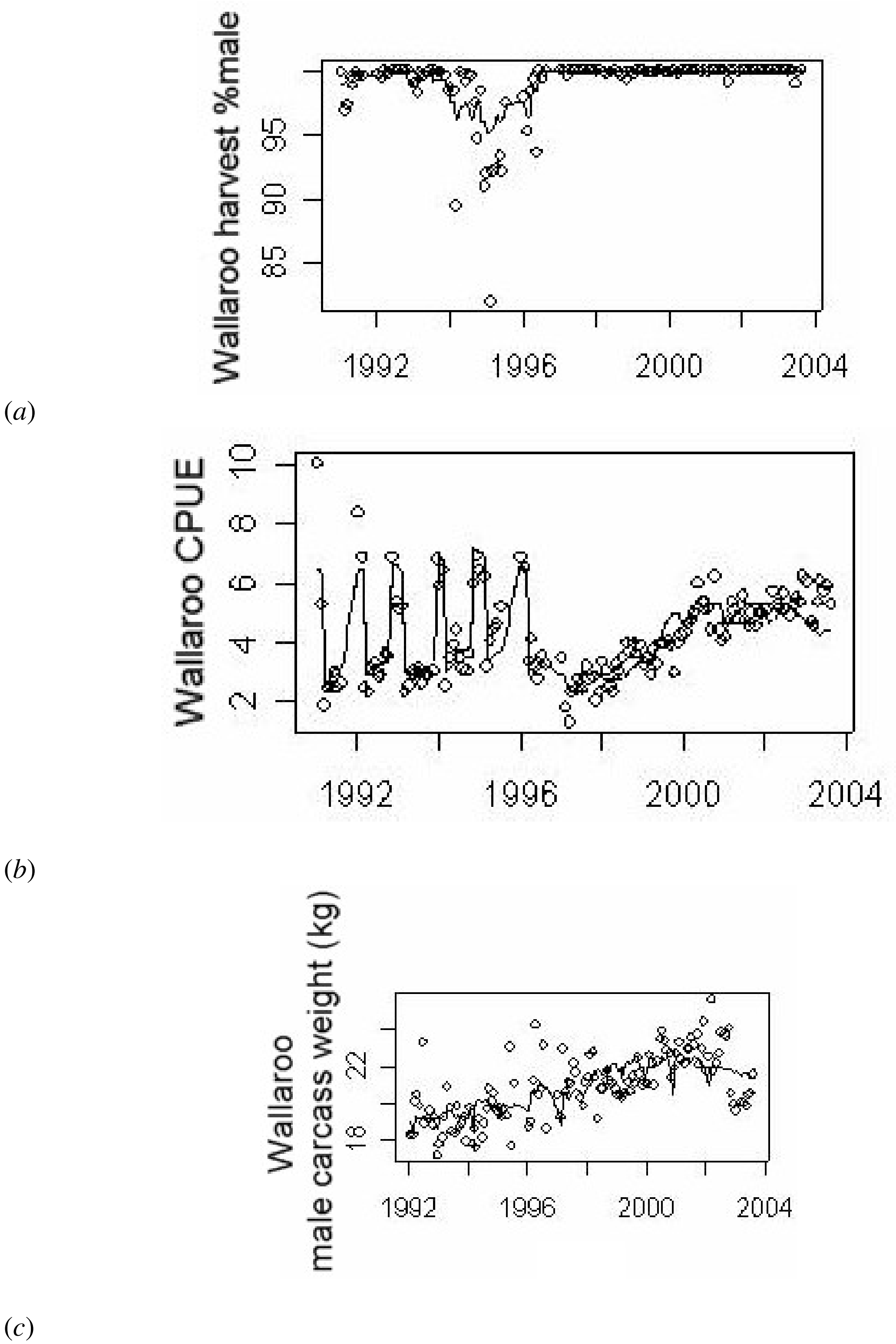


Fig. 13.18. Monthly (a) *%male* and (b) *CPUE* at Blackall and (c) average male carcass weight at Charleville for harvested wallaroos in Queensland. Fitted models (Table 13.3*c*) are shown as solid lines.

Predictive models for population statistics were possible in the higher density blocks for all species. Correlated error structures did not improve any models predicting population statistics. Approximate precision of predictions of density and harvest rate ranged 0.26-0.74 for red kangaroos, 0.27-0.79 for eastern grey kangaroos and 0.33-0.59 for wallaroos. These estimates of precision are comparable to direct estimates of population size using aerial survey. Examples of fitted models are shown in Figure 13.19.

13.4 Discussion

The models presented here show that kangaroo harvest statistics change over time in response to changes in population density and harvest rate. Usefully for management, these relationships are sufficiently precise to indirectly monitor populations. They could be used in two ways. Firstly, a consistent shift in a statistic over a number of months may indicate a decline in density or increase in harvest rate. If the likely density or harvest rate is of concern, then management action such as quota revision may be triggered. Other factors such as rainfall and season would need to be taken into account. Whether harvest rate or density or both were involved would need to be teased apart. The second use is for quota setting when direct estimates of population size (e.g. from aerial survey) are unavailable.

Important caveats to the preceding conclusions are that not all regions and blocks had useful relationships between harvest and population statistics and there was considerable variation among regions in the form of the relationship. There is certainly no one relationship that could be applied across an entire state or across species. Statewide trigger points for harvest statistics (i.e. values that trigger management action) that are used in Queensland (Queensland Parks and Wildlife Service 2003) are inappropriate. Regional and species-specific trigger points, as discussed above, could be used in many cases. This regional variation in harvest statistics is explored further in Section 14.

Unfortunately, economic factors such as prices paid for skins and carcasses could not be incorporated into the analyses here. Prices fluctuate with both demand for product and availability of kangaroos to shooters and should influence CPUE and the selectivity of shooters. Inclusion of economic data would be expected to tighten the relationships described here. The fact that good relationships were found without economic data highlights the strength of the connection between harvest and population statistics.

If harvest statistics are to be used to indirectly monitor populations in kangaroo management, then they must be considered within the framework described in Section 5 and compared with the alternative of using rainfall to predict rate of increase that described in Section 9. Reductions in survey frequency are most appropriate in the lower harvest regions and more mesic regions within each state. Rainfall models were poor predictors of rate increase in central and northern Queensland, in lower density regions in South Australia and to some extent New South Wales. Harvest statistics can fill some but not all these gaps, and can supplement rainfall models in regions where both forms of indirect monitoring have good relationships. Harvest statistics are most likely to be useful in Queensland. The relationships

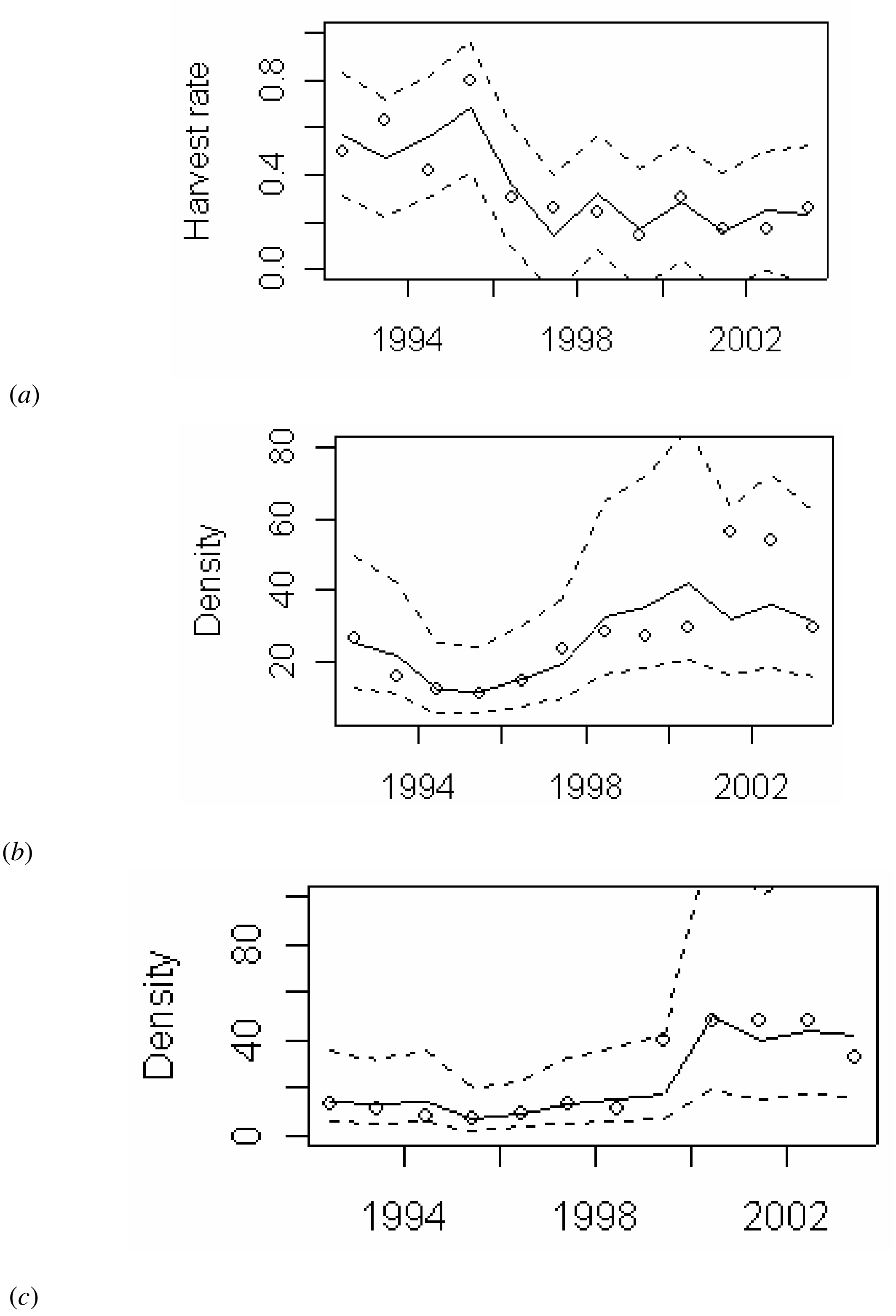


Fig. 13.19. Fitted models (solid line, Table 13.3*d*, *e* and *f*) and 95% prediction intervals (dashed lines) for (a) red kangaroo harvest rate at Charleville, (b) eastern grey kangaroo density (km^{-2}) at Bollon and (c) wallaroo density (km^{-2}) at Blackall in Queensland.

between harvest and population statistics were not explored outside the core survey area in Queensland. In these areas survey frequency is already less than annual. However, the relationships described here cannot be readily extrapolated to new areas, as the regional variation in the relationships demonstrated.

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14. Determinants of spatial variation in kangaroo harvest composition, catch-per-unit-effort and harvest rate

14.1 Introduction

Kangaroo harvest rate, harvest composition and catch-per-unit-effort (*CPUE*) will vary regionally for a number of reasons. These include the density of all harvested kangaroo species, extent of the road network, distance to major towns that provide a base for many shooters and contain the dealer sites where carcasses and skins are brought for sale, and factors influencing access to animals such as vegetation. An understanding of the spatial determinants of harvest rate will allow kangaroo managers to identify likely areas of over- or under-harvest. This is particularly useful when direct estimates of harvest rate are unavailable, such as in Queensland where aerial surveys of kangaroos have incomplete geographic coverage (see Section 9, Fig. 9.2).

If managers are to use harvest statistics to indirectly monitor kangaroo populations, then an appreciation of the geographic variation in harvest statistics and its likely determinants will help. In Section 13, regional variation in harvest statistics was recognised and so the relationship between harvest and population statistics was examined for each region separately. However, there are unsurveyed or infrequently surveyed areas for which relationships could not be developed. Assessment of the spatial variation in harvest statistics may allow interpretation of harvest statistics in these areas, although such extrapolation should be conducted cautiously. Again, in Queensland, incomplete coverage by aerial survey meant that temporal variation in harvest statistics could only be assessed in monitor blocks in Section 13. Trends in harvest statistics outside these blocks can only be interpreted in terms of changes in density or harvest rate if the spatial variation in the relationship between harvest and population statistics is understood. For example, an unsurveyed area with a low percentage of males in the harvest cannot be interpreted as reflecting low density or high harvest rate until other factors have been discounted. A baseline value for harvest statistics where harvest rate and kangaroo density are held constant in each area is therefore required.

This section firstly describes geographic variation in kangaroo harvest rate, harvest composition and *CPUE* across the main harvest area in eastern Australia. The relationship between harvest composition and population statistics on a broad scale across the study area is then examined graphically. Finally, a more detailed, finer-scale assessment of the determinants of kangaroo harvest rate, harvest composition and catch per unit effort in the main harvest area of Queensland is presented.

14.2 Methods

The study area is the sheep rangelands of eastern Australia described in Section 13. Temporal variation in kangaroo harvest rate has been incorporated as a response or explanatory variable in regional harvest and population models in Sections 9, 10 and 13. These trends are compared here in simple plots of harvest rate over time. For these plots, harvest rate was calculated as the harvest between consecutive aerial survey estimates of kangaroo density divided by the geometric mean of those two density estimates (see Section 9). Harvest rate in

South Australia was multiplied by 0.63 for red kangaroos and 0.79 for western grey kangaroos to account for the likely underestimate of densities in that state and make them comparable to harvest rates in New South Wales and Queensland (see Section 12). For each species, monthly proportion of males in the harvest and average male carcass weight (see Section 13) were then averaged across the study period for each region and plotted against average density and harvest rate across the period. Sex ratio was only calculated for > 50 harvested animals in any month. In South Australia, data were only calculated for 1997-2001 when full carcasses were dressed. Prior to 1997, carcasses were dressed to a much lower weight. For these plots, average harvest rate and density was calculated as the average of interpolated monthly values (see Section 13). Standard errors were calculated for harvest statistics from the monthly averages. The ability of kangaroo density and harvest rate to predict harvest sex ratio and carcass weight was assessed by multiple regressions.

In Queensland, harvest data were available for grid squares (½^{o} blocks) annually from 1986 (except 1987), providing seven years of overlap with the aerial survey data (see Section 1). The survey data were restricted to the 180 grid squares in the core area (see Section 3, Fig. 3.2) and these were the unit of analysis. Response and explanatory variables used in linear models are detailed in Table 14.1. Analyses with harvest rate as the response covered all seven years. However, analyses with percentage of the carcass harvest that is male and *CPUE* and as response variables were restricted to three years, 1991, 1992 and 2001. Analyses with average male carcass weight as the response variable were restricted just to 1992 and 2001. The percentage of the landscape within 10 km of the transect line that was ‘open’ (woody foliage projective cover < 12%) within each grid square was calculated from the Statewide Landcover and Trees Study (SLATS) (Department of Natural Resources and Mines 2003) using FRAGSTATS (McGarigal and Marks 1994) and arcsine transformed to improve normality. The density of ‘edge’ between these open areas and wooded areas was calculated from the same data. The 1991 SLATS coverage was used for the 1986-1992 survey and harvest data, while the 1999 coverage was used for the 2001 survey and harvest data. Skin quality in kangaroos declines north of about 23^{o} S because of tick damage (Kelly 1997), so a dummy variable distinguishing north and south of this latitude was included in analyses. The minimum distances from the centre of each grid square to towns with a population > 1,000 and to primary roads were also used and log transformed to improve normality. Annual rainfall data were obtained for recording stations in the study area from the Bureau of Meteorology. Rainfall surfaces were then calculated using inverse distance weighting and annual values extracted for each grid square. Wallaroo harvest density was included as a proxy for wallaroo density.

Table 14.1. Response and explanatory variables, and associated codes, used to predict kangaroo harvest statistics within the core area of Queensland (see Section 3, Fig. 3.2). See text for details.

Code	Variable
Response variables	
red.%male	Percentage of the red kangaroo carcass harvest that is male
red.cpue	Catch-per-unit-effort (i.e. harvest per shooter night) of red kangaroos
red.mwt	Average male carcass weight of red kangaroos
grey.%male	Percentage of the eastern grey kangaroo carcass harvest that is male
grey.cpue	Catch-per-unit-effort (i.e. harvest per shooter night) of eastern grey kangaroos
grey.mwt	Average male carcass weight of eastern grey kangaroos
Response and explanatory variables	
red.zhr	Instantaneous harvest rate of red kangaroos, spatially standardised
grey.zhr	Instantaneous harvest rate of eastern grey kangaroos, spatially standardised
Explanatory variables	
red.zd	Density of red kangaroos, spatially standardised
grey.zd	Density of red kangaroos, spatially standardised
wall.zh	Harvest of wallaroos, spatially standardised
year	1986, 1988-1992, 2001
edge	Density of 'edge' (between open and wooded areas)
%open	Percentage of the grid square that is open
road.dist	Minimum distance from centre of grid square to a primary road
town.dist	Minimum distance from centre of grid square to a town with a population > 1,000
zrain	Annual rainfall, spatially standardised
poc	Dummy variable distinguishing areas north (1) or south (0) of latitude 23^{o}

For the Queensland grid square data, the percentage of males in the harvest was modelled using logistic regression, while the other response variables were modelled using multiple regressions. All analyses were performed using R 1.9.1 (R Development Core Team 2003). Models were simplified by stepwise removal of even weakly significant ($P > 0.01$, to avoid overparameterisation) terms from the full model (Crawley 2002). Spatial correlation structure was not considered important at the scale of a grid square. Overdispersion was corrected by using a quasibinomial error structure. Annual rainfall, kangaroo harvest rate, kangaroo density and wallaroo harvest density were all standardised spatially across all 180 grid squares to a mean of zero and unit variance to remove year-to-year variation in their means, which was not of primary interest here (*cf* Section 13). For the remaining response variables, a year dummy variable was incorporated in the models to account for any year-to-year variation in their means. A curvilinear term was also included for kangaroo density in the models to account for a possible saturation effect (see Section 13). Year-to-year variation in the parameter estimates was assessed by incorporating a year interaction with explanatory variables from the most parsimonious model without interactions.

Temporal trends in harvest rate over 1986-2001 and trends in harvest sex ratio were examined by mapping the slope of the regression of these statistics over time. This was done for kangaroo density in Section 12. Trends in harvest rate were restricted to the core area, but the entire commercial harvest zone in Queensland (see Section 3, Fig. 3.1) was included in the analysis of sex ratio trends. However, many grid squares were harvested only in some years of the 13-year period. A slope was only calculated for a grid square if there was a statistic in the periods 1991-1995, 1996-2000, 2001-2003, thereby including the main periods of decline and increase in kangaroo density (see Section 12) and covering the variation in effort and the amount of skin-only shooting (see Section 13).

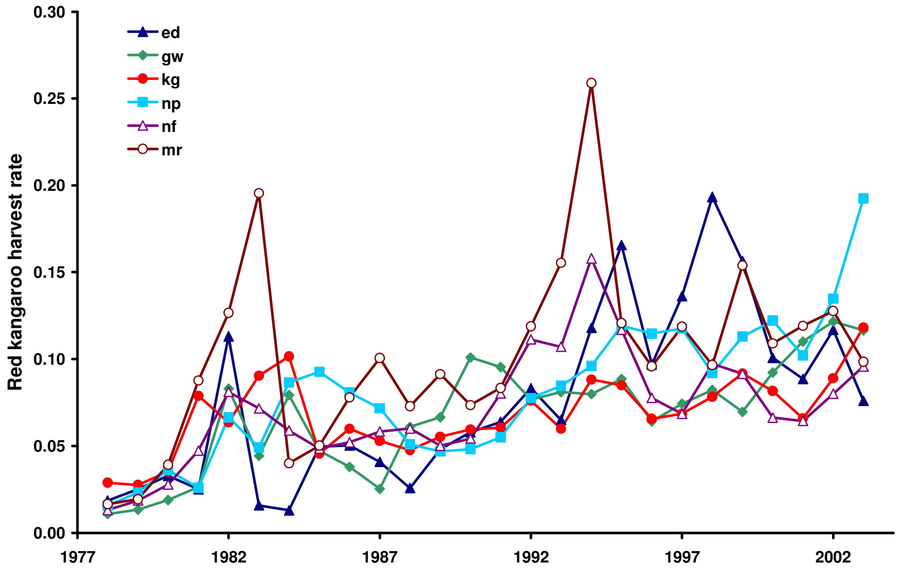
14.3 Results

14.3.1 Regional variation in harvest rate across eastern Australia

Regional harvest rate for each kangaroo species in each of the three states is shown in Figures 14.1-14.3. There is a striking variation in harvest rate amongst regions, both in the average harvest rate and the pattern of change over time. An exception is red kangaroos in South Australia where the six regions showed broadly parallel trends over time (Fig. 14.1*a*). In New South Wales, differences among regions have become more marked since 1990, and this has happened for all three species (Fig. 14.2). All regions and species in Queensland showed the same dramatic drop in harvest rate in the late 1990s (Fig. 14.3).

14.3.2 *Regional variation in harvest composition across eastern Australia*

Harvest composition has varied widely both among and within states (Figs 14.4-14.11) as expected from the data presented in Section 9. In most cases, it is difficult to see any pattern, although the Queensland data tend to dominate the plots with harvest rate. Male carcass weight tends to decline with increasing harvest rate for red kangaroos (Fig. 14.5*b*) and eastern grey kangaroos (Fig. 14.7*b*). The proportion of males in the eastern grey kangaroo harvest also declined with increasing harvest rate (Fig. 14.6*b*). Notably, high kangaroo density tended to be associated with relatively low proportions of males in the harvest and relatively lower carcass weights for all species. A likely explanation is that harvest rate is higher where density is higher. Only one regression was significant, with harvest rate a significant predictor of the sex ratio of the eastern grey harvest ($F_{1,16} = 6.26$, $P<0.05$, $R^2 = 0.24$). Multiple regression models with both variables were not supported for either statistic or species. The often inconclusive relationship between harvest statistics and harvest rate suggests other factors are involved.



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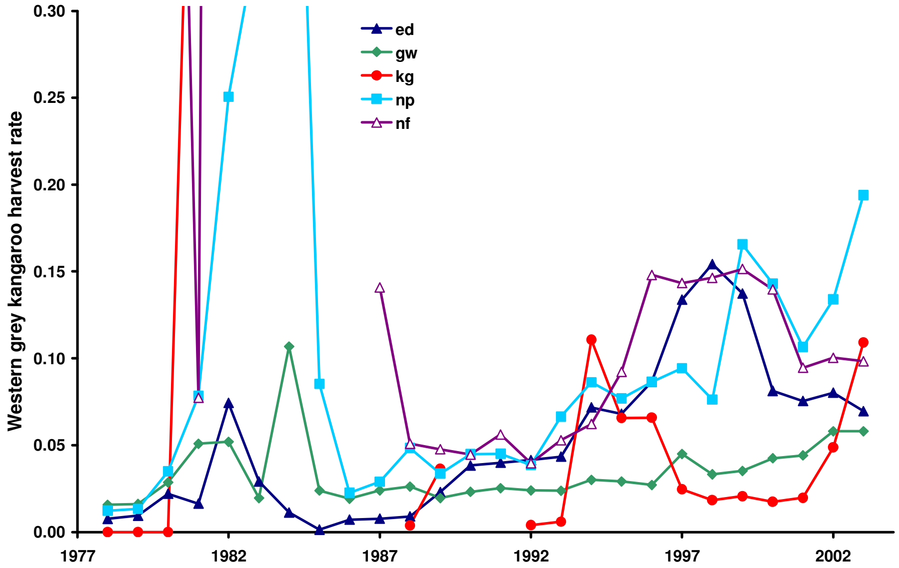

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Fig. 14.1. Trends in the instantaneous harvest rate of (a) red kangaroos and (b) western grey kangaroos in six soil conservation boards in the South Australian pastoral zone (see Section 9, Fig. 9.1).

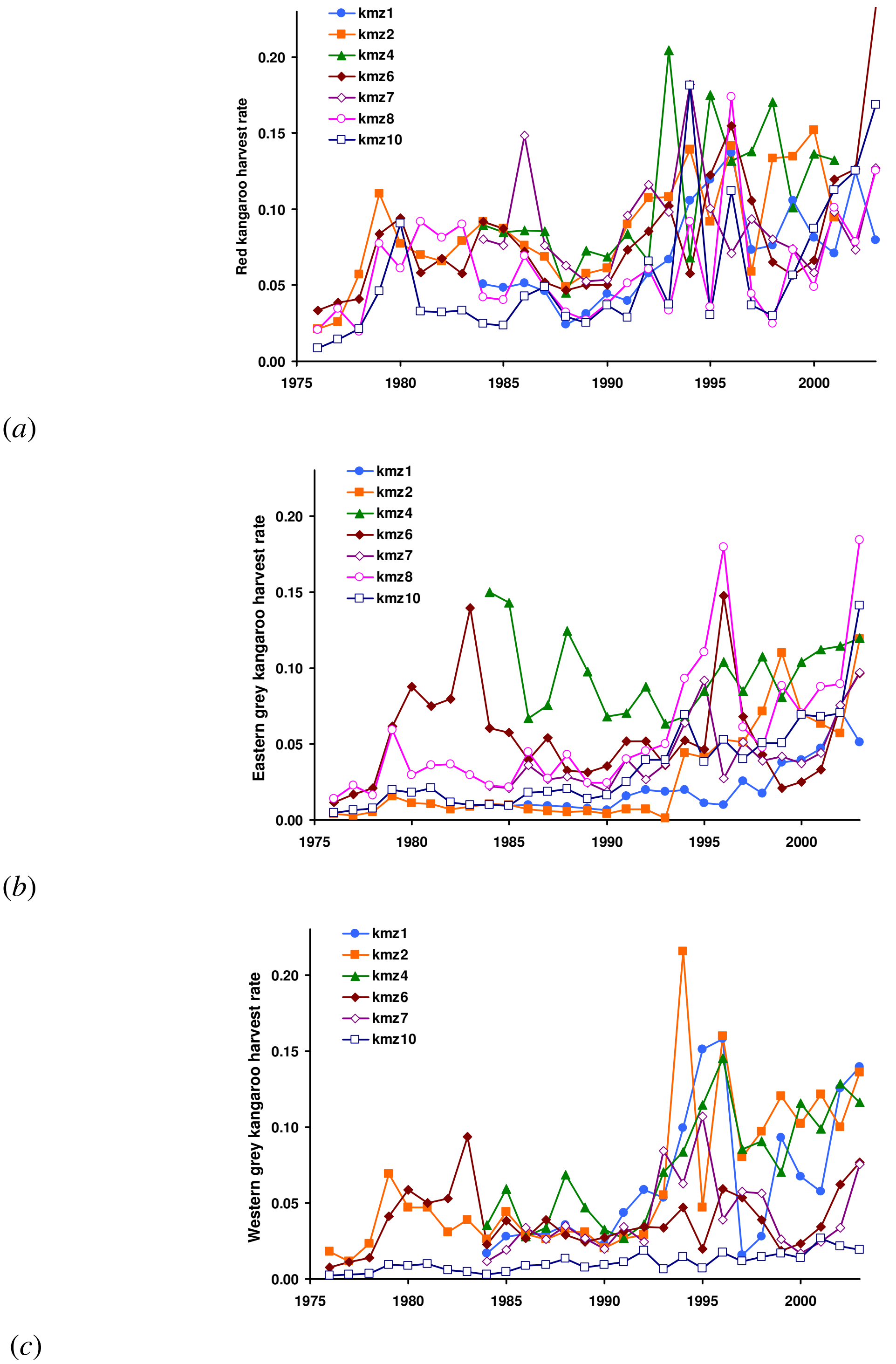

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Fig. 14.2. Trends in the instantaneous harvest rate of (a) red kangaroos, (b) eastern grey kangaroos and (c) western grey kangaroos in kangaroo management zones (KMZs) in New South Wales (see Section 9, Fig. 9.1).

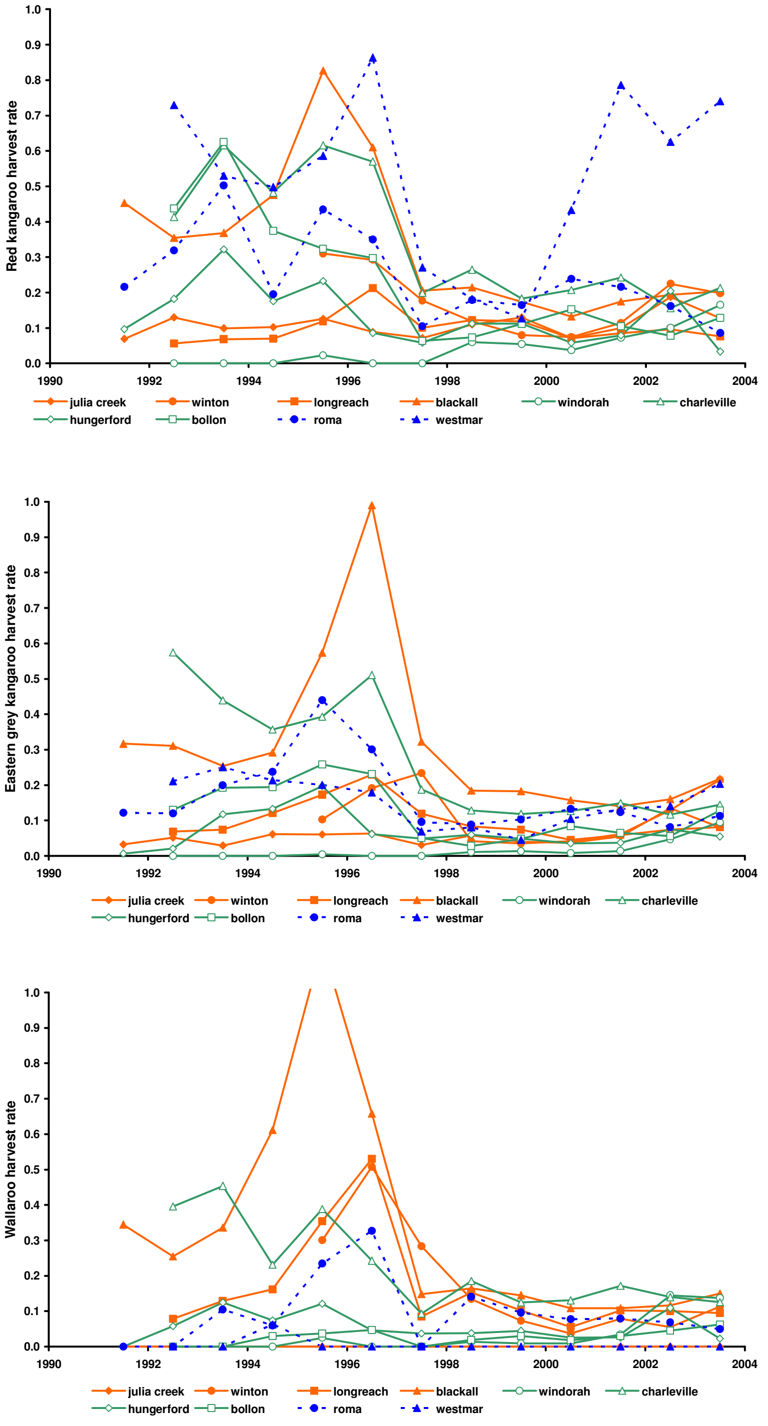

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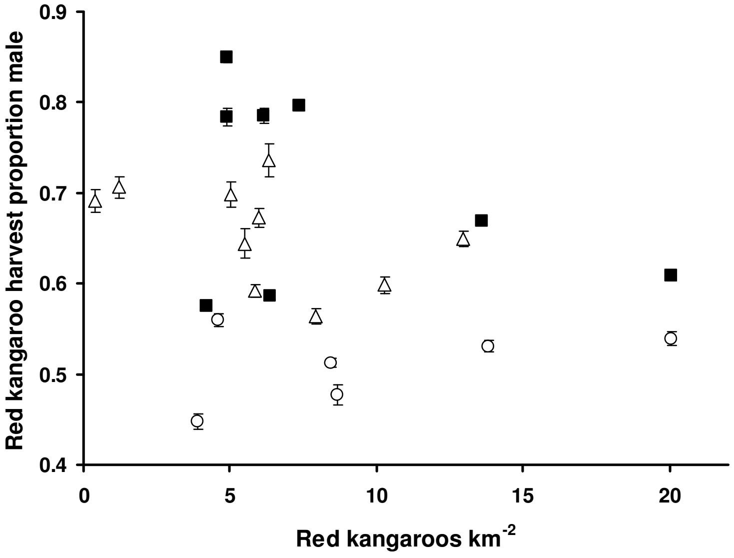
Fig. 14.3. Trends in the instantaneous harvest rate of (a) red kangaroos, (b) eastern grey kangaroos and (c) wallaroos in helicopter survey blocks in Queensland (see Section 9, Fig. 9.2).



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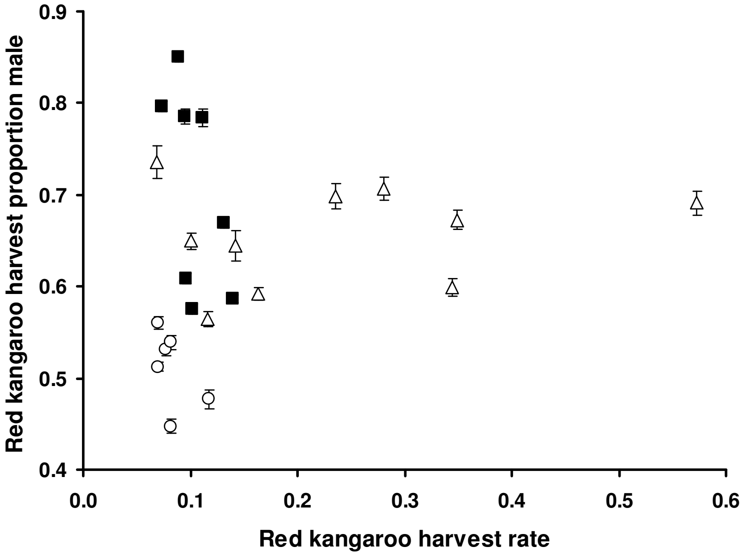

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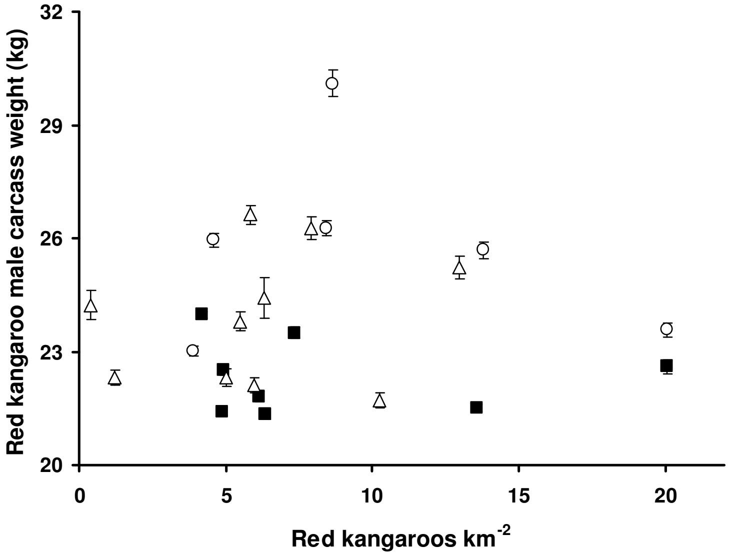
Fig. 14.4. Relationship between the average monthly proportion of males (± SE) in the red kangaroo harvest and red kangaroo (a) density (km^{-2}) and (b) instantaneous harvest rate. Each point represents a region or survey block in South Australia (circles), New South Wales (squares) or Queensland (triangles) (see Section 9, Figs 9.1 and 9.2).



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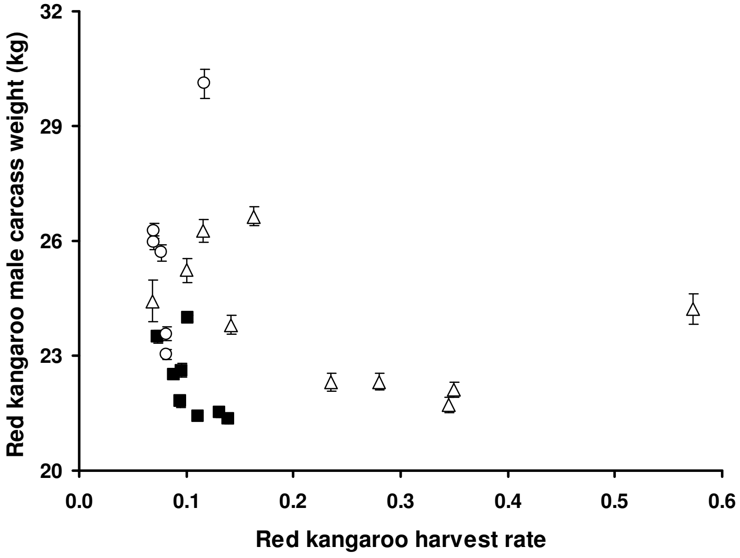

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Fig. 14.5. Relationship between the average monthly male carcass weight (± SE) in the red kangaroo harvest and red kangaroo (a) density (km^{-2}) and (b) instantaneous harvest rate. Each point represents a region or survey block in South Australia (circles), New South Wales (squares) or Queensland (triangles) (see Section 9, Figs 9.1 and 9.2).

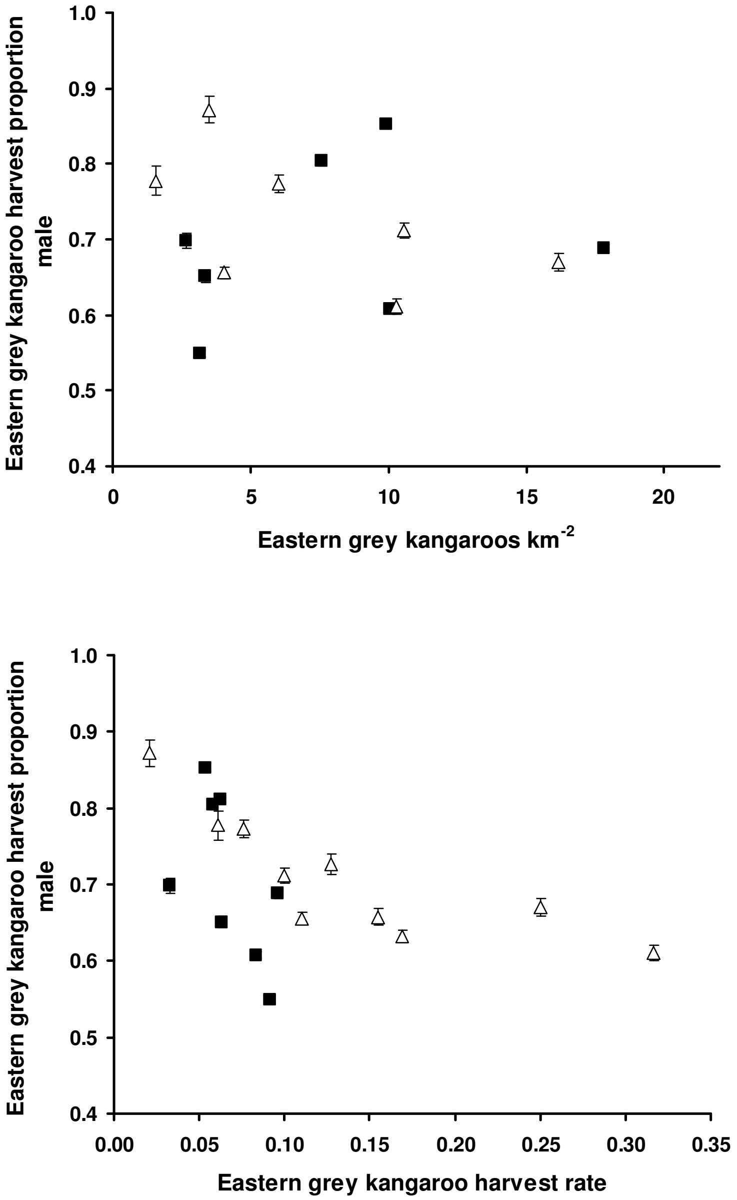

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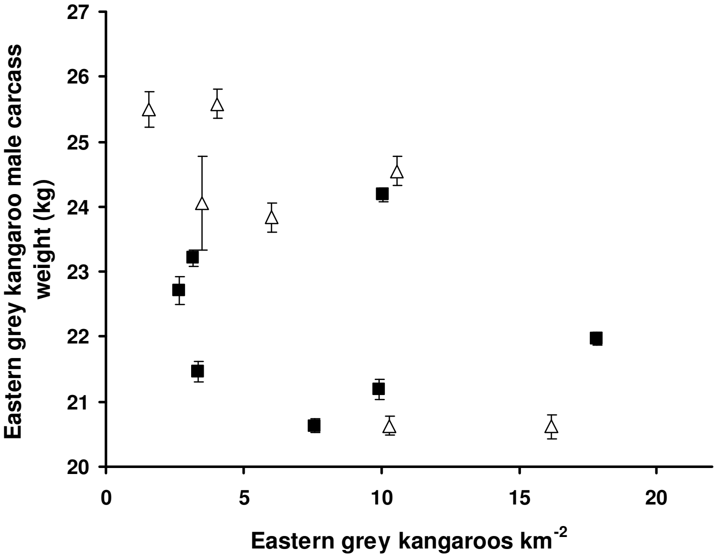
Fig. 14.6. Relationship between the average monthly proportion of males (± SE) in the eastern grey kangaroo harvest and eastern grey kangaroo (a) density (km^{-2}) and (b) instantaneous harvest rate. Each point represents a region or survey block in New South Wales (squares) or Queensland (triangles) (see Section 9, Figs 9.1 and 9.2).



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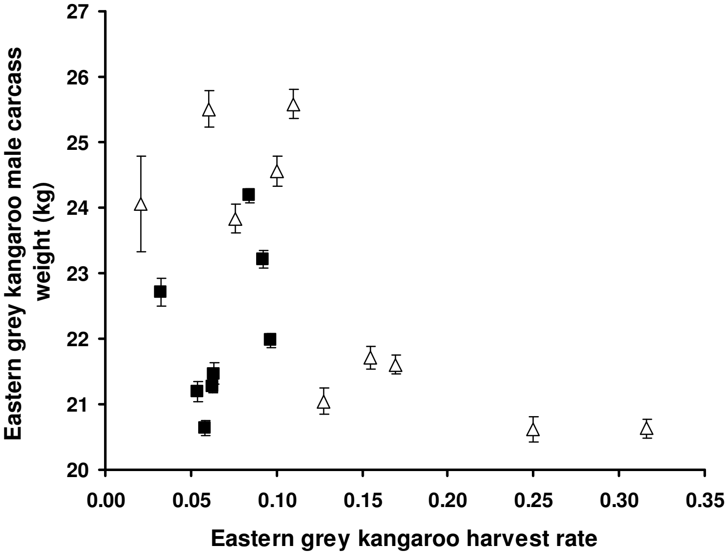

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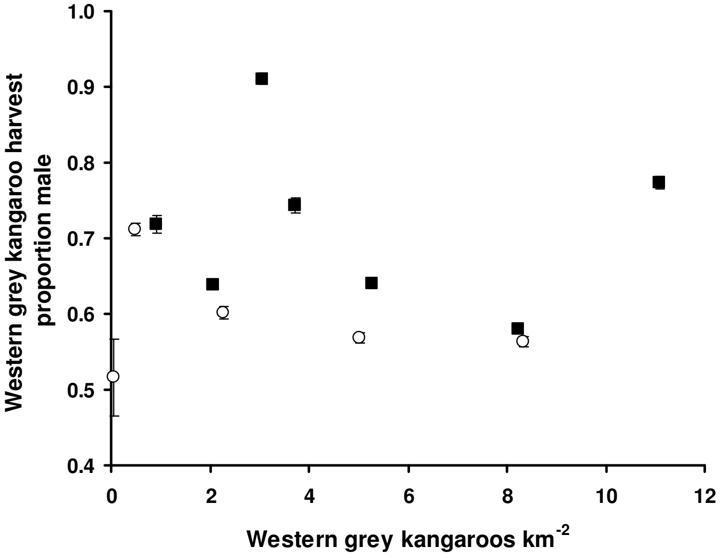
Fig. 14.7. Relationship between the average monthly male carcass weight (± SE) in the eastern grey kangaroo harvest and eastern grey kangaroo (a) density (km^{-2}) and (b) instantaneous harvest rate. Each point represents a region or survey block in New South Wales (squares) or Queensland (triangles) (see Section 9, Figs 9.1 and 9.2).



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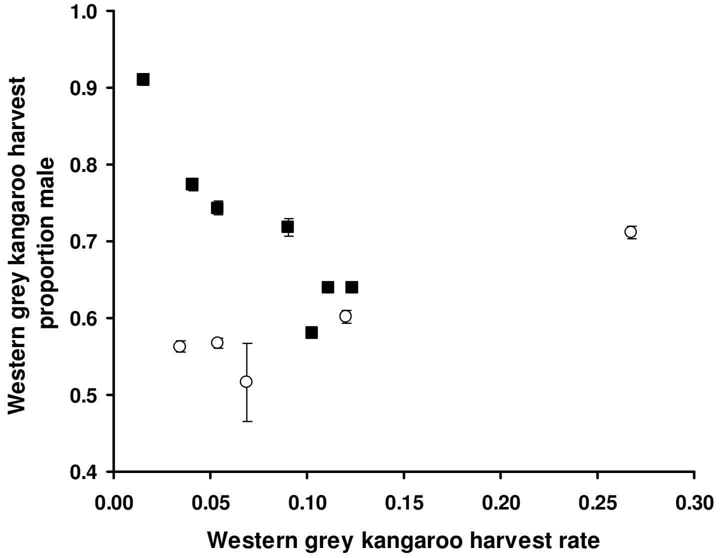

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Fig. 14.8. Relationship between the average monthly proportion of males (± SE) in the western grey kangaroo harvest and western grey kangaroo (a) density (km^{-2}) and (b) instantaneous harvest rate. Each point represents a region in South Australia (circles) or New South Wales (squares) (see Section 9, Fig. 9.1).

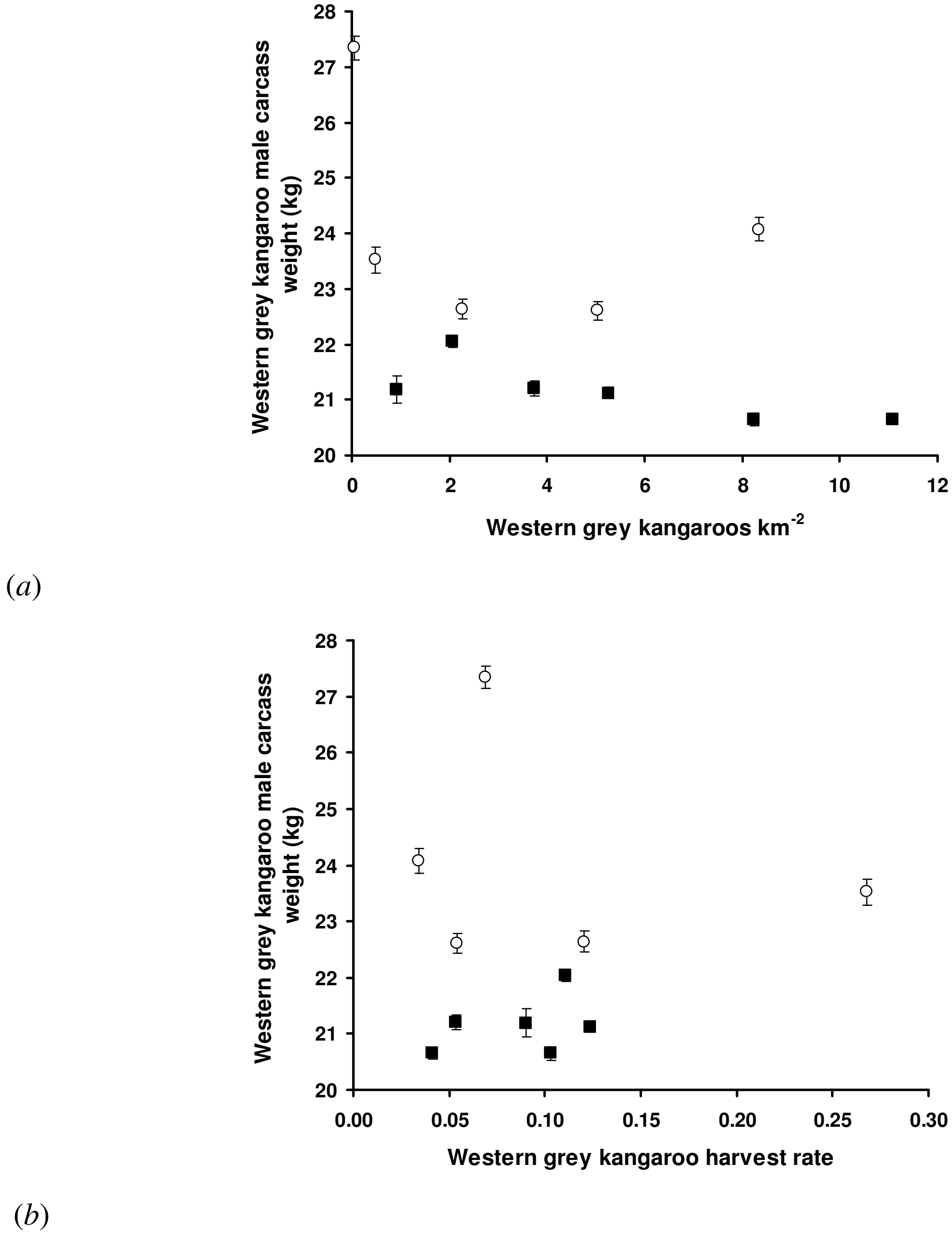
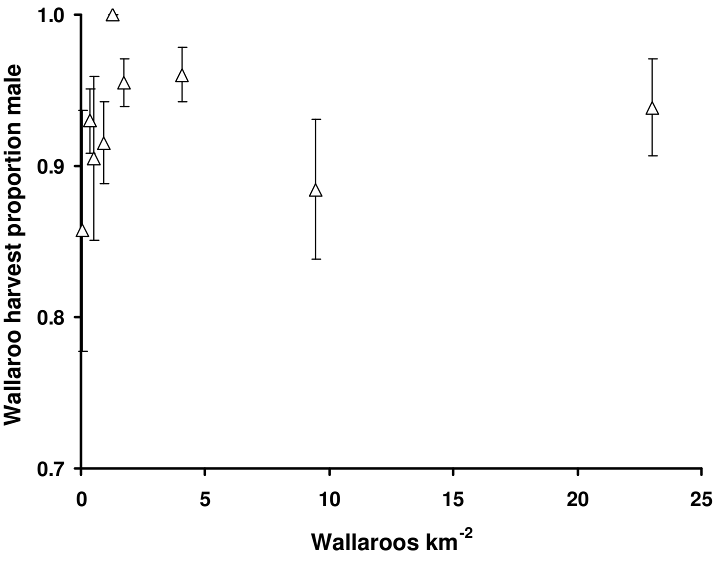


Fig. 14.9. Relationship between the average monthly male carcass weight (± SE) in the western grey kangaroo harvest and western grey kangaroo (a) density (km^{-2}) and (b) instantaneous harvest rate. Each point represents a region in South Australia (circles) or New South Wales (squares) (see Section 9, Fig. 9.1).



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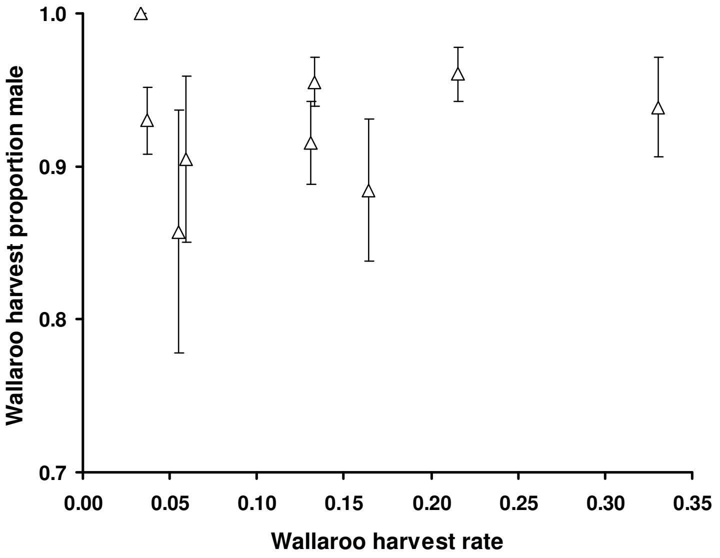

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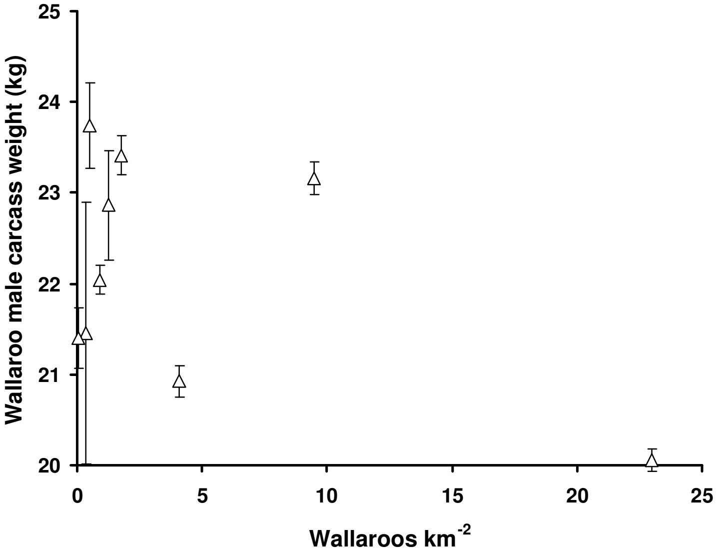
Fig. 14.10. Relationship between the average monthly proportion of males (± SE) in the wallaroo harvest and wallaroo (a) density (km^{-2}) and (b) instantaneous harvest rate. Each point represents a region or survey block in Queensland (see Section 9, Fig. 9.2).



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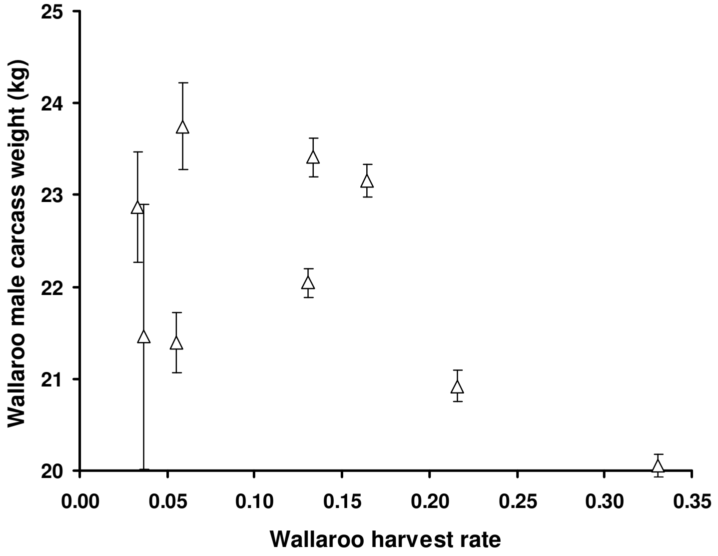

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Fig. 14.11. Relationship between the average monthly male carcass weight (± SE) in the wallaroo harvest and wallaroo (a) density (km^{-2}) and (b) instantaneous harvest rate. Each point represents a survey block in Queensland (see Section 9, Fig. 9.2).

14.3.3 *Determinants of spatial variation in harvest statistics in Queensland*

The results of the regression modelling predicting spatial variation in four harvest statistics are summarised in Table 14.2. The parameter estimates are standardised and so reflect the relative importance of each explanatory variable.

For red kangaroos, the percentage of males in the harvest varied among years with a higher percentage harvested more recently. There was a similarly strong latitudinal effect with fewer males taken in northern Queensland. These trends are shown in Section 14.3.2 below and in Figure 14.13*a* and *c*. The density of red kangaroos and wallaroos had a smaller but significant and surprisingly negative influence. Not surprisingly, *CPUE* was higher in areas of high red kangaroo density with high harvest rates but lower densities of eastern grey kangaroos and wallaroos. *CPUE* was also higher in 1992 and greater in grid squares that were more open and in southern latitudes. Surprisingly, a greater distance to towns and higher rainfall, particularly in 1992, had positive effects on *CPUE*. Carcass weight for red kangaroos was lower in grid squares with higher harvest rates, higher grey kangaroo and wallaroo density, but was higher in more open areas. Red kangaroo harvest rate was higher primarily where red kangaroo density was lower, but was higher where the densities of other species, particularly wallaroos, were higher. In the early part of the time series, more open grid squares had lower harvest rates.

For eastern grey kangaroos, there was again a strong influence of latitude and year-to-year variation in the percentage of males in the harvest. The density of eastern greys and wallaroos and the harvest rate had a smaller, negative influence. More edge, probably reflecting access, in a grid square and surprisingly higher rainfall were associated with more males in the harvest. *CPUE* was again higher in higher density areas and areas harvested at a higher rate. The densities of other species again had a negative influence. Amount of edge and openness, usually associated with higher densities of greys, had negative effects in contrast to the result for red kangaroos. Carcass weight was higher at higher densities and declined with harvest rate. The positive effects of wallaroo density, openness and latitude are not readily interpretable. Harvest rate was again higher where density was lower, although the relationship was curvilinear. Red kangaroo density had a negative effect and wallaroo density a positive effect. As expected, harvest rate was lower in more open areas, closer to towns and following rain.

14.3.2 *Shifts in the pattern of harvest statistics in Queensland*

The spatial pattern of harvest rate for red and eastern grey kangaroos across the core area (see Section 3, Fig.3.4) in Queensland has changed little over 1986-2001 (Fig. 14.12). There is some suggestion of a general increase in the harvest rate of red kangaroos in the southwest and north of the region and a decline in the central west and southeast, but the trend is not strong and generally restricted to a small number of disconnected grid squares. For eastern grey kangaroos, harvest rate has tended to decline in the north and increase in the west and southeast.

Table 14.2. Standardised parameter estimates and adjusted R^2 for the most parsimonious (according to backwards elimination) linear models predicting (a) red kangaroo harvest statistics and (b) eastern grey kangaroo harvest statistics. Descriptions of explanatory variables are given in Table 14.1 and in the text. Only significant parameter estimates are shown for individual year and year interactions, with the relevant year shown in brackets. The reference or baseline year to which parameter estimates relate, are 1986 for harvest rate (*zhr*), 1991 for *%male* and *cpue* and 1992 for average male carcass weight (*mwt*). The baseline value for *poc* is south of latitude 23^{o}.

(a) Red kangaroos

Response	Explanatory variables											Adj. R^2
	red.zd	*red.zhr*	*grey.zd*	*wall.zh*	*year*	*%open*	*town.dist*	*zrain*	*poc*	*year* × *zrain*	*year* × *%open*	
%male	-0.06			-0.05	0.45 (01)				-0.45			
cpue	2.01	1.39	-2.06	-0.75	2.39 (92)	0.75	1.07	1.07	-1.57	2.26 (92)		0.62
mwt		-0.72	-0.76	-0.41		0.88						0.33
zhr	-0.62		0.08	0.30							-0.27 (91) -0.34 (92)	0.39

(b) Eastern grey kangaroos

Response	Explanatory variables												Adj. R^2
	grey.zd	*grey.zd*^{2}	*grey.zhr*	*red.zd*	*wall.zh*	*year*	*edge*	*%open*	*town.dist*	*zrain*	*poc*	*year* × *grey.zd*	
%male	-0.15		-0.17		-0.03	0.12 (92) 0.80 (01)	0.12			0.07	-0.37		
cpue	3.42		1.66	-0.71	-0.80	-0.77 (01)	-0.38	-0.44	0.31			-0.83 (01)	0.76
mwt	1.05		-0.61		0.35			0.52			0.82		0.56
zhr	-0.38	0.13		-0.18	0.25			-0.24	-0.28	-0.11			0.25

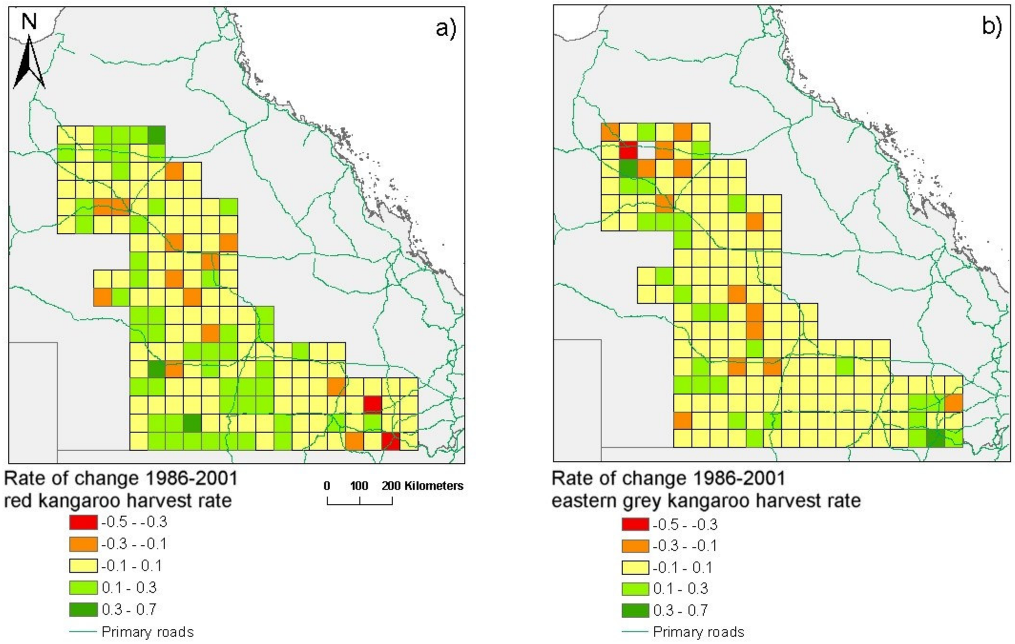

Fig. 14.12. Annual rate of change in harvest rate of (a) red kangaroos and (b) eastern grey kangaroos in grid squares in the core area (see Section 3, Fig. 3.2) of Queensland over 1986-2001.

Across the entire commercial harvest zone in Queensland, the percentage of males in the red and eastern grey kangaroo harvest was highest in the south (roughly centred around Charleville) in 2003 (Figs 14.13*a* and *b*). Over 1991-2003, this pattern has become more pronounced for both species (Figs 14.13*c* and *d*), as the percentage of males in the harvest for the harvest zone combined increased (Table 14.2, see Section 13, Fig. 13.14). There has been a decline in the percentage of males for red kangaroos in the northwest, whereas the overall increase was simply greatest for eastern greys in this broad area.

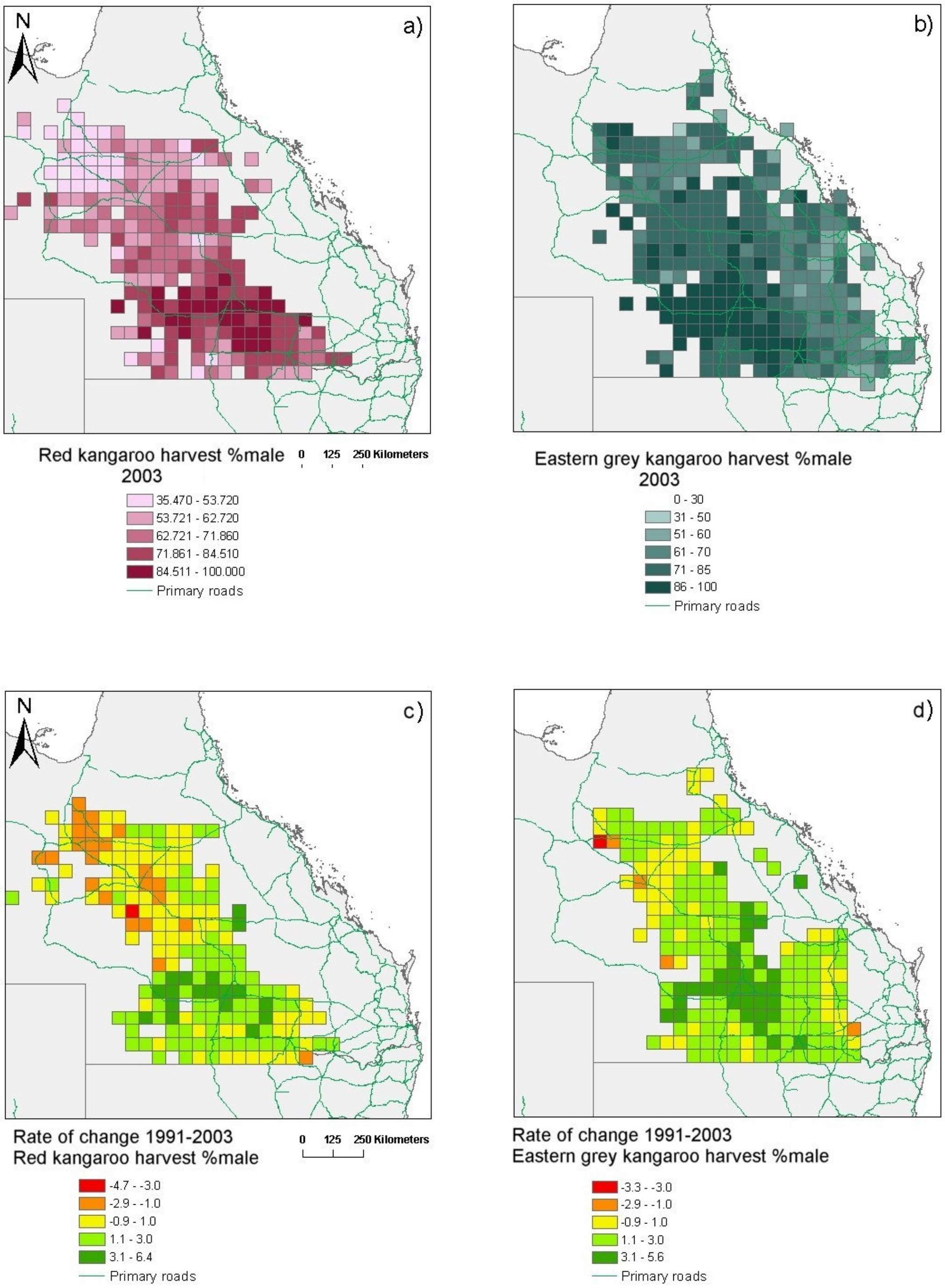

Fig. 14.13. Average %male in the 2003 carcass harvest of (a) red kangaroos and (b) eastern grey kangaroos and annual rate of change over 1991-2003 in %male in the harvest of (c) red kangaroos and (d) eastern grey kangaroos in grid squares in the commercial harvest zone (see Section 3, Fig. 3.1) of Queensland.

14.4 Discussion

Across eastern Australia, there are marked differences among regions in kangaroo harvest statistics. This reaffirms the need to consider harvest statistics regionally that was identified in Section 13. Though not shown, this pattern has been fairly stable over the past decade. This relative stability can be seen for harvest rate in Figures 14.1-14.3 and for sex ratio in broad regions in Queensland in Section 3, Figure 13.12. The differences among regions do change, but generally over a protracted period. The determinants of this spatial variation at this scale are not simply kangaroo density or harvest rate.

At the finer scale of a grid square (½° block), the spatial pattern of harvest rate and sex ratio for both red and eastern grey kangaroos in Queensland was also remarkably stable over a 10-15 year period. The increasing percentage of males in the harvest, particularly in the south, presumably reflects the decline in skin-only harvesting in Queensland, discussed in Section 13.

At the scale of a grid square, the determinants of harvest statistics were not always as expected. Certainly there was marked year-to-year variation in *CPUE* and the percentage of males harvested and this often accounted for a substantial part of the overall variation. Harvest rate declined with increasing density as has been reported elsewhere (Bayliss 1987; Pople and Cairns 1995; Pople 1996). Harvest rate was also higher where other harvested species were present and this is expected from theory (Caughley and Sinclair 1994) and has been reported previously for kangaroos. The harvest rate of red kangaroos, which use relatively open habitats, has been found to be affected more by the presence of eastern greys, which use more wooded country, than *vice versa* (Sinclair 1977; Pople 1996). The results of the analysis here is consistent with that result, although wallaroos are also an important influence in Queensland.

The move away from skin-only shooting is the likely explanation for the poor relationships between the percentage of males in the harvest and density and harvest rate. The relationship between *CPUE* and density was expected, but the influences of vegetation structure, distance to towns and rainfall are harder to explain. *CPUE* also increases with harvest rate, a result also seen in Section 13. Theory suggests that *CPUE* should decline with effort (Hilborn and Walters 1992).

Male carcass weight declined with increasing harvest rate as expected, but there were other factors with a similar influence such as the openness of the vegetation, possibly reflecting the ability to be selective. Other influences were not consistent among the two species, such as the density of other species.

There are a number of applications for these data. The first is that by mapping changes in harvest statistics (e.g. Figs 14.13*c* and *d*), areas of over- or under-harvest can be identified. This should be useful for managers who regulate the harvest and industry who may place their own restrictions in order to optimise aspects of the harvest such as the overall weight or the proportion of males and therefore large carcasses. These changes were examined on a broad, regional scale in Section 13, but there are finer scale patterns and broader-scale changes that do not always match up with administrative regions. A second application is to use the harvest data to extrapolate density estimates from aerial surveys, particularly when the surveys have incomplete geographic coverage such as the helicopter survey blocks in Queensland. This will require models with density as a function of harvest statistics. An alternative is use habitat variables to model density or a combination of harvest and habitat variables (see Section 17).

14.5 Acknowledgements

Norbert Menke provided the maps in this section. Norbert and Wayne Rochester interpolated the rainfall data.

14.6 References

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Section 15

Tenhumberg, B, Tyre, D, Pople, A, and Possingham, H (2004). Do harvest refuges buffer kangaroos against evolutionary responses to selective harvesting? *Ecology* **85:** 2003-2017.

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DO HARVEST REFUGES BUFFER KANGAROOS AGAINST EVOLUTIONARY RESPONSES TO SELECTIVE HARVESTING?

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Abstract. There is a wealth of literature documenting a directional change of body size in heavily harvested populations. Most of this work concentrates on aquatic systems, but terrestrial populations are equally at risk. This paper explores the capacity of harvest refuges to counteract potential effects of size-selective harvesting on the allele frequency of populations. We constructed a stochastic, individual-based model parameterized with data on red kangaroos. Because we do not know which part of individual growth would change in the course of natural selection, we explored the effects of two alternative models of individual growth in which alleles affect either the growth rate or the maximum size. The model results show that size-selective harvesting can result in significantly smaller kangaroos for a given age when the entire population is subject to harvesting. In contrast, in scenarios that include dispersal from harvest refuges, the initial allele frequency remains virtually unchanged.

Key words: body size; environmental stochasticity; genetic effects; harvest refuge; individual-based model; kangaroo; Macropus rufus; *size-selective harvesting.*

INTRODUCTION

Changes in body size in response to selective harvesting are of great interest and there are several models of the underlying mechanisms of this phenomenon. Ratner and Lande (2001) review empirical and theoretical work in this area and summarize the mechanisms proposed to explain observed changes in body size in harvested populations. They identify three categories of possible mechanisms: (1) abiotic factors influencing fish growth and development, e.g., large-scale ocean regime shifts that change water temperature, salinity, or eutrophication; (2) biotic factors, including relaxing density-dependent effects on growth due to changes in the population density; and (3) effect of harvesting on population demography and genetics. Their review concentrates on marine and freshwater organisms, but applies generally to harvested animals.

Among terrestrial animals, "trophy" species, such as the Saiga antelope (*Saiga tatarica*), elephants, moose, or elk, are selectively harvested because antlers or tusks have a higher value than animal meat. Theoretical work on moose (*Alces alces*) (Hundertmark et al. 1993) and elk (*Cervus elaphus*) (Thelen 1991) suggests that selective harvesting of bulls with a minimum antler length can change the frequency of alleles favoring antler growth. There is also empirical evidence for the potential of selective harvesting to influence the distribution of traits. For example, in South Luangwa National Park in Zambia, the proportion of tuskless elephants (*Loxodonta africana*) increased from 11% to 38% in only 20 years due to ivory poaching (Jachmann et al. 1995).

Changing allele frequencies in terrestrial species has important implications for conservation managers as well. For example, sanctuaries for endangered species are occasionally so successful that managers are forced to control population density through translocations or culling (e.g., Sukumar 1991, Armbruster and Lande 1993, Chapman et al. 1998, Treydte et al. 2001). In this case, potential indirect genetic effects of "harvesting" cannot be ignored.

In Australia there is increasing concern about the possible consequences of selective harvesting of kangaroos (Croft 1999). This paper uses a stochastic simulation model to explore the impact of harvesting on potential genetic controls of growth and survival in kangaroos. The results are directly relevant to the specific issue of kangaroo management. Management strategies can influence harvesting rate, minimum size of the target animal, and the size and location of harvest refuges. We also use the model to make more general comments on the evolutionary impact of size-selective harvesting in a stochastic environment.

Selective harvesting can alter the pattern of age- or size-specific mortality, which also can produce evolutionary change in life history and morphological traits (Miller 1957, Handfort et al. 1977, Ricker 1981, Wohlfarth 1986, Nelson and Soulé 1987, Edley and Law 1988, Law 1991, Policansky 1993, Rijnsdorp 1993, Murphy et al. 1994, Hutchings 1999). Models exploring the evolutionary dynamics of body size under harvesting often make the simplifying assumption that harvesting is the only source of selection on size (Law

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1991, Law and Rowell 1993). Ratner and Lande (2001) criticize these assumptions because most populations experience natural selection with respect to polygenic (quantitative) morphological traits. In their view, "stabilizing viability selection and directional fecundity selection on size traits interact with size-selective harvesting, and models that omit these interactions may produce incomplete or misleading results." Our model therefore includes increased mating success for larger males and reduced survival in drought as other sources of selection on body size.

Theoretical work usually considers harvesting strategies that differ in their degrees of size selectivity, i.e., a range of minimum sizes (Law 1991, Law and Rowell 1993). In fish the minimum size is often determined by the mesh size of the fishing nets, and fish above that size have the same probability of being caught regardless of population density. In terrestrial animals, the size selectivity is more complex. The minimum size is usually dictated by economic factors or regulations, but the probability of harvesting an individual depends on the population density and the individual's size relative to the size of other animals. If the population density is low, it takes harvesters a long time to find an animal; consequently, they harvest it as long as it is above the minimum marketable size. With increasing population density, the encounter rate increases and harvesters become more selective because large animals are often more valuable and there is usually a limit to the number that can be harvested in a single foray (e.g., vehicle size). Such capacity effects also have the potential to affect size selectivity in marine systems (Gillis et al. 1995*a*, *b*).

In this paper, one of the primary questions is how dispersal of individuals from a nonharvested area (a refuge) may counteract the genetic impact of size-selective harvesting. There is a growing interest in the role of marine reserves to conserve the genetic viability and identity of marine stock (Trexler and Travis 2000, Conover and Munch 2002). Such systems can be described as source–sink metapopulations, in which the refuge population acts as source and the harvested population as sink. Theoretical work (e.g., Wootton and Bell 1992, Donovan et al. 1995, Dias 1996, Gaona et al. 1998) suggests that metapopulations with at least one source population have a lower probability of extinction. Thus, we can expect that harvest refuges will increase the demographic viability of the kangaroo population. The existence of harvest refuges in the kangaroo system and their potential effect on demographic and genetic viability depend on the spatial variability in harvest and the mobility of kangaroo populations.

The maximum annual rate of kangaroo harvesting is determined by state conservation agencies and is a quota for an entire state. The annual quota varies between 15% and 20% of the statewide population estimated with harvest-independent surveys. However, harvesting is usually concentrated in some areas whereas others are not harvested at all because of differences in accessibility and the location of refrigeration units for carcass storage. This spatial variation in harvesting rates implicitly creates harvest refuges, which may replenish kangaroo abundance in the harvested areas (Pople 1996). It is reasonable to assume that only natural selection influences kangaroo populations in refuge areas.

Whether or not spatial variability in harvest actually improves the demographic and genetic viability of a harvested population depends on the movement rates between harvested and nonharvested areas (Trexler and Travis 2000). If movement rates are too low, the two areas will function as independent populations, and both natural and artificial selection will lead to genetic divergence. If movement rates are too high, the two areas effectively become one, and there also will be no genetic benefit to harvest refuges. Kangaroos, particularly red kangaroos (*Macropus rufus*), are in general very mobile (Frith 1964, Bailey 1971, Denny 1980, Priddel 1987, Priddel et al. 1988*a*, *b*, Croft 1991, Norbury et al. 1994). The majority of the population does not move more than 10 km/year, but some individuals disperse over distances of tens or hundreds of kilometers. Exactly where this places kangaroos on the scale of movement effects on genetics just described is unclear, so in what follows, we explore the sensitivity of our results to a broad range of movement rates.

This paper describes a model of the genetic consequences of selective harvesting on the frequency of genes determining kangaroo body size and survival in droughts. Analytical quantitative genetic models usually assume a normal phenotype distribution, random mating, and constant genetic variance (Lande 1976, Falconer and Mackay 1996, Ratner and Lande 2001). In many biological systems these assumptions are violated. Our model is a stochastic, individual-based simulation model that allows us to consider more complex scenarios that would not be feasible in an analytical model. Comprehensive stochastic computer simulations are increasingly used to test predictions of analytical models (e.g., Bürger 1999, Reeve 2000). The results of the model suggest that size-selective harvesting results in a higher frequency of genotypes with smaller asymptotic size or growth rate, in agreement with other models of size-selective harvesting (e.g., Law 1991, Law and Rowell 1993, Ratner and Lande 2001). If there is dispersal from refuge populations, the initial gene frequency remains virtually unchanged. This model is tailored to red kangaroos, but we believe that the predictions would apply to a variety of other species living in arid environments, such as the African savannah or the Arabian Peninsula.

MODEL OVERVIEW

In the literature there are numerous attempts to model the population dynamics of kangaroos as a function of rainfall, resource availability, density dependence, and environmental stochasticity (see review in Cairns 1989, McCarthy 1996). Our objective is not to create a complex model of population dynamics as it relates to the environment, but to evaluate the potential for evolutionary change as a result of size-selective harvesting. Thus we ignore interspecific competition (e.g., with sheep) and the interactions of pasture growth and kangaroo performance. Instead, we use rainfall as a surrogate for resource availability. Large kangaroos are gregarious; the only permanent grouping is between a female and her dependent young-at-foot (Jarman and Coulson 1989). Although relatively large groups sometimes form, these groups are unstable in their composition (Croft 1980). In the interests of keeping the model from becoming too complex, we ignore small-scale group structure in our model.

The model includes demographic and environmental stochasticity. Demographic stochasticity means that at any point in time there is a probability that an individual dies or reproduces. The random nature of sex determination of offspring is also included. Environmental stochasticity enters the model through rainfall. Rainfall strongly influences the population dynamics of arid-zone kangaroos through food availability. The population size fluctuates to a great extent as a consequence of including environmental stochasticity in the model.

The model is individual based, and therefore each individual is tracked as a unique and discrete entity. Individual-based modeling is a widely used tool for simulating ecological systems (see review in Grimm 1999, Grimm et al. 1999), especially for models where individual variability is critical for the population dynamics. Our model keeps track of the individual properties of age, size, sex, and genotype. At every time step (= two months), the model cycles over lists of males and females and determines the fate of each individual. The different population processes occur in the following sequence:

1. *Rainfall.*—At the beginning of each year the annual rainfall is determined by randomly drawing a number from historical rainfall data that have been collected for 123 years at Menindee (near Kinchega National Park) in western New South Wales, Australia. This parameter is treated as an indicator for the availability of resources, such as food and water, for the whole year.

2. *Harvesting.*—In our model, harvesting starts 100 years after the beginning of a simulation run, to allow the gene frequencies and age distributions to approach equilibrium. At the beginning of each year, the number of kangaroos to be harvested is calculated from the kangaroo density of the previous year and the harvesting quota. Individuals are chosen randomly from male and female lists and are exposed to harvesting. The probability of being shot depends on the size of the chosen kangaroo and overall kangaroo abundance.

3. *Mating and reproduction.*—Each female without a pouch young mates and gives birth to a pouch young with probability f; the sex is assigned randomly with a sex ratio of 1:1. The father of the offspring is determined in two steps: first, the female encounters a male chosen randomly from the list of mature males, and second, the probability that this male successfully mates with the female depends on his size relative to all other males. Both successful and unsuccessful males go back to the list and may be selected again. This process is repeated until the female is successfully mated. It is possible that a male can have more than one opportunity to mate with a particular female, and sometimes even very small males will mate successfully. Newborn kangaroos can die at birth; the probability of death increases with increasing kangaroo abundance.

4. *Natural mortality, aging, and growing.*—At each time step there is a chance that an individual will die. If a female dies, her dependent offspring die with her. The surviving individuals age by one time step and increase in size. Based on its new age, an individual may move up one stage class. For example, at the age of 8 months, pouch young turn into "young-at-foot," and at the age of 12 months, young-at-foot turn into subadults. New subadults are independent of their mother and, depending on their sex, they are added to female or male lists. Whether female subadults reach maturity depends not only on age, but also on their size and the amount of rainfall.

5. *Dispersal.*—At every time step some individuals move between harvested and nonharvested populations. Dispersing individuals from the refuge population replace harvested individuals to some extent and increase the genetic variability of the harvested population.

Note that processes (1) and (2) occur only every sixth time step.

MODEL ASSUMPTIONS

We use the following notational conventions in what follows: i and j index individuals in a population, and i usually refers to a "focal" individual, whereas j is used in summations over entire populations; y is size, z is sex, and x is age in time steps; μ is a probability of dying during a time step; p is always a probability of an event occurring during a single time step, and the subscript identifies the event. All model parameters are listed in Table 1, and the estimation of the parameters is described in Appendix A.

Sex ratio

In large, sexually dimorphic, polygynous mammals such as kangaroos, the variance in the reproductive success of males is greater than in females. Current theory suggests that in these animals, a mother that is in good condition should preferentially conceive sons and provide them with above-average parental care, and a mother that is in poor condition should preferentially conceive daughters and provide them with below-average parental care (Trivers and Willard 1972,

TABLE 1. Base value of model parameters, and the probability distribution functions (PDF) used in the sensitivity analysis.

Parameter				
Description	Symbol†	Conditions	Base value	PDF‡
Maturity				
Intercept	w_0 (3)		1.137	normal (1.137, 5)
Weight	w_1 (3)		0.653	normal (0.653, 0.14)
Age	w_2 (3)		−8.298	normal (−8.298, 3.4)
Rain	w_3 (3)		−0.046	normal (−0.046, 0.016)
Age : rain	$w_{2,3}$ (3)		0.033	normal (0.033, 0.01)
Male bias in birth	α		0.5	beta (12, 5)
Male dominance	v (4)		5	gamma (5, 1)
Birth rate	f		0.95	beta (40, 2)
Dispersal				
From harvested to nonharvested	$\varepsilon_{\mathrm{H}\rightarrow\mathrm{NH}}$ (13)		0.001	gamma (2, 400)
From nonharvested to harvested	$\varepsilon_{\mathrm{NH}\rightarrow\mathrm{H}}$ (14)		0.001	gamma (3.5, 150)
Male bias	θ		0.6	beta (6, 4)
Mortality				
Age	ρ (5)	age $< x^*$	0.05§	gamma (60, 1600)
		age $\geq x^*$	0.05§	gamma (60, 1600)
	κ (5)	age $< x^*$	0.3§	gamma (10, 33)
		age $\geq x^*$	10§	normal (10, 1)
	x^*		14	normal (14, 1.5)
Rainfall	μ_0 (8)	males	0.5	beta (12, 12)
		females	0.55	beta (14.5, 12)
		young	0.2	beta (2, 14)
	b (7)	males	0.01	gamma (10, 1000)
		females	0.01	gamma (10, 1000)
		young	0.014	gamma (20, 1430)
Density dependence	ω (9)	young only	0.001	beta (4, 3000)
Genes	m (C1)‖		0.085	gamma (4, 47)
	d (C1)‖		0.009	gamma (4, 444)
Growth				
Age	y_∞ (10)	males	190	normal (190, 10)
		females	160	normal (160, 10)
	c (10)	males	0.25	beta (20, 60)
		females	0.47	beta (45, 50)
	x_0 (10)	males	−3.4	normal (−3.4, 0.3)
		females	−2	normal (−2, 0.3)
Rainfall	g (12)		1.2	gamma (20, 17)
	h (12)		0.015	gamma (10, 666)
Genes	$\sigma_{\text{growth, 1}}$	genes→y_∞	8	normal (8, 1.5)
	$\sigma_{\text{growth, 2}}$	genes→c	0.05	normal (0.05, 0.01)
Harvesting	k (1)		0.0001	normal (0.0001, 0.00003)
Mortality rate	μ_{harvest} ϕ (1)		0.5	normal (0.5, 0.2)
Minimum size	$y_{\min}$		142 mm (≈25 kg)	normal (25, 5)
Quota	q		0.15	normal (0.15, 0.03)

† Numbers in parentheses indicate the equation in which the parameter is used.

‡ Numbers in parentheses are the parameters of the PDF used in the sensitivity analysis.

§ Parameters that were varied independently for both sexes in the sensitivity analysis.

‖ Eq. C.1 in Appendix C.

Maynard Smith 1980). In the empirical literature, there is mixed support for this theory. Some researchers found that the sex ratio of newborns varies with environmental conditions (kangaroos; Johnson and Jarman [1983]), maternal age, social rank, and body condition (red deer; Clutton-Brock et al. [1982]; red-necked wallabies *Macropus rufogriseus* and eastern grey kangaroos *M. giganteus*; Stuart-Dick and Higginbottom [1989]). In contrast, in an extensive study over three years on red kangaroos *M. rufus* ($n > 2000$), Pople (1996) detected little sex bias in pouch young and no relationship between pouch young sex and maternal age or condition.

For reasons of parsimony, we assume in our model that environment and size do not affect the sex ratio. It is unlikely that variation in the sex ratio would change the model predictions notably because under size-selective harvesting, the largest individuals of each sex are killed, resulting in natural selection favoring smaller individuals.

Harvesting

In the model we assume that a given proportion, q, of the kangaroo population is harvested each year. Based on q and the kangaroo abundance, n, the number of harvested individuals (= target) is calculated and individuals are removed randomly at the beginning of each year. In the model we assume the following scenario: If a shooter encounters a group of animals (s)he usually shoots the largest one first and the other animals in the group escape. Group size is bigger when kangaroo abundance is larger, and at very low density, only solitary animals are encountered. Therefore, the probability of a kangaroo surviving harvest, $1 - \mu_{\text{harvest}}$, depends on its size relative to the size of the other kangaroos, and kangaroo abundance, and is calculated as follows:

$$\mu_{\text{harvest},i} = \begin{cases} 0 & \text{if } y_i < y_{\min} \\ \phi \dfrac{y_i^{kn^2}}{\sum\limits_j y_j^{kn^2}} & \text{if } y_i \geq y_{\min} \end{cases} \tag{1}$$

where y_i is the size of kangaroo i, ϕ is a scaling constant to adjust for different harvesting pressure, n is the abundance of adult and subadult kangaroos, and k is an index determining how size-selective harvesters are. With increasing n, the selectivity for bigger animals increases, and if kn^2 is close to 0, all animals above the minimum size, $y_{\min}$, have an equal probability of being shot. We use n^2 rather than n to increase the effect of abundance on μ_{harvest}.

To determine which animal is harvested and removed from the population, we randomly choose males and females from the population. Chosen individuals are "shot" with the probability μ_{harvest}, and are removed from the population. If a female is shot, all of her dependent young die with her. However, the young are not counted toward the harvesting target. Surviving individuals remain in the population. Individuals can be chosen more than once and there is a chance that relatively small individuals will be harvested. The random selection process continues until the target quota proportion q of the current population has been harvested.

Reproduction

In the model, the probability that a female will reach maturity, p_{mature} depends on her age (x), size (y), and the current rainfall (R), and is given by

$$p_{\text{mature}}(y, x, R) = \frac{e^{\text{lp}}}{1 + e^{\text{lp}}} \tag{2}$$

$$\text{lp} = w_0 + y_i w_1 + x w_2 + R w_3 + x R w_{2,3} \tag{3}$$

where lp is the linear predictor.

We have no data to estimate the probability of maturation for males. Therefore, we assume that males randomly mature between 2.5 and 3.5 years. For males, the timing of maturity has only a small influence on fitness because males less than 4 years old are relatively small in size compared to the rest of the male population and, consequently, have a very low probability of mating.

The probability that male i will mate successfully after encountering a female, $p_{\text{mating}}(y, v)$, is given by

$$p_{\text{mating}}(y, v) = \frac{y_i^{v}}{\sum\limits_j y_j^{v}}, \qquad v \geq 0 \tag{4}$$

where y_i is the size of kangaroo i, and the summation is over all mature males, and v determines how much the relative size of individual i influences mating success. For $v > 1$, the influence is large; for $0 < v < 1$, the influence is small; and for $v = 0$, the mating success is independent of size.

Mortality

The natural mortality depends on age, sex, and rainfall (Frith and Sharman 1964, Newsome 1965, Bayliss 1985, Shepherd 1987, Pople 1996). For very young animals, there is an additional independent mortality event, the probability of which is a function of total population abundance. Independence means that surviving one phase does not alter the probability of dying in a later phase. The mortality probability that we calculate, $\overline{\mu}_{R,x,z}$, where R is the annual rainfall for the current year, x is the age of the individual, and z is the sex, is the average across the genetic variation in the population; the mortality probability for a particular individual also incorporates the effect of its genome (see *Genetics*).

We use a Weibull function (McCallum 2000) to include the effect of age on the instantaneous death rate. The age-specific death rate at age x, also known as the hazard function in the survival literature, is

$$\kappa\rho(\rho x)^{\kappa - 1} \tag{5}$$

where ρ is the rate and κ is the shape parameter. If $\kappa > 1$, the death rate increases with age; if $\kappa < 1$, the death rate decreases with age. When $\kappa = 1$, the death rate is a constant and the distribution of survival times reduces to the exponential distribution. By changing κ for first part of the age range, we can let the instantaneous death rate decrease with age as a result of increasing experience (e.g., habitat selection), and during the last part of the age range, we can let the instantaneous death rate increase as a result of senescence, where x^* is the age in years at which senescence starts affecting survival.

The model uses discrete time steps, so we calculate the probability of dying from age x to $x + 1$ when rainfall is not limiting (i.e., $R = \infty$), $\overline{\mu}_{\infty,x,z}$, from Eq. 5:

$$\bar{\mu}_{\infty,x,z} = 1 - \exp\left[-\int_x^{x+1} \kappa\rho(\rho u)^{\kappa-1}\, du\right]$$
$$= 1 - e^{(\rho x)^\kappa - [\rho(x+1)]^\kappa}. \quad (6)$$

where u is a temporary integration variable.

In general, the survival probability of females is higher than that of males, and the survival probability of pouch young and young-at-foot is lower than that of adults. Survival in juveniles is lowest in late pouch life and among young-at-foot (Frith and Sharman 1964, Newsome 1965, Shepherd 1987, Pople 1996). In the model, we therefore assume that, given the mother stays alive, young only die of natural causes at 5–12 months of age (i.e., $\overline{\mu}_{R,x,z} = 0$ for $x < 5$ months). This limits females to attempting to rear a maximum of three offspring each year.

We assume that rainfall causes mortality to decrease from an upper limit ($\overline{\mu}_{0,x,z}$) to a lower limit when rainfall is not limiting (Eq. 6; $\overline{\mu}_{\infty,x,z}$) along a logistic curve (McCallum 1995):

$$1 - \mu_{R,x,z} = (1 - \mu_{\infty,x,z})\left(\frac{e^{a_{x,z}+Rb_{x,z}}}{1 + e^{a_{x,z}+Rb_{x,z}}}\right)$$

or

$$\mu_{R,x,z} = \frac{1 + \mu_{\infty,x,z}e^{a_x+Rb_x}}{1 + e^{a_x+Rb_x}} \quad (7)$$

where $b_{x,z}$ determines the slope (the estimation of this parameter is described in Appendix A), and $a_{x,z}$ is related to the maximum mortality ($\mu_{0,x,z}$) by the following relationship:

$$a_{x,z} = \ln\left(\frac{\mu_{0,x,z} - 1}{\mu_{\infty,x,z} - \mu_{0,x,z}}\right). \quad (8)$$

This means that, in years of high rainfall, kangaroos experience the lowest mortality ($\mu_{\infty,x,z}$) probability for a given age and sex, but with decreasing annual rainfall, the mortality increases to $\mu_{0,x,z}$. How much the mortality increases depends on the degree of drought resistance (see *Genetics* and Appendix B).

Pouch young and young-at-foot experience a second independent mortality event, the density-dependent phase, in which mortality rates depend on the abundance of the kangaroo population. In our model, the density-dependent mortality of juveniles, μ_n, increases exponentially with kangaroo abundance, n, at rate ω:

$$\mu_n = 1 - e^{-\omega n}. \quad (9)$$

Growth

In our model we used head length as a surrogate of kangaroo size. We used head length rather than mass because head length cannot decrease as a result of unfavorable environmental conditions. Head length also continues to increase well after maturity and to a greater extent than limb measurements such as pes length (Ealey 1967). We modeled growth of head length with the von Bertalanffy equation (Koojiman 1993):

$$y_x = y_\infty[1 - e^{-c(x-x_0)}] \quad (10)$$

where y_x is the head length of an individual at age x, y_∞ is the asymptotic head length, c is a growth rate, and x_0 is a shift parameter to allow head length at age 0 to be greater than zero. It is straightforward to rearrange Eq. 10 into a form that estimates the increment of growth over a single time step starting from size y_t (McCallum 1995):

$$\Delta y = (y_\infty - y_t)(1 - e^{-c}). \quad (11)$$

Growth is also influenced by rainfall, R, and the growth increment is reduced by a fraction:

$$\Delta y_R = \Delta y(1 - ge^{-hR}) \quad (12)$$

where g and h are parameters determining the shape of the exponential curve. Under good conditions, individual growth follows the von Bertalanffy growth equation ($\Delta y_R \rightarrow \Delta y$), but with decreasing rainfall, the growth slows down and reaches zero in severe droughts ($\Delta y_R \rightarrow 0$). For a small number of the extreme parameter combinations in the sensitivity analysis, Eq. 12 leads to small negative growth increments under the most severe drought conditions used in the model (annual rainfall <55 mm, <1% of years). In these circumstances, the growth increment was rounded to zero.

Dispersal

Refuge and harvested populations undergo the same population processes and are affected by the same environmental conditions (i.e., rainfall). At every time step, individuals disperse from the refuge population (NH) to the harvested population (H) and vice versa. We assume that this movement is determined by: (1) the basic dispersal rate, $\varepsilon_{\mathrm{H}\rightarrow\mathrm{NH}}$, or $\varepsilon_{\mathrm{NH}\rightarrow\mathrm{H}}$, (2) the proportion of males among migrants, θ, and (3) the ratio of the kangaroo numbers in both populations. Therefore the individual dispersal rate for males is

$$\varepsilon_1 = \theta\varepsilon_{\mathrm{H}\rightarrow\mathrm{NH}}\frac{N_{\mathrm{H}}}{N_{\mathrm{NH}}} \qquad \varepsilon_2 = \theta\varepsilon_{\mathrm{NH}\rightarrow\mathrm{H}}\frac{N_{\mathrm{NH}}}{N_{\mathrm{H}}} \quad (13)$$

and for females it is

$$\varepsilon_1 = (1 - \theta)\varepsilon_{\mathrm{H}\rightarrow\mathrm{NH}}\frac{N_{\mathrm{H}}}{N_{\mathrm{NH}}}$$

$$\varepsilon_2 = (1 - \theta)\varepsilon_{\mathrm{NH}\rightarrow\mathrm{H}}\frac{N_{\mathrm{NH}}}{N_{\mathrm{H}}} \quad (14)$$

where N_{H} and N_{NH} are the number of kangaroos in the harvested population and refuge population, respectively. The dispersal rate for any particular sex or direction, ε, is converted to the probability that an individual will disperse in a single time step, p(dispersal) using the following equation:

$$p(\text{dispersal}) = 1 - e^{-\varepsilon}. \qquad (15)$$

Because p(dispersal) depends on the ratio of the kangaroo numbers in both populations, the smaller population acts as a sink and the larger population as a source until both populations are equal in size. This mechanism is consistent with the concept of an ideal free distribution, in which foragers redistribute themselves so that the resource exploitation rate is the same for all animals (Fretwell and Lucas 1970). The rate ε is kept small to reduce the likelihood of time-delayed fluctuations in population size.

In real kangaroo populations, movement between harvested and refuge areas is likely to be influenced by differences in habitat quality. Harvesting often concentrates in open, more easily accessible areas, which seem to be more favorable for red kangaroos compared to refuge areas. In the model, we can account for a dispersal preference by using different values for $\varepsilon_{\mathrm{H}\rightarrow\mathrm{NH}}$ and $\varepsilon_{\mathrm{NH}\rightarrow\mathrm{H}}$ in Eqs. 13 and 14.

Genetics

In life history theory, it is usually assumed that growth is a trade-off with survival, such that the cost of being large is a reduced survival probability (Roff 1992, Stearns 1992). In the absence of such trade-offs, there would be a tendency for fixation at the highest possible trait values. Kangaroo surveys over many years suggest that, in drought years, large individuals are more likely to die than smaller ones. Furthermore, reproductive success is positively correlated with size: size influences mating success in males, whereas size effects initiation of maturity in females. Hence, it appears that there is a trade-off between size and drought resistance in kangaroos, but as far as we know, details on the underlying genetics of this trade-off are unknown. Our goal was to examine the ability of dispersal from nonharvested populations to buffer this trade-off against selection pressure imposed by size-selective harvesting. We employed simulation-based quantitative genetic modeling to generate a range of possible evolutionary responses to harvesting.

We assume that drought resistance and size are additive, quantitative traits. The genome is diploid, with characters being modeled by 20 diallelic autosomal loci with free recombination among them. All of the loci are pleiotropic; at every locus, the allele increasing growth also decreases drought resistance, so that there is always a complete trade-off between the characters (genetic correlation of negative one). Each parent contributes 50% to the genes of their offspring, chosen at random from the alleles at each locus. Thus, if an individual homozygous for drought resistance (i.e., all drought resistance alleles) mates with an individual homozygous for size alleles, the resulting offspring will have half dought resistance alleles and half size alleles.

There is no dominance between alleles; trait expression depends entirely on the number of alleles for each trait that an individual possesses. Thus, the degree of drought resistance depends on the total number of drought resistance alleles in the whole genome, whereas the growth rate depends on the total number of "size" alleles. Higher or lower numbers of alleles are mapped to trait values using an inverse normal distribution. Genotypes of the population at the beginning of the simulation were sampled independently among loci such that the expected allele frequency at each locus was 0.5. Model runs based on 100 loci for each trait resulted in the same equilibrium allele frequency as runs using 20 loci, but it took longer to reach the equilibrium. Therefore, we have limited our analyses to 20 loci for the sake of simplicity.

Size genes.—In our model there are two benefits of increased growth rate. First, male size is correlated with mating success (Walker 1995). If two or more males compete for access to a female, the largest one usually wins. This does not mean that small individuals are excluded from mating, but their probability of mating successfully is reduced compared to that of larger counterparts. Second, age at maturity depends on size. Larger females tend to reach maturity earlier than smaller individuals. In the model the genetic make up of an individual determines size at birth and the age at which individuals reach the sex-specific asymptotic size.

Size genes could influence growth in different ways. In this model we consider two different mechanisms. First, we assume that the entire growth curve is shifted up or down depending on the frequency of size genes. This means that an individual with a small number of size genes starts out small and never catches up in size relative to an individual with many size genes. Second, we assume that the number of size genes determines the growth rate, c, in Eq. 10. Following this latter assumption, individuals approach the same asymptotic head size at different rates. The number of size genes is mapped to asymptotic size, y_∞, or growth rate, c, associated with a particular number of size genes using an inverse Gaussian function with mean $\bar{y}_\infty$, or $\bar{c}$, and standard deviation, σ_{growth}. The exact value for an individual depends on the number of size alleles (S) that they have relative to the maximum possible ($S_{\max}$),

$$y_\infty = \bar{y}_\infty + \sigma_{\mathrm{growth}}\Phi^{-1}(S/S_{\max}) \qquad (16)$$

where Φ^{-1} is the inverse normal distribution function. Using the baseline parameters, the effect of the different number of size genes causes the asymptotic male head size to vary between 168 mm (no size alleles) and 201 mm (100% size alleles) in the first growth model. Under the second growth model, male kangaroos reach 170 mm head size between 3 and 12 years of age (100% and 0% size alleles, respectively).

Drought resistance genes.—Annual rainfall greatly influences water availability and plant growth and, consequently, kangaroo mortality (Bayliss 1985). Therefore, in this paper we use drought resistance as being analogous to stress tolerance caused by poor nutrition

TABLE 2. Starting conditions of all simulations.

Parameter	Term	Value	PDF†
Number of males	n_{males}	50	constant
Number of females	n_{females}	50	constant
Proportion of size alleles	γ	0.5	Beta (5, 5)

† Probability distribution function for the sensitivity analysis.

and dehydration. The number of "drought resistance" alleles results in a particular survival rate in exactly the same manner as for growth effects (see Eq. 16), but with mean $\overline{\mu}_{R,x,z}$ (see Eq. 7), and standard deviation $\sigma_{\mathrm{drought}}$. We model the increasing influence of drought resistance allele with decreasing rainfall by increasing $\sigma_{\mathrm{drought}}$ as rainfall decreases. Therefore, in a run of "good" years there is no advantage to having drought resistance alleles, because the survival of all individuals of the same sex and age is virtually the same. See Appendix C for a more detailed description of how $\sigma_{\mathrm{drought}}$ influences survival.

Sensitivity analysis

Our model is very complex and there is considerable uncertainty in estimates of the input parameters. We want to know how changes in the input parameters would alter the model predictions. Sometimes the effect of changing one parameter value depends on the values of other parameters. The technique that we used is called Latin Hypercube Sampling (LHS) and is described in Appendix D. It has been used in the analysis of complex ecological models elsewhere (Rushton et al. 2000*a*, *b*). We consider four scenarios within which the parameters are varied: (1) size alleles determine asymptotic growth, no dispersal from nonharvested population; (2) size alleles determine growth rate, no dispersal from nonharvested population; (3) size alleles determine asymptotic growth, dispersal from nonharvested population; or (4) size alleles determine growth rate, dispersal from nonharvested population.

We also varied the initial proportion of size genes in the population (Table 2). We keep track of genetic changes by examining the number of size alleles as a proportion of its maximum (S). For example, $S = 0.6$ means that kangaroos have, on average, 60% size alleles and 40% drought resistance alleles. To allow the allele frequency to stabilize in the absence of harvesting, the populations were not harvested in the first 100 years. We calculated S in the year before harvesting commences (S_1) and after 100 years of harvesting (S_2), and used the difference in S ($\Delta S = S_2 - S_1$) as an indicator for the magnitude of genetic change. A negative value of ΔS indicates that kangaroos grow more slowly or have a lower asymptotic size. We also present results for the effect of harvesting on abundance in the harvested population, calculated as the difference between the population size at the onset of harvesting (n_1) and abundance after 100 years of harvesting (n_2), $\Delta n = n_2 - n_1$.

The relationship between variation in the input parameters and the magnitude of genetic change is quantified with Partial Rank Correlation Coefficients (PRCC; Blower and Dowlatibadi 1994). Although we calculated PRCCs for all combinations of inputs and outputs, for the sake of brevity we present only the values for the combinations that we are most interested in: the effect of management controls and dispersal rates. We plot the relationship between inputs and ΔS or Δn only for combinations with correlations significant at $P < 0.01$. Note that the graphs do show the median genetic or abundance change for all parameter combinations; we simply are not presenting them as functions of inputs with weak relationships or that are beyond the control of managers.

Heritability estimates

The magnitude of a genetic response to selection depends on the amount of additive genetic variation that contributes to the overall phenotypic variation observed and the heritability of that additive genetic variation. Therefore we calculated the heritability of the rate of growth to maturity (calculated as size at maturity/age at maturity), using all females maturing between year 50 and year 100 in a single baseline run, a total of 3926 individuals. We calculated an offspring–midparent regression (Hartl and Clark 1989), which is the phenotypic covariance between the average growth rate to maturity of the two parents and the growth rate to maturity of their offspring, divided by the phenotypic variance of growth rate to maturity. We then calculated a bootstrap standard error for this estimate using 1000 bootstrap replicates.

RESULTS

The population dynamics of the simulated kangaroo populations are strongly influenced by annual rainfall. In years of high rainfall, the population size increases; in drought years, the numbers sharply decrease (Fig. 1). This pattern is consistent with that observed in natural populations (Caughley et al. 1984, Bayliss 1985, 1987, Cairns and Grigg 1993). Harvesting reduces simulated kangaroo abundance, and kangaroo numbers fluctuate around a lower mean value.

Despite the large fluctuation in population numbers, the average allele frequency across loci is quite stable prior to the onset of harvesting (Fig. 2). However, with no dispersal between populations and the highest minimum size for harvesting ($y_{\min}$), the proportion of size alleles decreases markedly in the harvested population

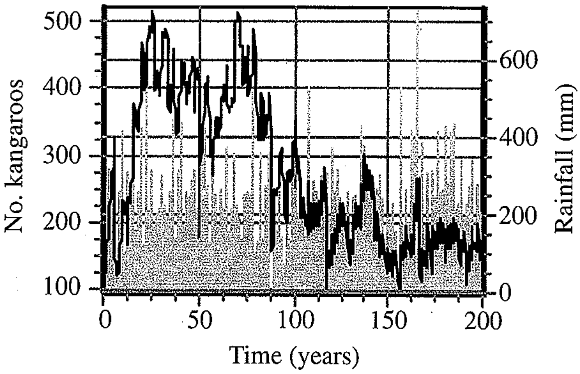

FIG. 1. Simulated population dynamics of red kangaroos (solid line) and the corresponding rainfall (gray bars). Harvesting commences after 100 years, size alleles determine asymptotic growth, and there is no dispersal from the nonharvested population.

after harvesting commences, whereas the proportion of size alleles in the refuge population remains unchanged (Fig. 2). A reduction in the proportion of size alleles ($\Delta S < 0$) means that size-selective harvesting reduces the average age-specific size of kangaroos. This result is consistent with data on heavily harvested populations of several different aquatic species (see review in Ratner and Lande 2001). As a result of the particular tradeoff chosen in our model, size-selective harvesting also increases the degree of drought resistance (or stress tolerance). In the scenarios with dispersal between the refuge population and the harvested population, the median proportion of size alleles remains at about the pre-harvesting level in both populations ($\Delta S \approx 0$). In the majority of runs, the change in allele frequency due to harvesting does not disappear after the cessation of harvesting.

We used the sensitivity analysis to evaluate (1) how sensitive the model predictions are to the uncertainty in the parameter estimates, and (2) the ability of management controls to counteract the effect of size-selective harvesting. Kangaroo managers can manipulate the harvesting rate, q, the size distribution of harvested animals (i.e., $y_{\min}$), and they can set aside harvest refuges. In scenarios with no dispersal from harvest refuges, 100 years of size-selective harvesting resulted in a reduced proportion of size genes (median $\Delta S < 0$) in 85% of the runs, with 37% decreasing by -0.1 or more (Fig. 3A, B). The largest change was -0.35. The partial rank correlation coefficients (PRCCs; Table 3) indicate that the proportion of size alleles decreases with increasing harvesting rate (q) and increasing minimum size ($y_{\min}$) for both growth models (PRCCs < 0). Increasing the harvesting rate has a relatively larger effect than increasing the minimum size (see also Fig. 3A, B).

In contrast, in the scenarios with dispersal from harvest refuges, only 54% of runs had a reduced proportion of size alleles, with only 2% of runs with a reduction greater than -0.1 (Fig. 3). The largest reduction was -0.19. The dispersal rate from the harvesting population into the refuge population, $\varepsilon_{H \rightarrow NH}$, has a small negative effect on the reduction of size genes (Table 3; Fig. 3C) when size alleles influence the asymptotic size. The minimum harvested size ($y_{\min}$) also has a significant negative effect on the median change in both growth models (Table 3), but the magnitude is considerably smaller than that observed when there is no dispersal (Fig. 3D).

The effect of harvesting on the change in abundance is very consistent between growth models and the presence of harvest refuges. Increasing the harvest quota results in a greater decrease in abundance in all scenarios (Fig. 4A,C, Table 3). Increasing the minimum harvested size ($y_{\min}$) reduces the change in abundance in all scenarios (Fig. 4B,D, Table 3). The effect of harvesting on abundance is not greatly affected by the presence of harvest refuges; the median change in abundance is -102 without harvest refuges and -89 with refuges.

The heritability of growth rate to maturity for females in the model is 0.14 (bootstrap SE 0.008).

DISCUSSION

It is believed that refuges help to preserve genetic diversity and to maintain population size and age structure, which are thought to permit evolutionarily adaptive responses in the face of environmental uncertainty (Carr and Reed 1993, Quinn et al. 1993). This paper assesses the value of refuges to prevent evolutionary change due to size-selective harvesting. Our model suggests that it is likely that size-selective harvesting reduces the proportion of size alleles when the entire population is subject to harvesting. Moderate dispersal from nonharvested areas has the potential to counteract this directional change toward smaller kangaroo sizes. These results are not an artifact of random genetic drift

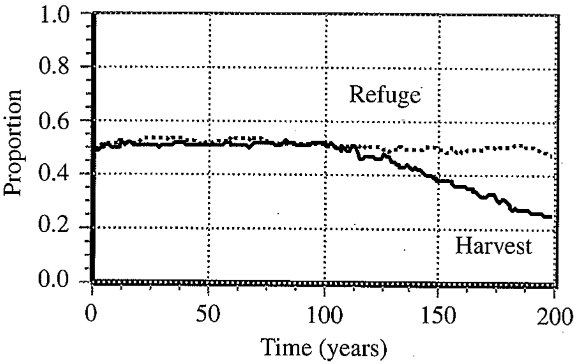

FIG. 2. Average number of size alleles as a proportion of the maximum number for the harvested (solid line) and the nonharvested population (dotted line) when harvesting is maximally size selective. Harvesting commences after 100 simulated years, with minimum size $y_{\min} = 35$ kg, size alleles determine asymptotic growth, and there is no dispersal between populations.

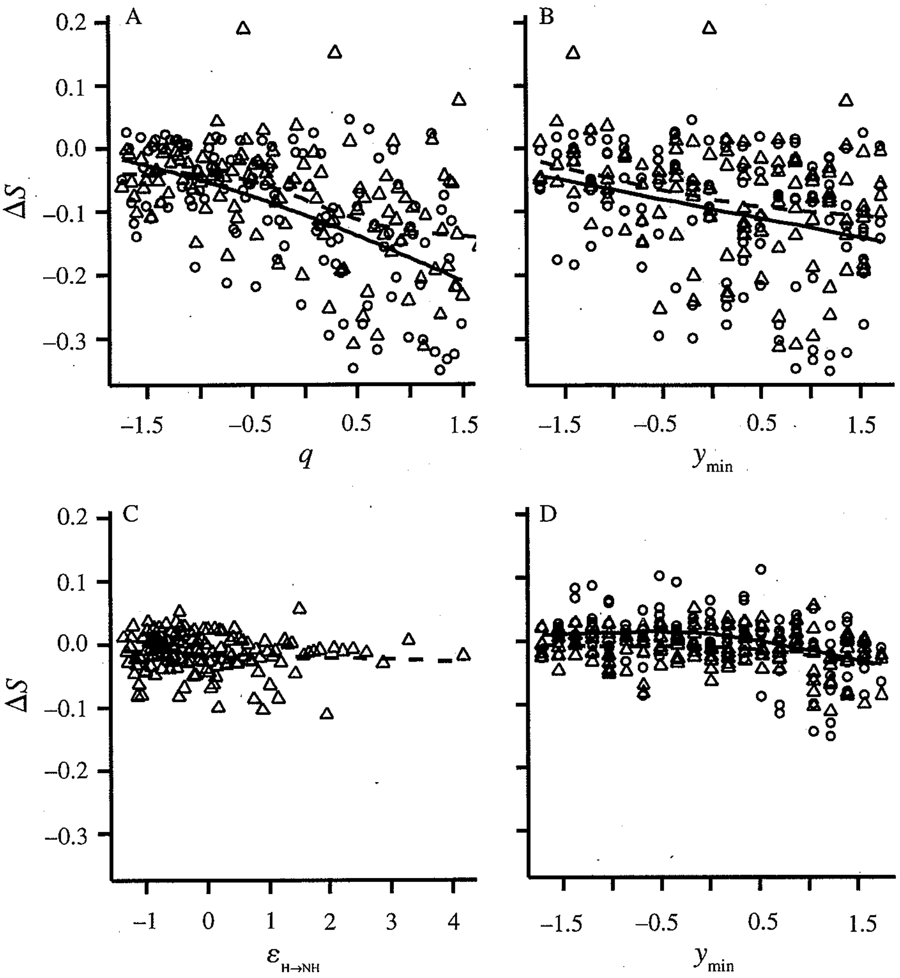

FIG. 3. Influence of size-selective harvesting on the frequency distribution of size alleles of the scenarios with no dispersal (A, B) and with dispersal from harvest refuges (C, D). Each symbol is the median of the 20 replicate runs at a single parameter set; all 150 parameter sets are shown in each panel. Open circles (solid lines) indicate the runs where the size alleles determine the growth rate, c, and the open triangles (dashed lines) indicate those runs where the size alleles determine the asymptotic size, y_∞. The lines are created using a smooth spline function. Variation around the line is due to variation in the parameters other than the one displayed. ΔS specifies the change in the proportion of size alleles after 100 years of harvesting; there is no change if $\Delta S = 0$. Parameter values for harvesting rate (q), the minimum size ($y_{\min}$), and the dispersal rate from the harvested population into the nonharvested population ($\varepsilon_{H\to NH}$) are expressed as standard deviations above or below the mean (0 indicates the mean parameter value).

TABLE 3. Partial rank correlation coefficients (PRCC).

Parameter	Size alleles→	No dispersal		With dispersal	
		ΔS	Δn	ΔS	Δn
q	c	**−0.58**	**−0.23**	−0.16	**−0.36**
	y_∞	**−0.49**	**−0.25**	−0.02	**−0.42**
$y_{\min}$	c	**−0.32**	**0.36**	**−0.32**	**0.26**
	y_∞	**−0.32**	**0.36**	**−0.29**	**0.24**
$\varepsilon_{H\to NH}$	c			−0.14	−0.02
	y_∞			**−0.33**	0.05
$\varepsilon_{NH\to H}$	c			0.01	0.05
	y_∞			−0.10	−0.06

Note: Boldface indicates results significant at the 0.01 level and shown in Figs. 3 and 4.

in small populations. First, our model includes balancing selection, which has a stabilizing effect on allele frequency. Second, ΔS did not change if we ran the model without harvesting and adjusting the degree of density dependence in juveniles such that the average population size ≈100 (results not shown). Third, random genetic drift would equally likely result in fixation of size or drought resistance alleles, resulting a large scatter around the zero line in Fig. 3A and B. In contrast, in our simulations ΔS significantly decreases with increasing harvesting rate and increasing degree of size selectivity. Finally, the sensitivity analysis is based on the median of 20 replicate runs at each parameter combination. Genetic drift would lead to random variation around the median response, but it should be equally

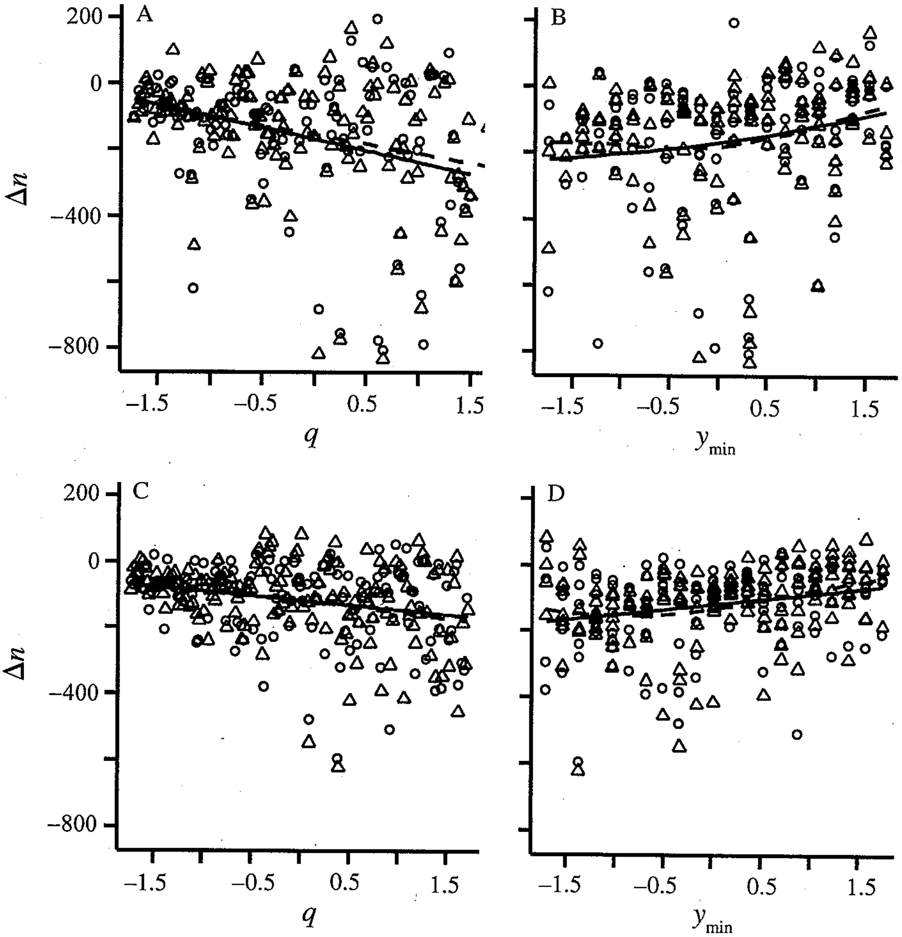

FIG. 4. Effect of size-selective harvesting on the median change in abundance (Δn) between the onset of harvesting and 100 years later. All symbols and lines are as in Fig. 3.

likely to be in either direction, and therefore the median should be a good representation of how the model is responding to changes in parameters despite random drift in genetics and demographic stochasticity in abundance.

Hale (2001) examined the genetic diversity of red kangaroos and wallaroos (*Macropus robustus*) by analyzing allozymes and microsatellite loci. He did not find any significant differences in levels of allelic diversity between nonharvested and harvested areas. In his analysis he included samples from areas with harvesting rates close to 30%. These results might lead to the conclusion that size-selective harvesting is not affecting allele frequencies in kangaroos. Our model highlights two alternative explanations for Hale's (2001) findings:

1) Currently the size of the nonharvested area and the dispersal rate between harvested and nonharvested populations are sufficiently large to counteract the effect of size-selective harvesting. This situation may change. There is a movement to promote kangaroo products (Grigg 1988, 1997, Grigg et al. 1995, Switala 1995, Grigg and Pople 2001), which might result in a decreasing refuge area. A large percentage of the kangaroo population is not harvested because they live in areas where harvesting it is not economical because of poor accessibility (remoteness, difficult terrain, thick vegetation, or poor road network). Ron Hacker (*unpublished manuscript*) estimates that currently in New South Wales ≥5% of the kangaroo population lives in such "economical harvest refuges," in addition to 3% that live in national parks.

2) Our model suggests that the allele frequency changes gradually. Consequently, effects on wild populations will be detectable only over a long time. It could be that the populations have not been exposed to sufficient harvesting pressure long enough to generate any measurable change in the gene frequency. Few estimates are available prior to 1980, so the historical harvest rate that was imposed is unclear. Since 1980, the harvest rate has generally increased nationally in Australia (Grigg and Pople 2001). However, substantial harvest rates of kangaroos comparable to

recent years have only been reported for some states (Pople and Grigg 1998).

Our model is tailored to the biology of kangaroo populations, but we believe that the value of harvest refuges demonstrated in our model would hold for a wide range of species that have to cope with a highly stochastic food supply and that experience size-selective harvesting. The advantage of constructing a species-specific model is that we know a great deal about the population processes in the model and our parameter estimates are based on empirical studies. This is particularly important because of the large uncertainty involved in modeling the genetics. The underlying genetics determining body size and the interactions with other traits are largely unknown. We now discuss the different aspects of this uncertainty.

Heritability of body size.—Heritability is the proportion of phenotypic variation due to the additive effect of genes. There is an additive genetic component to size variation (Gjedrem 1983, 1986). Roff (2000) reviewed the heritability of size at maturity for a variety of species and reported values as low as 0.09 to as high as 0.90. The heritability of body size in natural fish populations is likely to be in the range of 0.2–0.3 (Stokes and Law 2000). Most studies on heritability of body size are concerned with size at maturity. In our model, size at maturity is determined by Eq. 3. What changes is how quickly individuals reach a particular size. The overall heritability of growth rate to maturity (0.14) created by our genetic model is comparable, albeit at the low end of the range, with that observed in natural populations. If the heritability is excessively large, the model is overestimating the response to selective harvesting, whereas if it is too small, the model is underestimating the response. Unfortunately no information exists on the heritability of size for kangaroos.

Growth model.—A common assumption in life history models is that all individuals follow more or less the same growth trajectory (Roff 1992, 2000, Klingenberg and Spence 1997). In this case, differences in adult size are caused by different birth sizes or variation in developmental time. Alternatively, evolution could act on selecting for different intrinsic growth rates (Arendt 1997). For most species, including kangaroos, we do not know which is more important. In our model we mimic both life history tactics by assuming that the number of size genes determines either the asymptotic size or the growth rate. The sensitivity analysis of our model suggests that the way in which genes control growth does not strongly influence the selection for smaller body size due to size-selective harvesting.

Genetic trade-off.—Life history theory is based on the hypothesis that evolution is constrained by the presence of trade-offs among some of the traits that contribute to fitness (Roff 1992, Stearns 1992). One commonly assumed trade-off is that between size and survival, with the fitness trade-off arising from a correlation between fecundity and body size. In kangaroos, larger body size decreases age at maturity (Dawson 1995) and increases male mating success because larger males are more successful in competing for females (Moss 1995, Walker 1995).

In our model we assume that size is traded off with survival under drought conditions. We consider annual rainfall as an indicator of food and water availability, which in our model influences growth, reproduction (via juvenile survival), and adult survival. We used drought resistance as a trade-off, rather than the age-dependent survival probability, for two reasons.

First, Tenhumberg et al. (2000) found that optimal life history strategies depend on whether individuals have a constant or stochastically varying food supply. Thus, kangaroos and other animals living in arid environments with a highly stochastic food supply are likely to have evolved appropriate life history strategies. By using drought resistance as a trade-off, we examined the effect of this stochastic selection pressure on the genetic response to size-selective harvesting. One alternative would be to allow the age-dependent survival probability to respond to genetic variation. This would disadvantage "large" individuals every year independent of the environmental conditions, resulting in a much stronger selection pressure for being small, and a more rapid evolutionary response to selective harvesting. Using an alternative trade-off would not alter our qualitative conclusions, because the aim of our model is not to make quantitative predictions about genetic change, but to evaluate the potential of harvest refuges as a management strategy to minimize the risk and amount of change in the allele frequency.

Second, Arendt (1997) and Reznick et al. (2000) review empirical evidence that, in a great many species, the cost of rapid growth is a reduced ability to respond to environmental stress, such as nutrient stress. Examples of stress-tolerant, relatively slow-growing species include lizards, frogs, snails, insects, and birds. Slow growth allows organisms that experience nutrient stress to use what nutrients are available most efficiently and to survive longer. In kangaroos, drought reduces the availability of water and food, resulting in increased mortality. Starving kangaroos are also particularly susceptible to hypothermia. Stress-resistant kangaroos might use nutrients to build a heavy fur or to develop greater fat reserves in favor of rapid growth. A range of possible physiological and behavioral differences is possible.

CONCLUSIONS

This study suggests that size-selective harvesting can result in smaller kangaroos of a given age with higher survival probability under drought conditions. The effect of size-selective harvesting increases with increasing harvesting rate and minimum size of the harvested animals. In scenarios with moderate dispersal from a nonharvested population, virtually all effects of harvesting on genetic structure disappear.

This paper highlights a potential conflict in sustainable use of wild life populations. Restricting harvesting to individuals with a high minimum size is commonly done to ensure the viability of a population. As a side effect, the balance of natural section changes to favor individuals with slower growth. Genetic change does not necessarily reduce the viability of a population. In the eyes of some kangaroo harvesters or conservation biologists, it would be beneficial to change the balance in favor of kangaroos with higher drought resistance because this would decrease the variance in the population dynamics of kangaroos. However, in a multitrait system, both positive and negative correlations can occur despite underlying physiological trade-off between pairs of traits (Charlesworth 1980, Charnov 1989). For example, Stokes and Law (2000) argue that genetic changes caused by size-selective harvesting in fish are large enough to affect the productivity of fisheries.

Because it is likely that there will be complex interactions between traits not considered in this paper, a precautionary management approach would be to minimize any genetic change, especially if we do not know that cessation of harvesting will reverse selection back to the original state (Stokes and Law 2000). Our model suggests that setting aside harvest refuges as a management strategy has a great potential to resolve this conflict. In order to determine the appropriate size and distribution of harvest refuges in the landscape, we need a better understanding of dispersal in the species in question, and the strength of selection under different harvesting regimes (i.e., different combinations of dispersal rates and degrees of size selectivity).

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APPENDIX A

Equations, regression tables, and graphs of parameter estimation for kangaroo maturity, mortality, and growth are available in ESA's Electronic Data Archive: *Ecological Archives* E085-056-A1.

APPENDIX B

A graph of kangaroo survival probabilities is available in ESA's Electronic Data Archive: *Ecological Archives* E085-056-A2.

APPENDIX C

A model and graph of the genetics of drought resistance are available in ESA's Electronic Data Archive: *Ecological Archives* E085-056-A3.

APPENDIX D

A discussion of sensitivity analysis is available in ESA's Electronic Data Archive: *Ecological Archives* E085-056-A4.

Section 16

Tenhumberg, B, Pople, AR, and Tyre, AJ (in prep.). Phenotypic variation in size at maturity in female red kangaroos.

Phenotypic variation in size at maturity in female red kangaroos

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Introduction

Evolutionary forces acting on the timing of sexual maturity (reviewed in Roff, 2002; Stearns, 1992) also influence population growth (first described by Cole, 1954). From an evolutionary point of view, the optimal length of the juvenile period is determined by trading off different factors influencing individual's fitness. For example, the shorter the juvenile phase the more time is left for reproducing, but a small size at maturity may negatively impact offspring survival and quality. An important component in the optimal length of the juvenile period is how quickly individuals grow, which is influenced by environmental factors such as food availability and temperature. Hence we can expect the onset of sexual maturity to exhibit patterns of phenotypic variation. This paper examines the onset of sexual maturity of female red kangaroos (*Macropus rufus*) under different environmental conditions. For males, the timing of maturity has only a small influence on fitness because males younger than 4 years are relatively small compared to the rest of the male population and consequently have a very low mating probability (Walker, 1995).

Red kangaroos are marsupials that live in most of inland Australia, including desert, grassland, mallee and mulga country. They prefer open plains with scattered trees, and graze on green grasses and dicotyledonous plants. Kangaroos are polygamous (Croft, 1980), and generally breed year round. Males and females continue to grow after they reach sexual maturity and can live for >20 years (Bailey & Best, 1992). In captivity, female red kangaroos reach sexual maturity at 15-20 months (Sharman and Calaby 1964), but in the field, age at maturity can be delayed by poor environmental conditions (Frith & Sharman, 1964; Newsome, 1965). Similarly, periods of extreme drought can result in suppression of the 35-day oestrus cycle (Newsome 1964). After drought breaking rains females come back into breeding condition. For more details on the reproductive biology of red kangaroos see the review by Tyndale-Biscoe and Renfree (1987).

Rainfall is a key environmental variable as it determines food availability and influences kangaroo growth and survival. Despite its important role, the relationship between rainfall and onset of maturity has not been quantified. Long-term studies are necessary to investigate the effect of rainfall on onset of sexual maturity because the response of kangaroos to rainfall may also depend on food availability in previous years. In good years kangaroos can accumulate a large fat body buffering against periods of low food availability, and it might take several years of low rainfall to affect kangaroo survival because primary cause of death in drought years is starvation and not thirst. In this study we used a ten year data set to study the timing of sexual maturity of female red kangaroos. Our results revealed that, while most females mature between 1 and 2 years of age, the probability of maturing increases with an index of body condition and rainfall. Compared to relative body condition the influence of rainfall is small.

Methods

Study area

The study was based at Currawinya National Park (1510 km^2) (28^{o}50'S 144^{o}29'E) in southwestern Queensland, 170 km southwest of Cunnamulla. Originally a pastoral property grazing mainly sheep, it was declared a National Park in 1991 and domestic stock were removed during the latter part of that year and in 1992. The property had not been harvested since the late 1970s. The region is dominated by open woodlands of mulga and poplar box, interspersed with sandplains and dunefields of buddabush (*Eremophila sturtii*), hopbush (*Dodonaea angustissima*) shrublands and numerous claypans and saltpans. Rainfall at Currawinya is summer dominant with an annual mean of 293 mm and a coefficient of variation in annual rainfall of 49% (Figure 3). The Queensland Parks and Wildlife Service monitored the densities of red kangaroos on Currawinya National Park between 1990 and 2000 using helicopter surveys (Figure 4, unpublished data). For details on the survey method see Clancy *et al.* (1997).

Sampling

Samples of male and female red kangaroos were shot in spring of each year over 1991-2000 as part of a long-term study of demography in red kangaroo populations (Pople, 1996). All killings were compliant with the "code of practice for humane shooting of kangaroos" endorsed by the Council of Nature Conservation Ministers in 1990 (www.deh.gov.au/biodiversity/trade-use/publications/kangaroo-report/cop.html). Animals were shot at night from a vehicle using a spotlight and a high-powered rifle (usually a .222) with a telescopic sight. Pouch young and the few injured animals were killed as quickly as possible, usually with a heavy blow to the head. Red kangaroos were usually encountered in groups of 2-3. To randomise the sampling, the animal seen first in each group was targeted first, but frequently the animal offering the best shot was taken. It is possible that the age structure of the kangaroo sample may vary with shooting intensity, because some age classes are more vulnerable to shooters. To avoid any density-dependent bias we adjusted our initial sample size of 400 animals according to changes in population size between different years.

Animals were shot in the neck to avoid damaging the skull and then decapitated after body weight (minus pouch young weight and to a resolution of 0.5 kg) and pes length (from heel to base of the large toenail) were taken. Heads were tagged and boiled in water to deflesh the skull. All skulls were aged from their molar index (MI), calculated as the number of molars (to a resolution of 0.1) that had progressed past a reference line running across the anterior rim of the orbits. Kirkpatrick (1964, 1965, 1970) found a close relationship between this index and age in several captive macropod species including red kangaroos. Age for animals in this study was estimated using the equation developed by Kirkpatrick (1970) for red kangaroos of western Queensland stock:

$$\mathrm{Log}_{10}(\mathrm{age}) = 2.2278 + 0.359\mathrm{MI}$$

where age is determined in days.

Immature females were identified by four relatively small, 'capped' teats and a relatively tight pouch (Frith & Sharman, 1964). Prior to puberty, the teats of juvenile females are inverted and have associated mammary hair. At the onset of sexual maturity, these hairs are shed as the teats become everted (Sharman and Calaby 1964). Neither the teats, associated mammary glands nor the tightness of the pouch revert back to the pre-pubertal state in anoestrus females (Tyndale-Biscoe & Renfree, 1987). Where there was doubt, the reproductive tract was removed and assessed according to the macroscopic criteria of Sharman (1964). Following sexual maturity, the vaginae, uteri and urogential sinus all increase in size, although this will vary through the reproductive cycle. Ovaries will contain enlarging or mature Graafian follicles, and a corpus luteum of pregnancy or lactation. Old corpus luteum scars may not be readily identified in anoestrus females, in which case the state of the pouch and presence of elongated teats distinguish them from immature females (Frith & Sharman, 1964).

Data analysis

We calculated logistic regression and survival models using the software package R (version 1.8.0) to quantify factors influencing the probability to reach sexual maturity. We had the following explanatory variables to choose from: age in years (estimated from molar index), hind foot length in mm, weight in kg, and rainfall (mm) in the 12 months prior to sampling. Because hind foot length, age, and weight are highly correlated (Table 1), we calculated two additional explanatory variables: condition as the residual of the individual from the regression line of weight on hind foot length (Figure 1), and residual weight gain as the residual of the individual from nonlinear regression of weight on age (Figure 2). We used package nls to fit the nonlinear regression.

We examined models including the explanatory variables rain, age, hind foot length, condition, and residual weight gain (rwg). Because of the high correlations between these variables, we never combined age and condition with hind foot length and residual weight gain (Table 2). We tested the following three types of models:

(i) In the logistic model the probability that at female reaches maturity (p_m) is calculated by inverse logit transform on the linear predictor (lp).

$$p_m = \frac{\exp(lp)}{1+\exp(lp)}. \tag{1}$$

(ii) In the exponential model we test whether females mature at a constant rate, i.e. exponential distributed maturity times

$$p_m(t) = \exp(-\lambda t). \tag{2}$$

(iii) In the Weibull model we assume that the probability of females reaching sexual maturity is increasing with age.

$$p_m(t) = \exp\left(-(\lambda t)^{\kappa}\right). \tag{3}$$

(ii) and (iii) are cumulative survival functions, in which λ was modelled as a linear function of different explanatory variables (McCallum, 2000). Age is always included in these models, whereas in the logistic regression models age is not necessarily included. We used the cumulative survivor function rather than the hazard function because our data do not reveal when different individuals reached sexual maturity; instead we only know whether they were mature at the age of death.

We compared alternative models using Akaike's Information Criterion (AIC), which evaluates models based on both the likelihood of the model and the number of estimated parameters:

$$AIC = 2L + 2k \tag{4}$$

where L is the negative log-likelihood of the model and k is the number of parameters. We could compare these different model structures directly because the likelihood is based on the probability that a given female is mature, and therefore the likelihoods are directly comparable. Generally a model with a lower AIC value is considered to be better. However it is possible to go beyond a simple ranking of models by calculating Akaike weights, which are the probability that each model out of a set of models is closest to the correct one (Burnham & Anderson, 2002). First calculate a Δ_i value for each model by subtracting the AIC of the best model from the AIC of all models. The Akaike weight w_i for model i is then

$$w_i = \frac{e^{-\Delta_i/2}}{\sum_i e^{-\Delta_i/2}} \tag{5}$$

and this weighted distance between model i and the best model can be interpreted as the probability that model i is correct. Beginning with the best model, a 95% confidence set of models is constructed by adding models to the set until the sum of their Akaike weights exceeds 0.95. We used AIC rather than $\mathrm{AIC_c}$ because the number of data points exceeds the number of parameters by a ratio of nearly 100:1 for models with 4 parameters.

Results

Rainfall at Currawinya (Figure 3) was low in the early 1990s, but was above average during the latter half of the decade. As a result red kangaroo populations declined on the Park and surrounding grazing properties by >70% between 1991-1993 (Pople, 1996), but by the end of the decade, the population had recovered to pre-drought levels (Figure 4). Population decline during 1991-1993 was due to minimal recruitment into the population during (Pople, 1996) as is typical of kangaroo populations during drought (Frith & Sharman, 1964; Newsome, 1965; Shepherd, 1987), and an increase in mortality especially of adult male kangaroos causing a dramatic shift in the adult sex ratio towards females (Pople, 1996; Pople & Cairns, 1995).

Model selection:

Age strongly influences the probability of reaching sexual maturity. Including age as an explanatory variable in the logistic model reduced the AIC value of the null model by over 60% (Table 2). Size has also a large effect on AIC values, but size and age are highly correlated (correlation coefficient = 0.79, Table 1). Maturity times were not exponentially distributed; the probability of reaching sexual maturity increases with age (Weibull model). The absolute best model was the Weibull model including the explanatory variables residual weight gain and rain. However including residual weight gain in the model improved the fit to a much greater extent than rainfall. Including condition does not improve model fit probably because of its high correlation with age.

The third best model was the logistic model including age, rain and residual weight gain. Figure 5 and Figure 6 compares the predictions resulting from Weibull and logistic models. The effect of residual weight gain is much bigger in the logistic model than in the Weibull model. The logistic model predicts female kangaroos with a very high residual weight gain to reach sexual maturity below 0.5 years of age, which is physiologically impossible.

Discussion

Compared to eutherian mammals, life history diversity in marsupials has been subjected to little quantitative analysis (Fisher et al., 2001). A recent study by Fisher et al. (2001) analysing the pattern of marsupial life history traits found that age at maturity is a key variable describing life history pattern in marsupials. This paper scrutinizes phenotypic plasticity of age at maturity in marsupials using red kangaroos as a case study. Fisher et al.'s study (2001) suggests that the energetic value of food is shaping the evolution of marsupial life histories; this paper analyzes the plastic response of age at maturity to food availability in any given years.

Mathematical models have predicted that "norms of reaction" for age and size at maturity are adaptive (Berrigan & Koella, 1994; Stearns & Koella, 1986; Tenhumberg et al., 2000) and empirical studies have demonstrated that animals reach sexual maturity at an older age and smaller size under low food availability (e.g., Morita & Morita, 2002; Tenhumberg, 1992). Here we use rainfall as an indication of food availability in the current year and condition (individual weight relative to her size) and residual weight (individual weight relative to her age) to signify food availability in the past. However condition and age are correlated to some extent, making this variable less suitable as a signal for past food availability. Our analysis demonstrates that female red kangaroos mature earlier the higher their residual weight gain and the higher the rainfall. These findings are consistent with kangaroos growing at a faster rate (i.e. high residual weight gain) and so reaching a critical weight at an earlier age. Because age is correlated with kangaroo size (correlation coefficient = 0.36) our data do not reveal whether the growth rate also influences size at maturity.

There may be a trade-off between early maturity and subsequent growth because resources are diverted away from maintenance and growth towards the production of offspring (Cockburn & Johnson, 1988); this tradeoff could be particularly severe in kangaroos because they have an indeterminate growth pattern (Ealey, 1967). Early maturity increases population growth rate (Stearns & Hoekstra, 2000), so in the absence of significant costs to early maturity we would expect kangaroos to mature at the smallest size possible. However, annual fecundity may increase with female body weight as has been demonstrated for the ringtail possum, *Pseudocheirus peregrinus*, (Lee & Cockburn, 1985), or a larger body size might increase the chances of females resisting mating attempts by younger males (Cockburn & Johnson, 1988). In addition, it might be beneficial for kangaroos to mature at larger sizes if offspring survival or quality depends on female size. For example, larger mothers might be better in defending their young from predators, or they might provide better nutrition.

This paper quantifies the relationship between rainfall, residual weight gain and onset of maturity. Age at sexual maturity influences population growth rates, thus it is an important component in models projecting population growth in the future. Population models are used to evaluate different management strategies and are an important component in decision making, e.g. determining sustainable harvesting quota (Hacker et al., 2004). A good estimate of age at maturity at different growth rates is also vital for predicting evolutionary responses of kangaroo management because fitness is often more sensitive to changes in age at maturity than to changes in other life history traits (Stearns & Hoekstra, 2000). Tenhumberg et al (2004) constructed a model predicting genetic consequences of size selective harvesting. Their model assumes that kangaroos with a high growth rate have a higher probability of dying during drought years, but females reach maturity at an earlier age and male size is positively correlated with mating success. They found that without incorporating a positive relationship between age of maturity and individual growth rates genetic variation in kangaroo size is virtually lost in a few generations as a result of stabilizing selection (unpublished results), which is inconsistent with the large variation in sizes in kangaroo populations. Simulating genetic variation in kangaroo sizes is a prerequisite for predicting evolutionary responses to size selective harvesting.

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Tables:

Table 1: Correlations between explanatory variables.

	Rain	Age	Hind Foot Length	Weight	Condition	Rel. Weight Gain
Rain	1.00					
Age	0.01	1.00				
Hind Foot Length	0.10	0.76	1.00			
Weight	0.07	0.85	0.89	1.00		
Condition	-0.03	0.38	0.00	0.45	1.00	
Rel. Weight Gain	0.14	0.02	0.36	0.48	0.35	1.00

Table 2: AIC values for the fitted models. Size is measured as hind foot length and rwg is the residual weight gain (see text). *k* specifies the number of parameters fitted in the model. AIC weights less than 0.001 are omitted for clarity. ΔAIC is the difference in AIC between each model and the one with the lowest AIC value.

Model	Explanatory Variables	k	AIC	ΔAIC	weights
Logistic	null	1	455	332	
	size	2	201	79	
	size + condition	3	144	21	
	size + rain	3	203	80	
	size + rain + condition	4	143	20	
	age	2	169	46	
	age + rwg	3	141	18	
	age + rain	3	162	39	
	age + rain + rwg	4	137	14	
Exponential	null	1	314	191	
	condition	2	298	176	
	rain	2	310	187	
	condition + rain	3	293	170	
	rwg	2	293	170	
	rwg + rain	3	292	169	
Weibull	null	2	187	64	
	condition	3	189	66	
	rain	3	171	48	
	condition + rain	4	171	48	
	rwg	3	130	7	0.02
	rwg + rain	4	123	0	0.98

Table 3: Parameter estimates and 95% confidence limits (CL) for logistic and Weibull model with the lowest AIC values.

	Logistic Model		Weibull Model	
	Estimate	95% CL	Estimate	95% CL
κ	-	-	2.0282	(1.77, 2.27)
(Intercept)	-13.9893	(-18.0, -10.0)	-0.7033	(-0.83, -0.57)
Age	7.9330	(5.9, 10.0)	-	
Rwg	1.3662	(0.75, 1.98)	0.0493	(0.036, 0.065)
Rain	0.0050	(0.00099, 0.0090)	0.0005	(0.00018, 0.0007)

Figures:

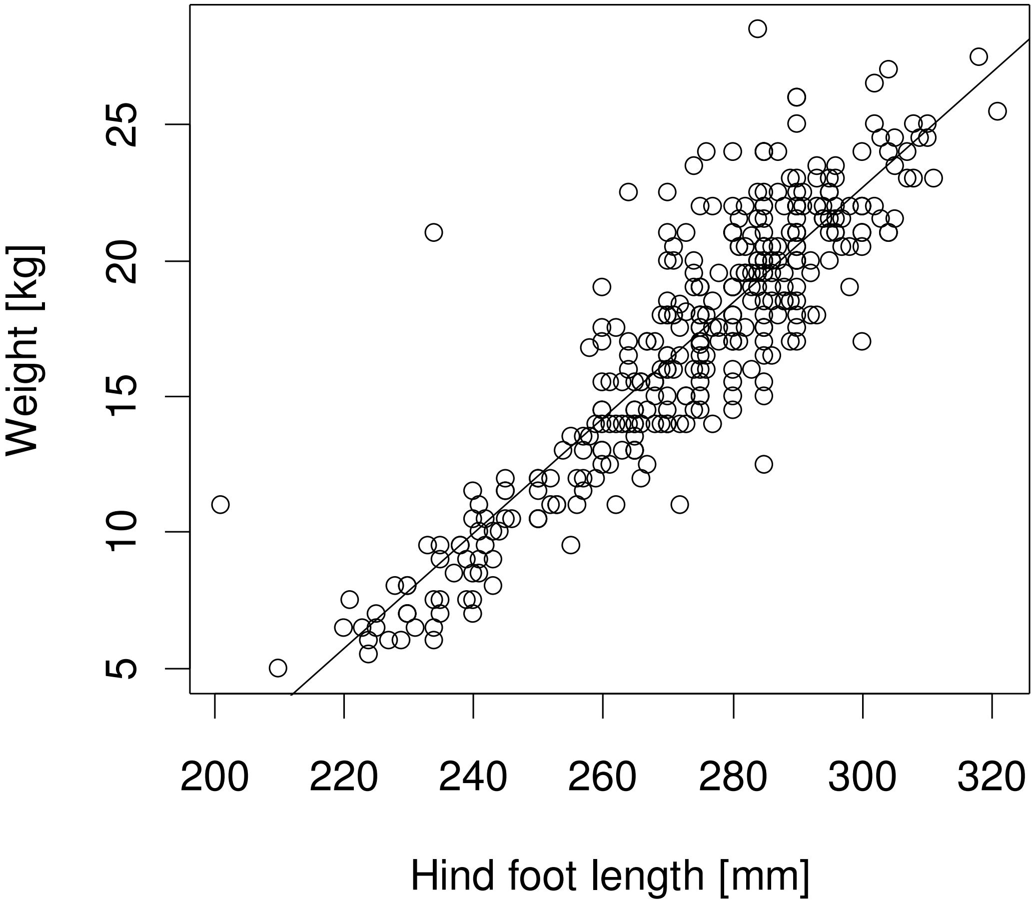


Figure 1: Weight as a function of hind foot length, HF. Weight = -40.9 (1.6) + 0.21 (0.005) * H.F., where values in parentheses are standard errors.

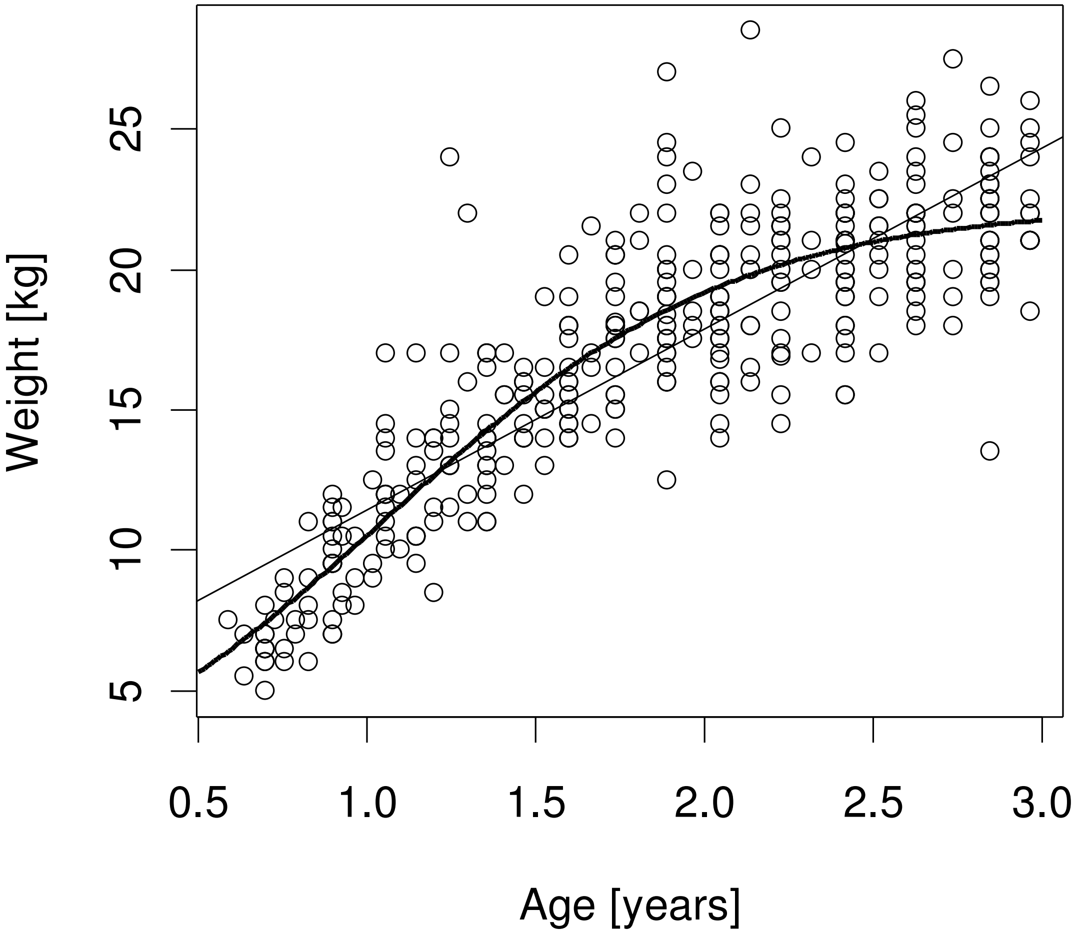


Figure 2: Weight as a function of age. The thick line is the logistic model that is used to calculate residual weight gain: $Weight = a/\left(1+\exp\left[\left(t-b\right)/c\right]\right)$, where t indicates age and a, b, c are constants with the following values: a = 22.26 (0.4), b = 1.06 (0.03), and c = 0.52 (0.04). The values in brackets are the standard errors. For comparison we also potted a linear model (thin line).

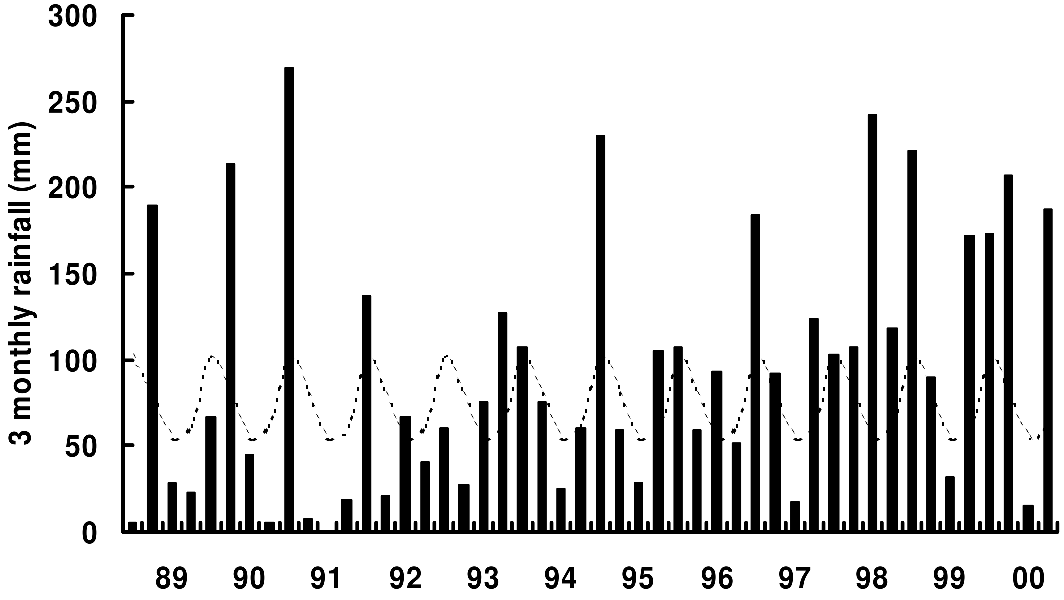


Figure 3: Three-monthly rainfall (solid bars) at Currawinya National Park over 1989-2000. Long-term average rainfall for each three-month period is shown as dotted lines.

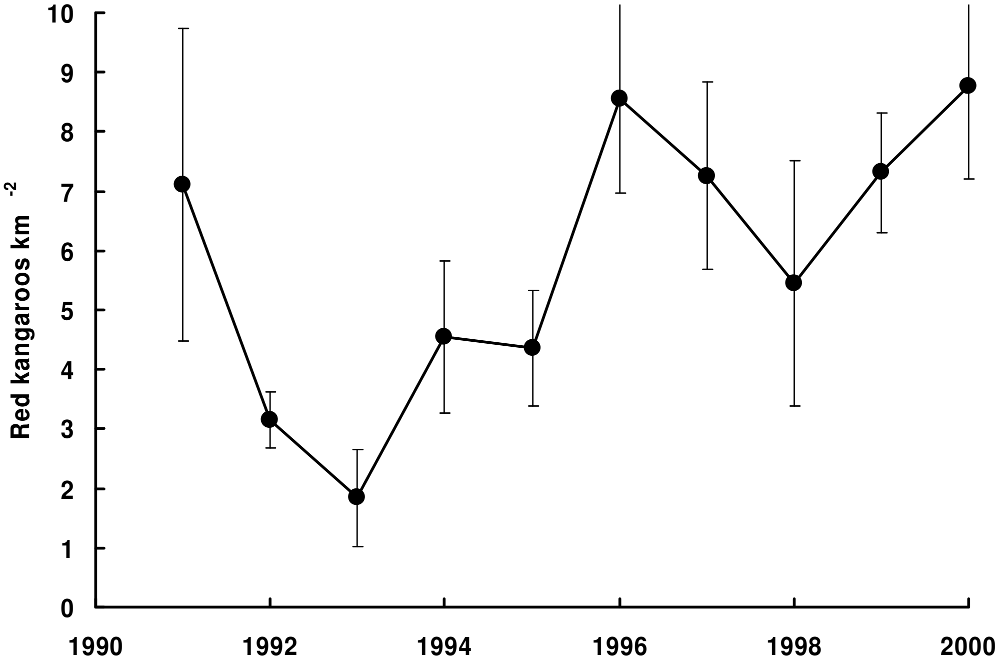
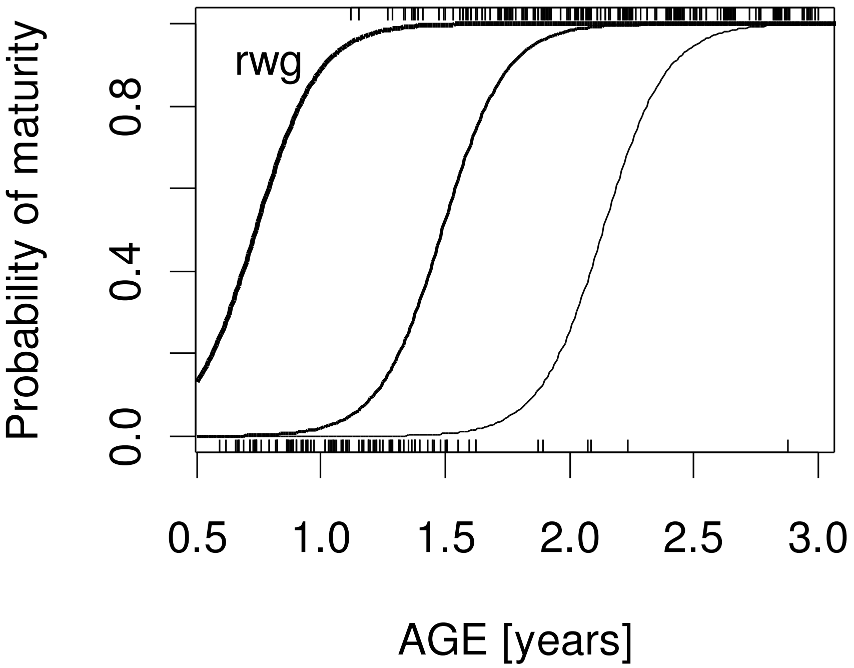


Figure 4: Densities (± standard errors) of red kangaroos per km^2 on Currawinya National Park between 1990 and 2000 as determined from helicopter surveys (Queensland Parks and Wildlife Service, unpublished data).



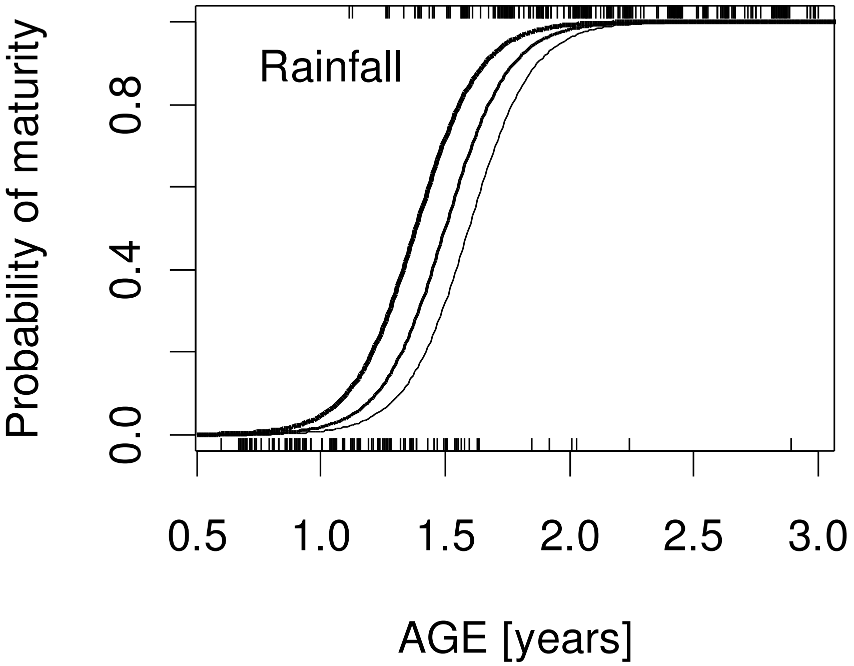


Figure 5: Predicted and observed maturity from the best logistic regression model. The lines are predictions for residual weight gain (rwg) or rainfall held at the 5%, 50% or 95% quantiles; the other variable is held constant at the mean. Rugs indicate the observed values.

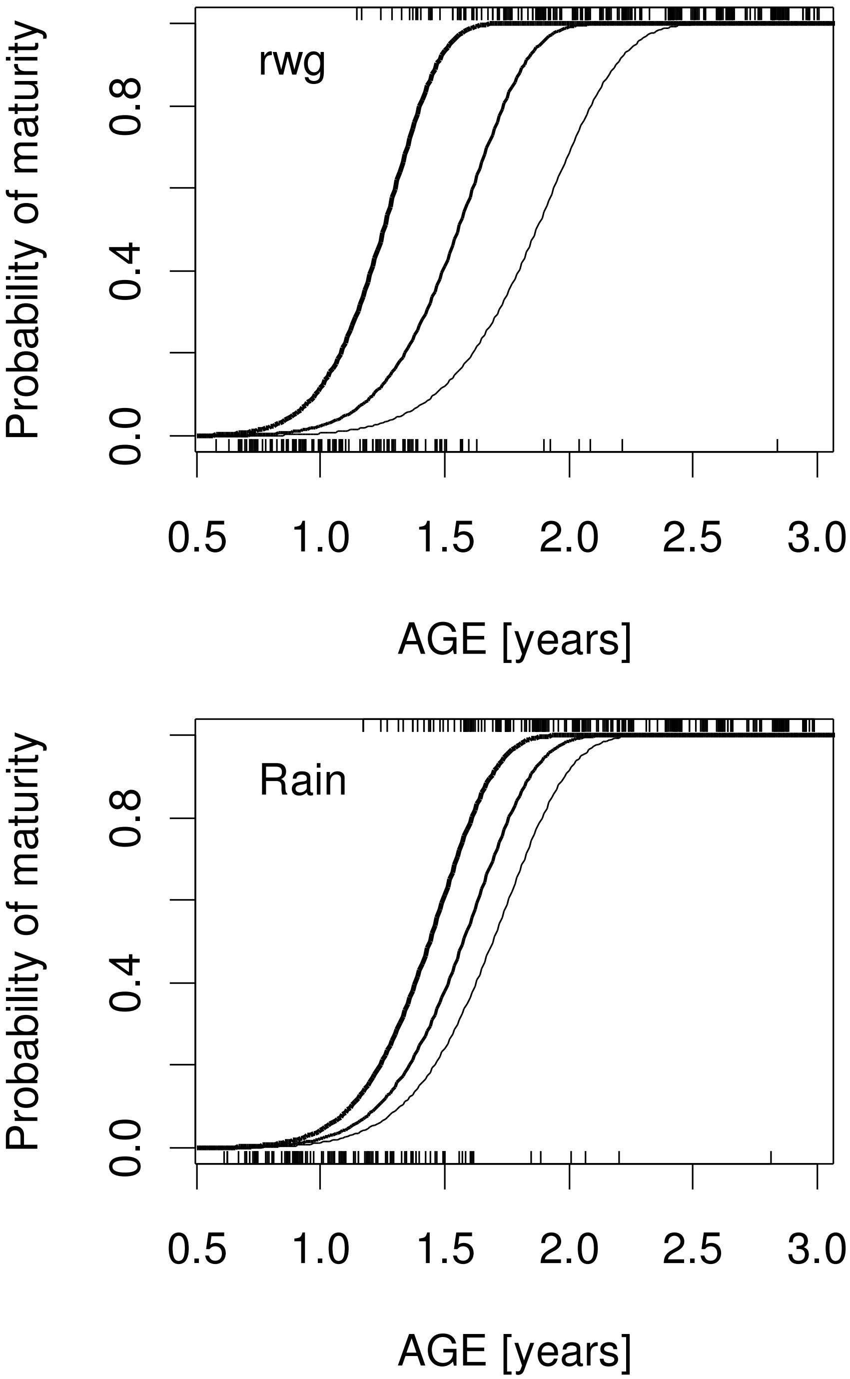


Figure 6: Predicted and observed maturity from the best Weibull distributed maturation time model. The lines are predictions for residual weight gain (rwg) or rainfall held at the 5%, 50% or 95% quantiles; the other variable is held constant at the mean. Rugs indicate the observed values.

17. Work to be completed

17.1 Introduction

There are a number of pieces of work that were either started or continued during the present project that are yet to be completed. These are described below and some preliminary results are presented.

17.2 Spatial modelling

Spatial modelling produces continuous density surfaces, providing alternative estimates of population size to that derived from the average of survey units. Integration under the density surface allows population size to be estimated for any area within the overall study area. Section 11 provided an example using kriging, but habitat covariates can also be used. In New South Wales and South Australia, annual quotas or tags or both are issued to properties within each region to put a ceiling on the number of kangaroos that can be commercially harvested. In all states, non-commercial culling (i.e. pest destruction) permits are also allocated to properties. All of these allocations are made largely on an *ad hoc* basis. A spatial model would therefore provide a more rigorous basis for allocating quotas and permits.

Aerial surveys provide regional estimates of abundance, but finer or local scale estimates generally have poor precision, which declines with size of an area for a given sampling intensity. Predicting future population size at a both scales adds further uncertainty in modelling births and deaths and, at a local scale, movement rates. There are two approaches to predicting future fine-scale abundance. A ‘bottom-up’ approach is to model temporal fluctuations at a fine or local scale. The estimate for each local area can then be combined to calculate an estimate of abundance for the region. An alternative, ‘top-down’ approach is to first predict future regional abundance, then divide this estimate up into its constituent, local areas using a spatial model.

17.2.1 South Australian habitat models

This latter method is the logical choice for kangaroo management in South Australia as it matches the quota setting process. Here, annual harvest quotas are set as proportions (~15%) of aerial survey estimates of red and western grey kangaroo population size for large management regions, generally > 10,000 km^2. Quotas are then issued to properties (ranging 20-2,000 km^2) within each region.

To predict red kangaroo distribution in South Australia, kangaroo density in 25 km × 25 km grids cells was ‘centred’ within each year (i.e. differences from the mean density over the study area, Quinn and Keough 2002) to avoid the need to account for annual variation in regional density within the study area. Four regions were modelled separately (Fig. 17.1) because it is this within-region variability that was of interest rather than the broader-scale variation across the whole pastoral zone. The latter has also been described before (Cairns *et al*. 1991). Year-to-year changes in broad-scale abundance were not of interest here; rather it was changes in the spatial pattern of density (= pattern of distribution). The modelling strategy involved constructing *a priori* multiple regression models relating red kangaroo density to sets of environmental variables, comprising aspects of the soil, vegetation, landform and climate. Landscape heterogeneity, considered important to red kangaroos (Pople 1989), was incorporated as the number of soil types, landforms and environmental associations (Laut *et al.* 1977) in each cell and the range in a number of soil attributes (e.g. nitrogen) in areas of increasing spatial extent surrounding each cell. More complex sets of explanatory variables were contrasted by combining variable sets and including curvilinear terms and interactions between likely variables. A particular interest was to describe any shift in the pattern of distribution and assess the influence of NDVI. This was possible through using year interactions with explanatory variables, including NDVI. To seek the most parsimonious model with the most predictive accuracy, models were compared using Akaike's Information Criterion and cross-validation. Spatial autocorrelation was assessed using a semivariogram (Isaaks and Srivastava 1989). If present, the correlation structure can be incorporated into the regression models using generalised least squares (Crawley 2002; Venables and Ripley 2002).

Year interactions with static variables would indicate changes in the pattern of distribution over time. Significant year interactions with NDVI would indicate an influence of this proxy for food supply in only some years. Both interactions were significant for the South Australian data. Figure 17.2 shows the predicted distribution and associated residuals for red kangaroos across the study area. These are relative densities that would be converted to absolute density from a model predicting average regional density (the 'top-down' approach from above). There is no obvious spatial pattern in the residuals.

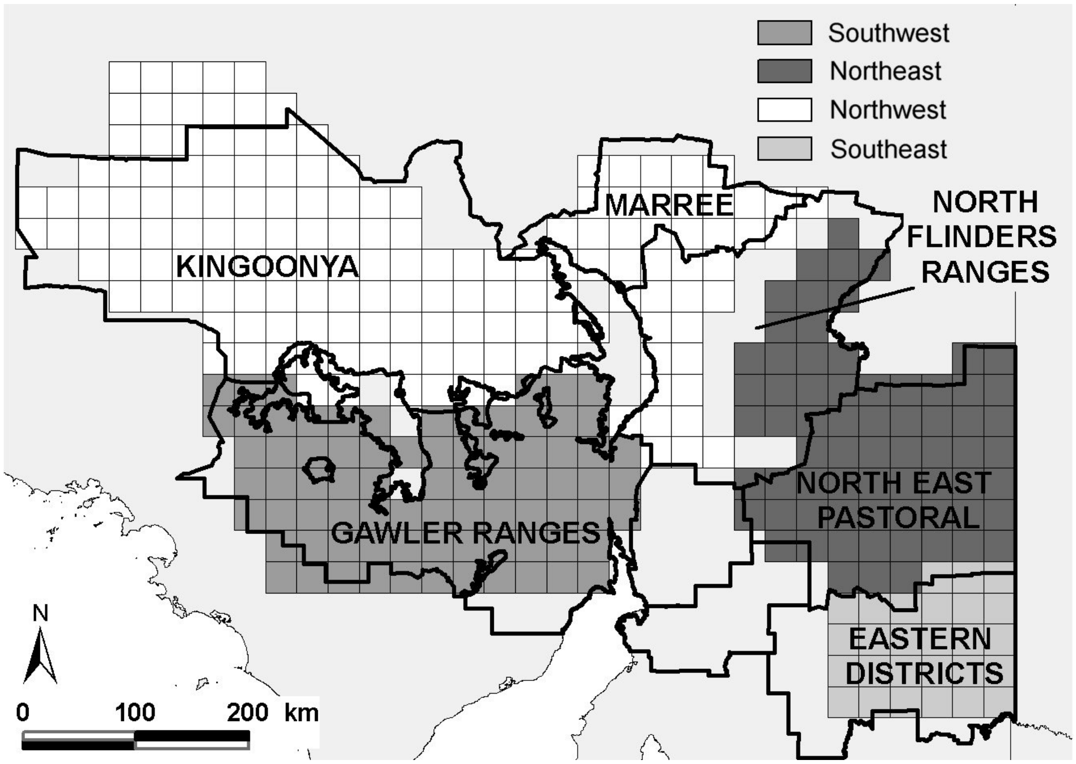


Figure 17.1. Four regions (shaded) modelled in South Australia in which relative kangaroo density was predicted. Boundaries of the existing management regions are also shown.

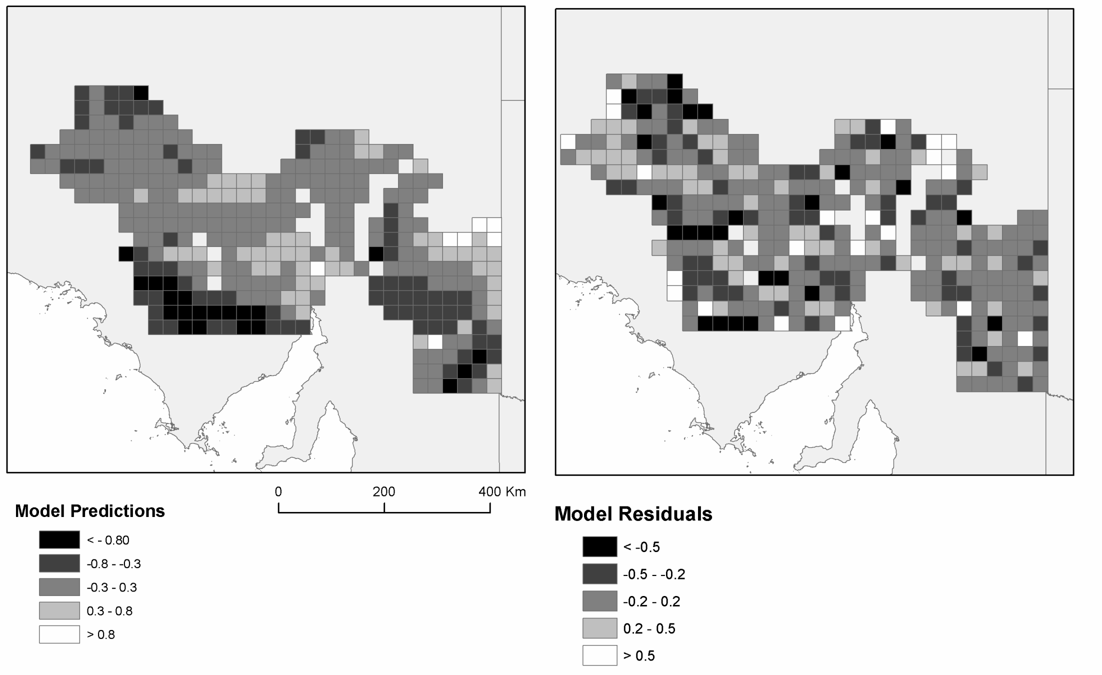


Figure 17.2. Predicted centred red kangaroo density in the South Australian pastoral zone and associated residuals.

17.2.2 Queensland habitat models

A similar approach was taken with Queensland data. As highlighted in previous Sections, surveys of kangaroos by helicopter in blocks result in incomplete geographic coverage of the harvest area and sampling is non-random. Extrapolating the average kangaroo density in these survey blocks to the rest of the harvest area therefore requires some strong and perhaps unrealistic assumptions. A spatial model can overcome these limitations by providing regional estimates of density through integration under a density surface. Estimates of kangaroo density from fixed-wing surveys were available in grid squares over 1980-2001 and averages for red and eastern grey kangaroos are shown in Figure 17.2. Density was spatially standardised in each year because spatial pattern rather than temporal fluctuation was of primary interest. A number of explanatory variables were included in multiple regressions to predict density and these are shown in Table 17.1. Harvest density was also spatially standardised and used as an explanatory variable. Recent rainfall and NDVI were temporally standardised in each cell and also used as explanatory variables. In addition to these variables that vary from year-to-year, a number of static habitat variables were included as explanatory variables including soil, landform, vegetation fragmentation and climate. Spatial correlation was assessed by examining variograms using the finer-scale unit data (5 km × 200 m, see Section 1) and then comparing models with and without a correlated errors using generalised least squares (`gls`) in R 1.9.1 (Crawley 2002; R Development Core Team 2003).

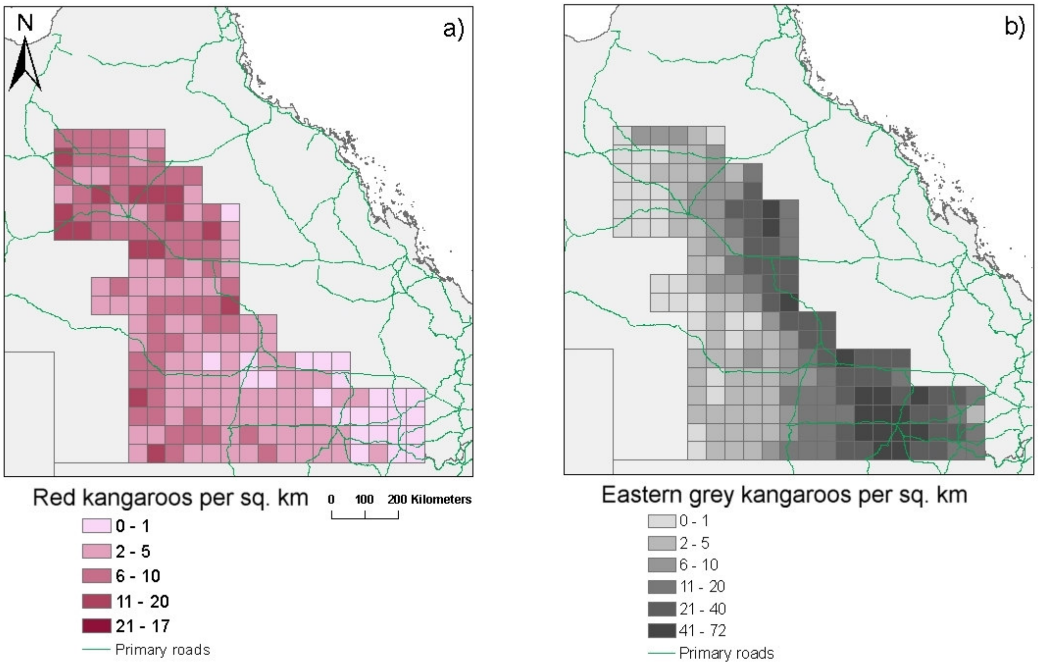


Figure 17.3. Average densities of (a) red and (b) eastern grey kangaroos in grid squares in Queensland from aerial surveys over 1980-2001.

Table 17.1. Explanatory variables used to model kangaroo density in grid squares in Queensland.

Rainfall
Temperature
Seasonality in climate
Variability in climate
Soil fertility
Soil water holding capacity
Soil diversity
Landform
Landform diversity
Range of fragmentation metrics
Average NDVI
Variability in NDVI
Recent rainfall
Recent NDVI
Harvest

Preliminary results indicate the data are not spatially correlated at this scale for either species. Akaike's Information Criterion and the coefficient of determination (R^2) are shown for four models predicting red kangaroo density in Table 17.2. The relationship between kangaroo density and just static aspects of habitat did not vary from year-to-year, as indicated by poor support for the model with a year interaction with habitat. NDVI improved on the relationship and its influence did not vary from year-to-year. Harvest density was a particularly useful predictor, being included in the most parsimonious model along with habitat variables. Model predictions are shown in Figure 17.4 with no obvious spatial pattern in the residuals.

Similar models were developed for eastern grey kangaroos. They explain a greater proportion of the variation ($R^2 > 0.5$) than the models for red kangaroos, which is not surprising given the greater concentration of greys in the readily predicted more mesic and more heavily wooded regions of the survey area (Fig. 17.3).

Table 17.2. Coefficient of determination (R^2) and Akaike's Information Criterion (AIC) for four models used to predict red kangaroo density in grid squares in Queensland (Fig. 17.3*a*).

Model	R^2	AIC
Static habitat variables	33	3051
Static habitat variables + NDVI	33	3048
Static habitat variables x year	34	3097
Static habitat variables + year x NDVI	33	3054
Static habitat variables + harvest	37	2967

These models provide a description of the relationship between habitat, harvest density and kangaroo density. In practice, densities are estimated regularly in the helicopter survey blocks and it is these that need to be extrapolated to the rest of the harvest area using a spatial model. This could be done in at least two ways. If local estimates of density were needed, then one option would be to use the average density among survey blocks, or a stratified estimate, in combination with harvest densities in grid squares to convert the standardised kangaroo densities in grid squares in the survey area from the models described above (Table 17.2, Fig. 17.4). However, the primary need is for regional and state-wide estimates of density, so a second option is to develop a spatial model from the helicopter survey blocks, for which there are now 15 years of data. This model could then be used to predict density outside the survey blocks. Finally, these models could then be cross-validated using the fixed-wing data. A complication is if the relationship between kangaroo density and habitat varies between years. For example, good rainfall over a number of years, but only in the Mitchell grass downs resulting in increases in red kangaroo density only there, would change the overall relationship between density and less wooded areas. This could be overcome with a year-specific spatial model, but annual sample size is small ($n = 16$). Sample size needs to be considerably larger than the number of explanatory variables (Tabachnick and Fidell 1996). The results in Table 17.2 suggest this may not be a problem, particularly if harvest density, a year-specific variable, is included as a predictor.

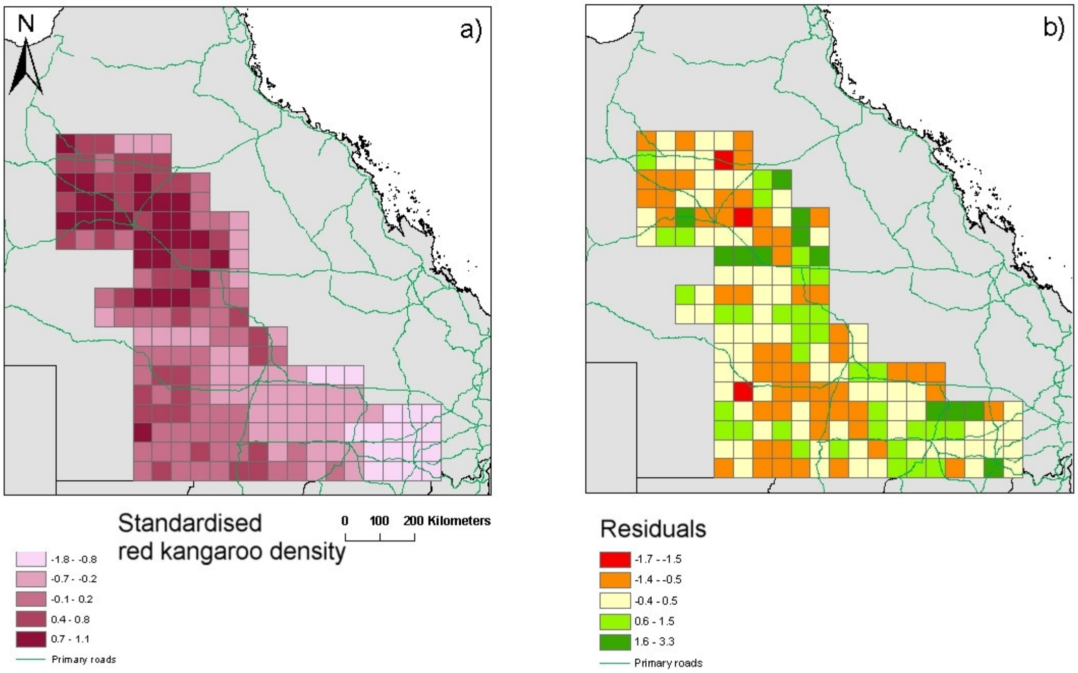


Figure 17.4. Predicted spatially-standardised densities of red kangaroos and model residuals in grid squares in Queensland.

17.3 Demography of an unharvested red kangaroo population

The dynamics of unharvested populations, including their underlying vital rates (i.e. survival and reproduction), provide an important contrast to their harvested counterparts. The contrast should allow a better understanding of the impact of harvesting, hopefully identifying the nature and strength of density dependence. However, a relatively long time series is required to encompass the broad range of environmental conditions experienced in arid and semi-arid areas.

Over a ten year period (1991-2000), age structure was determined annually for the red kangaroo population on Currawinya National Park (see Fig. 17.12) using large (200-400), random shot samples at approximately the same time each year. The study site is described in Section 16 along with sampling methods. Population density was also estimated at the same time using helicopter surveys. Currawinya was formerly a sheep grazing property and was gazetted as a National Park in 1991. However, there had been no authorised harvesting of kangaroos on the property for at least the ten years prior to 1991 and the shot samples were the only harvest, albeit small, since gazettal. Harvesting occurs regularly on the surrounding sheep grazing properties. Results for the first four years of this time series have been reported by Pople and Cairns (1995) and Pople (1996).

Annual survival rates were calculated from consecutive age structures and adjusted for population rate of increase (Caughley 1977; Pople 1996). Confidence intervals for age structures and survival were calculated from 1,000 bootstrap samples of the data.

Red kangaroo density on Currawinya and surrounding properties declined sharply during a protracted drought in the early 1990s (Figs 17.5 and 17.6). For the remainder of the decade, the population generally increased on the back of above average rainfall. By 2000, it had recovered to its pre-drought density. On the surrounding harvested properties, the overall recovery rate was lower so that that average densities on the two areas diverged (Fig. 17.5).

This difference between the two areas is likely to be the result of two factors. The first factor is harvesting, which is expected to have a greater impact when populations are increasing because harvest mortality is likely to be additive rather than compensated by a density-dependent increase in survival (Pople 1996; Pople and McLeod 2000). The second factor is the removal of sheep from Currawinya, which is likely to have freed up resources for kangaroos.

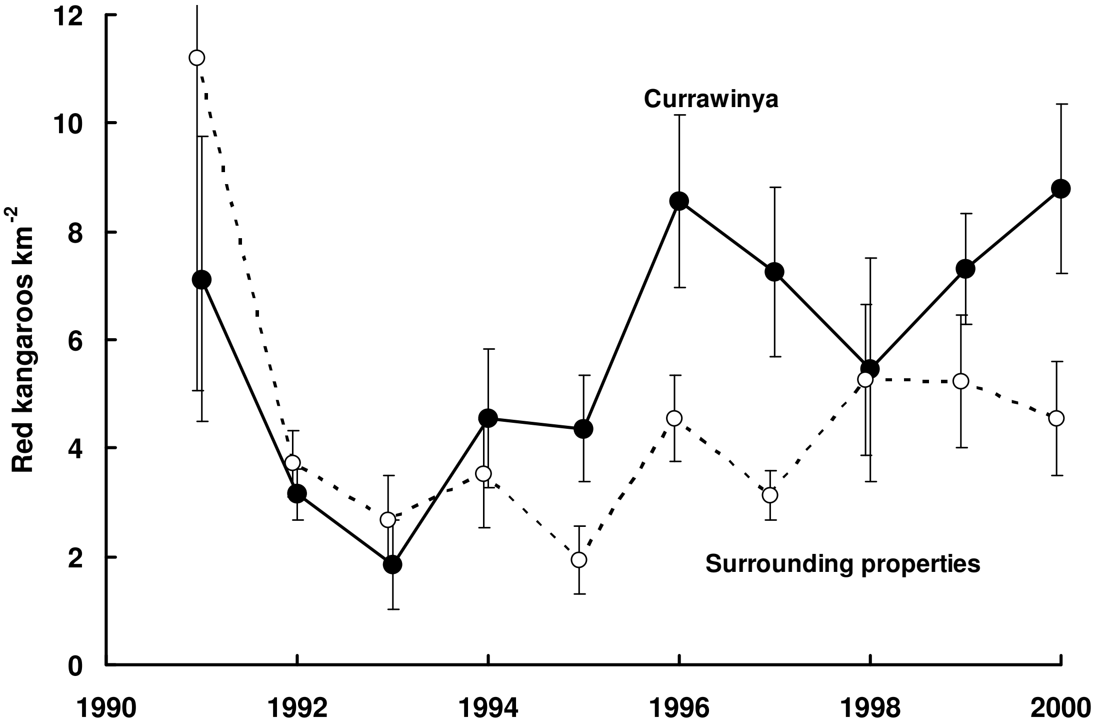


Figure 17.5. Trends in the density of red kangaroos (±SE) on Currawinya National Park, which is unharvested, and the surrounding harvested properties, as detrmined from helicopter surveys (Queensland Parks and Wildlife Service, unpublished data).

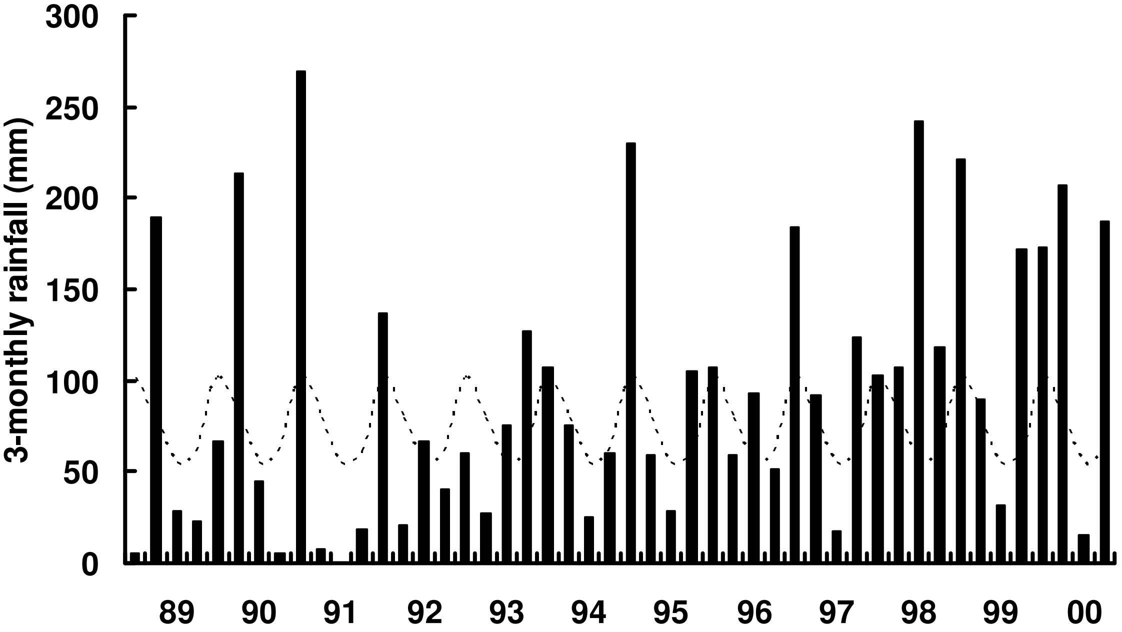


Figure 17.6. Quarterly rainfall (solid bars) at Currawinya National Park over 1989-2000. Long-term average rainfall for each three-month period is shown as a dotted line.

Mortality during the drought was strongly male biased, leaving an adult population comprising ~85% females (Fig. 17.7). This bias in mortality was across all age classes, resulting in a strong female bias in all sub-adult and adult age classes (Fig. 17.8). This result contrasts with another report of the age structure of red kangaroos dying during drought which was biased to larger, older animals, although population age structure was not determined (Robertson 1986). However, the subsequent recovery of the population on Currawinya saw a change in the age structure that could not be explained by survival alone. Annual survival rates > 1 indicated an influx of males and females in the sub-adult and adult age classes (Fig. 17.9). Survival rates in Figure 17.9 have therefore been termed 'apparent' survival.

The suggestion here is that the increase in red kangaroo density following the removal of sheep on Currawinya was delayed by the drought, but accelerated by an unstable age structure (i.e. few sub-adults, strong female bias amongst adults) and immigration following the drought. What is surprising is that immigration played such an important role in the population's dynamics over such a large area (1,510 km^2).

Reproductive data were also collected in this study. The proportion of adult females (≥ 3 years old) breeding to full potential (see section 17.6 for methods) over the study period are shown in Figure 17.10. This was predictably low during the drought, but subsequently recovered to 0.5-0.6 with the exception of 1999. These estimates broadly match the survival rates for juveniles (Fig. 17.9*a*), although the age class and likely time periods for influential environmental conditions are slightly different. A female's breeding status only reflects juvenile survival to weaning, whereas juvenile survival includes a period beyond weaning.

Variation in the sex ratio (proportion male) of pouch young is shown in Figure 17.11. These were often, but rarely significantly, above 0.5. A male bias is predicted by evolutionary theory for species with male-biased dispersal, such as red kangaroos, as it ensures equal investment in males and females (Maynard Smith 1978; Johnson 1989). Evolutionary theory also predicts that if males have more variable reproductive success than females, as in polygynous species such as kangaroos, and this success is influenced by parental investment, then females should invest more heavily in sons, but produce more daughters (Trivers and Willard 1973; Clutton-Brock *et al.* 1982). This may be achieved by varying either the sex of offspring relative to their body condition or the resources provided to offspring (Clutton-Brock *et al.* 1982). The relationship between maternal condition and age with pouch young sex ratio needs to be examined with these data. As an initial exploration, the relatively strong male bias in the drought year of 1991 is consistent with the negative correlation between the pouch young sex ratio (proportion male) in eastern grey kangaroos and rainfall reported by Jarman and Johnson (1983). However, over the entire time series at Currawinya, the proportion of pouch young that are male was not significantly correlated with rainfall in either the six or twelve months preceding sampling (six months rainfall: $r_8 = -1.55$, $P > 0.1$), as Jarman and Johnson (1983) also found. The data in this study differ to those of Jarman and Johnson (1983) in that they represent a long time series from the same study site rather than data from multiple sites.

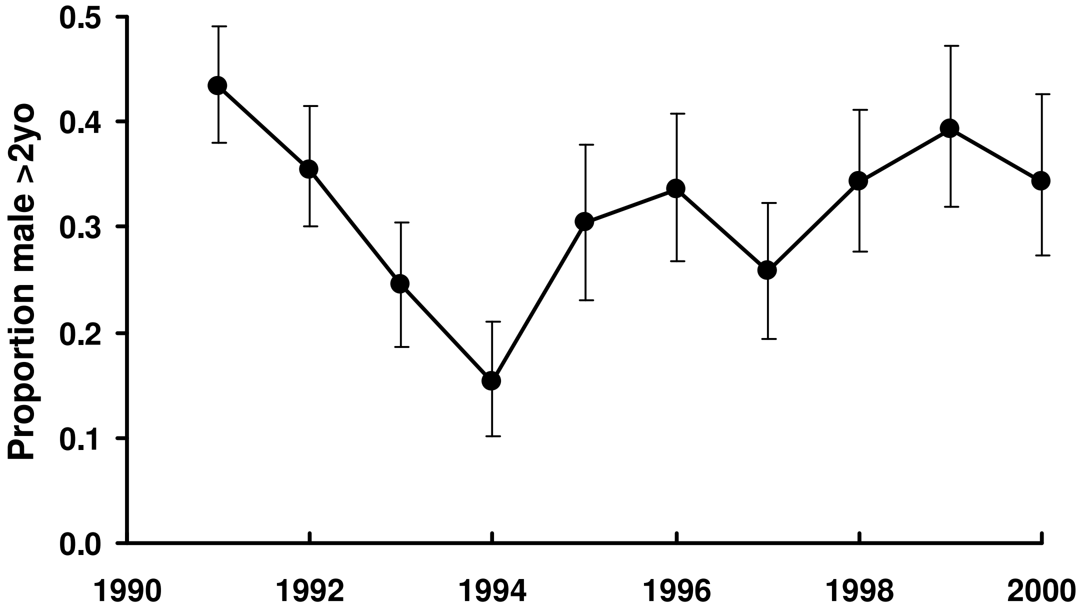
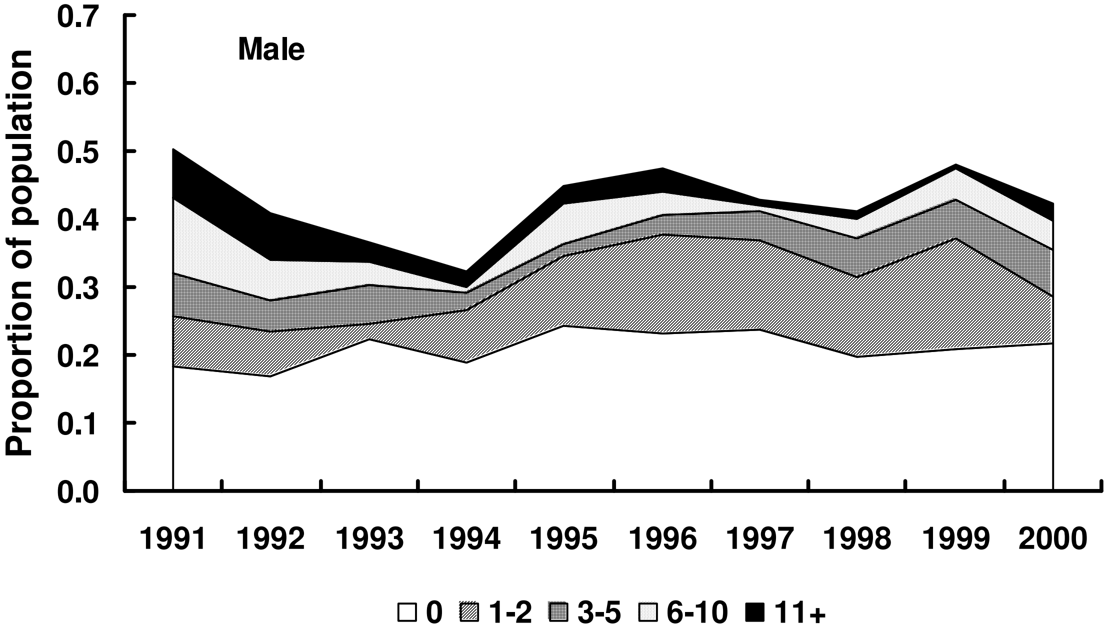
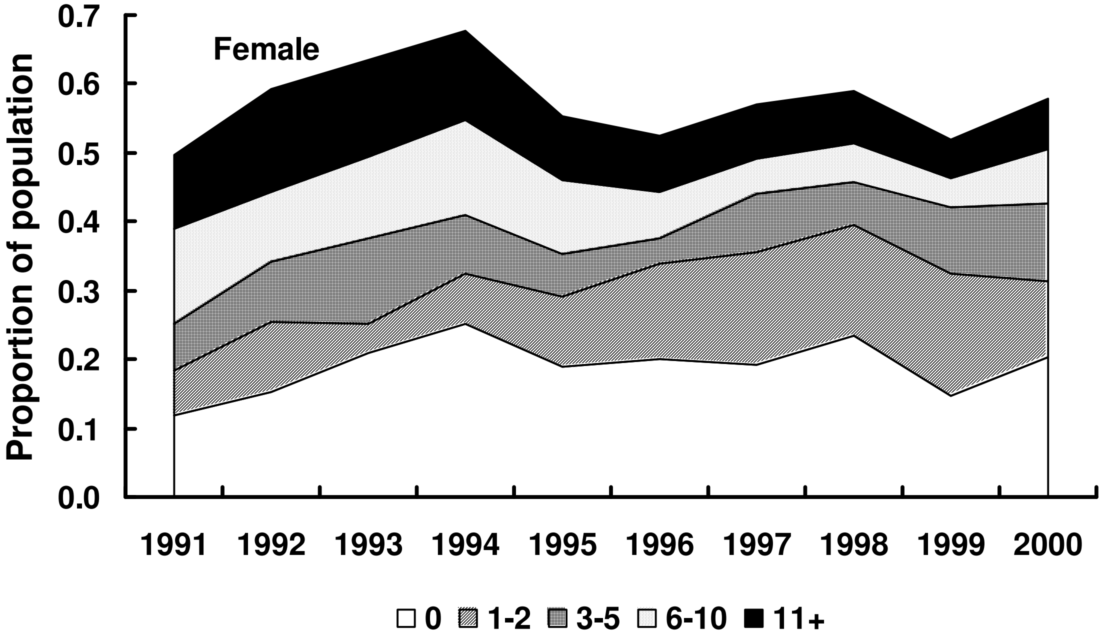


Figure 17.7. Changes in the proportion (± 95% CI) of males in the adult (≥ 3 years old) red kangaroo population on Currawinya National Park over 1991-2000.



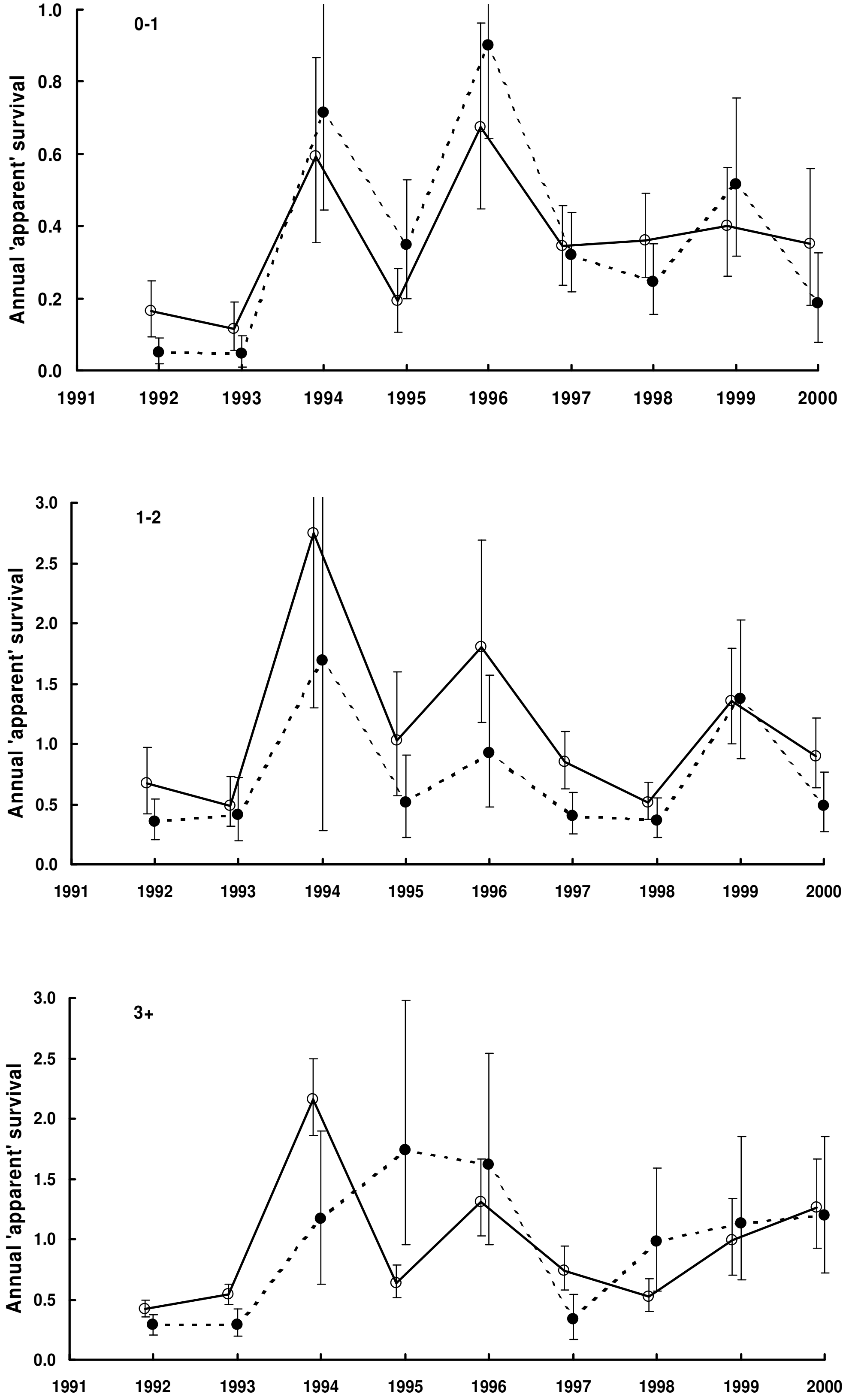
(*a*)



(*b*)

Figure 17.8. Proportion of the (a) male and (b) female red kangaroo population in five age groupings (0-1, 1-2, 3-5, 6-10, > 10 years old) at Currawinya National Park over 1991-2000.

Figure 17.9 (overpage). Annual 'apparent' survival (± 95% CI) of 0-1 (juvenile), 1-2 (sub-adult) and ≥ 3 year old (adult) male (dotted line, solid circle) and female (solid line, open circle) red kangaroos on Currawinya National Park over 1991-2000. The year on the *x*-axis refers to annual survival to that year.



(*a*)

(*b*)

(*c*)

Figure 17.9.

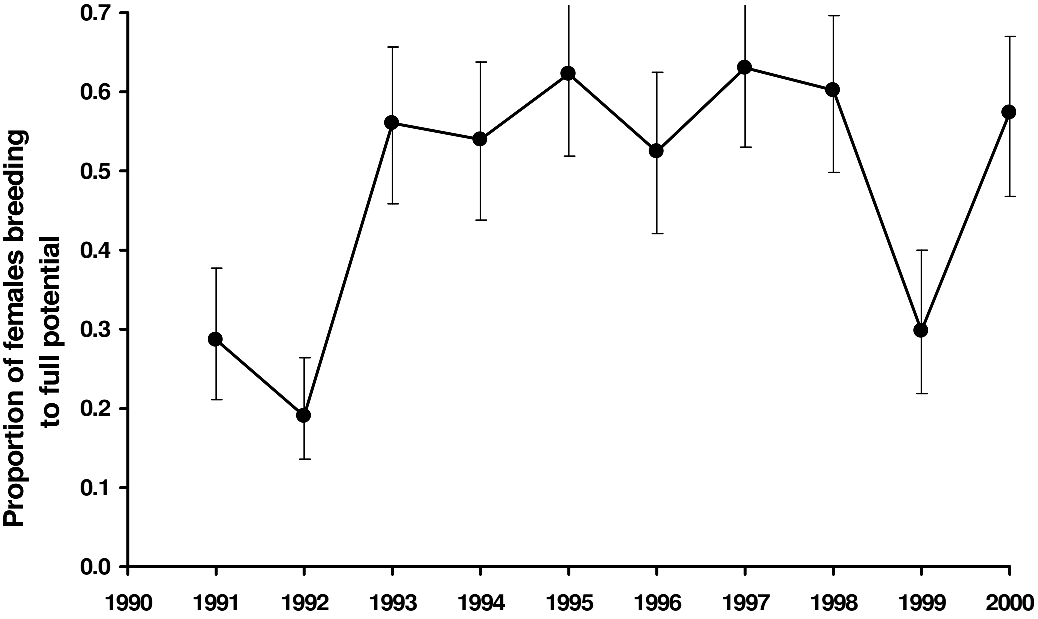


Figure 17.10. Proportion (± 95% CI) of mature (≥ 3 years old) red kangaroo females breeding to full potential at Currawinya National Park.

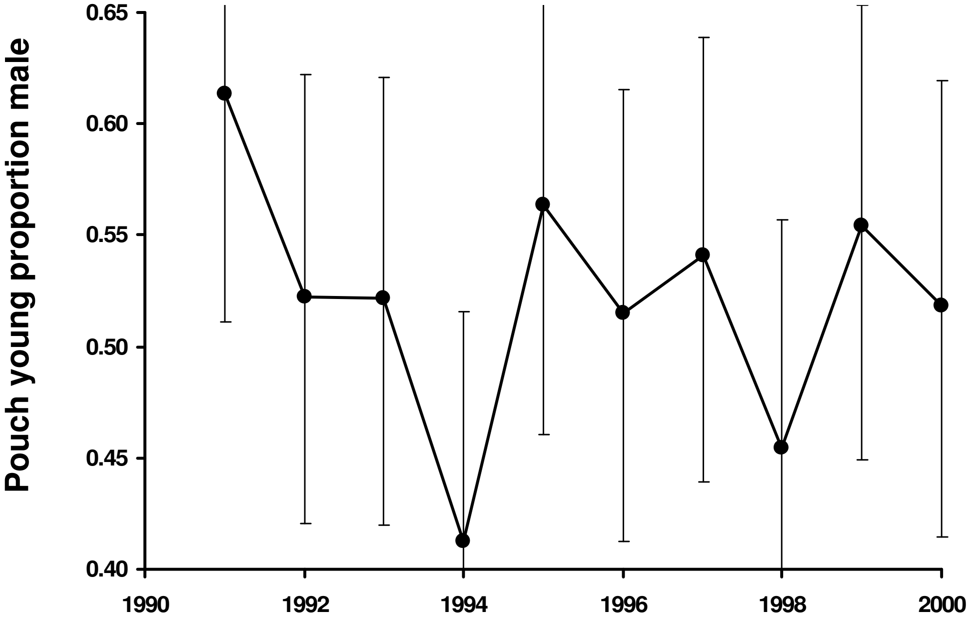


Figure 17.11. Sex ratio (proportion male ± 95% CI) of red kangaroo pouch young at Currawinya National Park.

17.4 Geographic variation in red kangaroo body size

The regional variation in growth patterns of male red kangaroos described in Section 13, Fig. 13.3, was drawn from data collected across eastern Australia (Fig. 17.12). There are also data for females which show a similar pattern. These data are consistent with Bergmann's rule which predicts that mammals will have a larger body size in colder climates. The rationale is that the lower surface area to volume ratio of larger mammals will allow them to radiate less body heat and therefore stay warmer in cold climates. Conversely, in warmer climates, the higher surface area to volume ratio will facilitate heat loss and cooling of the body. An exception to this rule was the unexpectedly large body size of kangaroos at the sites near Julia Creek in far northern Queensland.

Other morphometric measurements were taken in this study allowing an assessment of Allen's rule. This rule predicts that endotherms should have shorter limbs in colder climates, again as an aid to temperature regulation for similar reasons to Bergmann's rule.

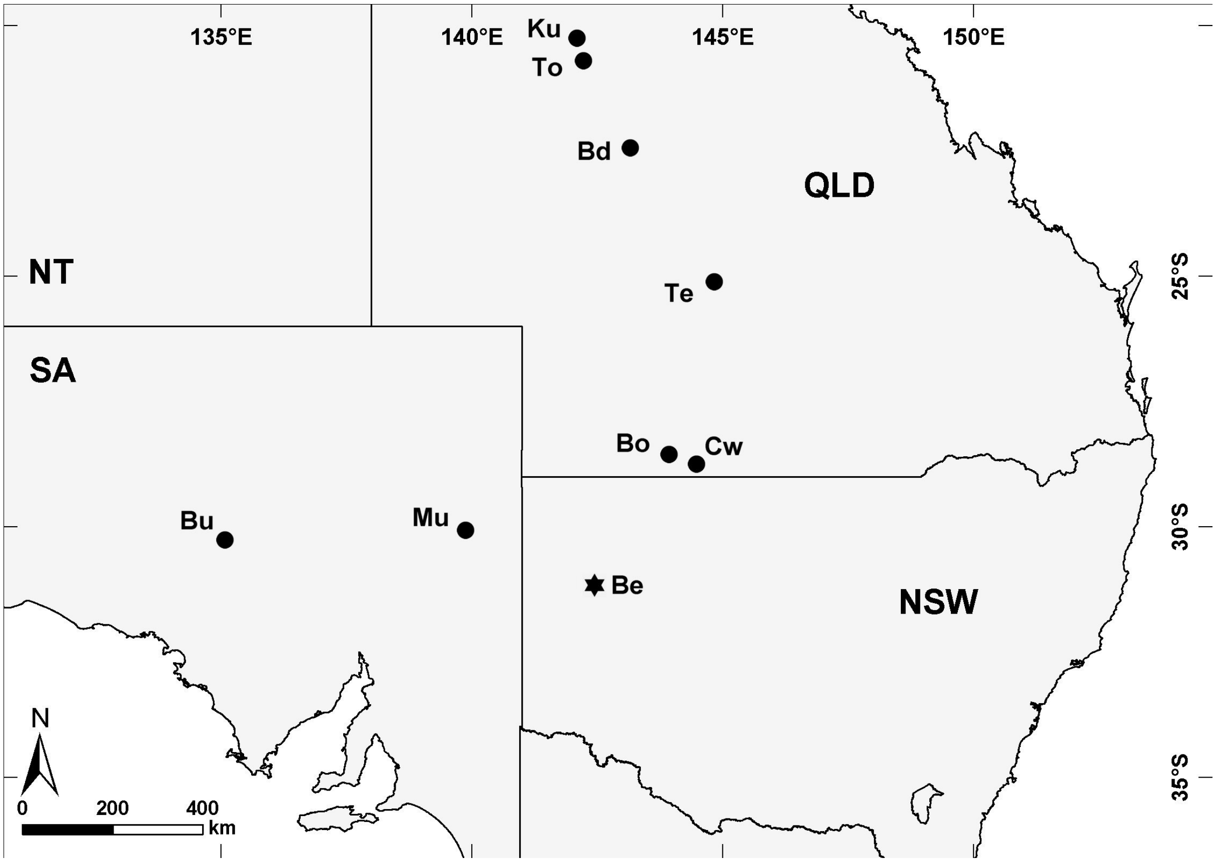
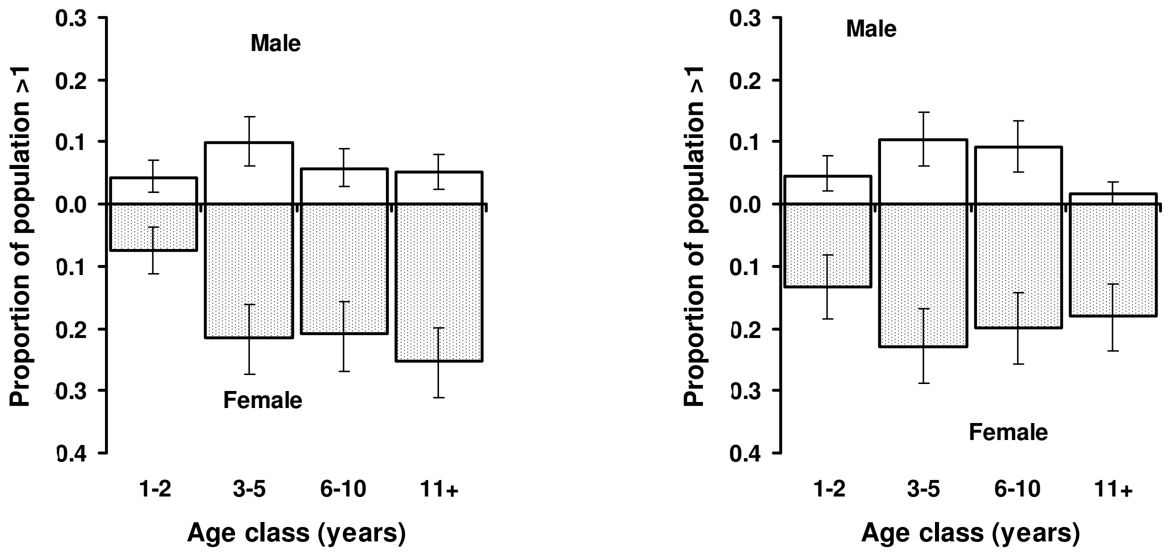


Figure 17.12. Location of study sites where random shot samples of red kangaroos were taken to determine population age structure. These data (circles) also formed the basis for assessing geographic variation in body size (Section 17.4; see Section 13, Fig. 13.3) and determinants of reproductive success and offspring sex ratio (circles and star) (Section 17.6). Ku, Kulwin; To, Toorak; Bd, Bladensburg; Te, Terrick Terrick; Bo, Boorara; Cw, Currawinya; Be, Boorungie; Mu, Mulyungarie; Bu, Bulgunnia.

17.5 Age structure and harvest selectivity

Random shot samples of red kangaroos (see Section 16 for a description of methods) were taken at sites throughout eastern Australia (Fig. 17.12) spanning a range of harvest rates. This allows an assessment of the effect of harvesting and past rainfall (as a proxy for food supply) on population age structure. Some of these data were reported in Section 13, Fig. 13.2. Age structures for these populations are shown in Figure 17.13. Ninety-five percent confidence intervals were calculated from 1,000 bootstrap samples. In far northern and southern Queensland, samples were taken from a harvested and a nearby unharvested site.

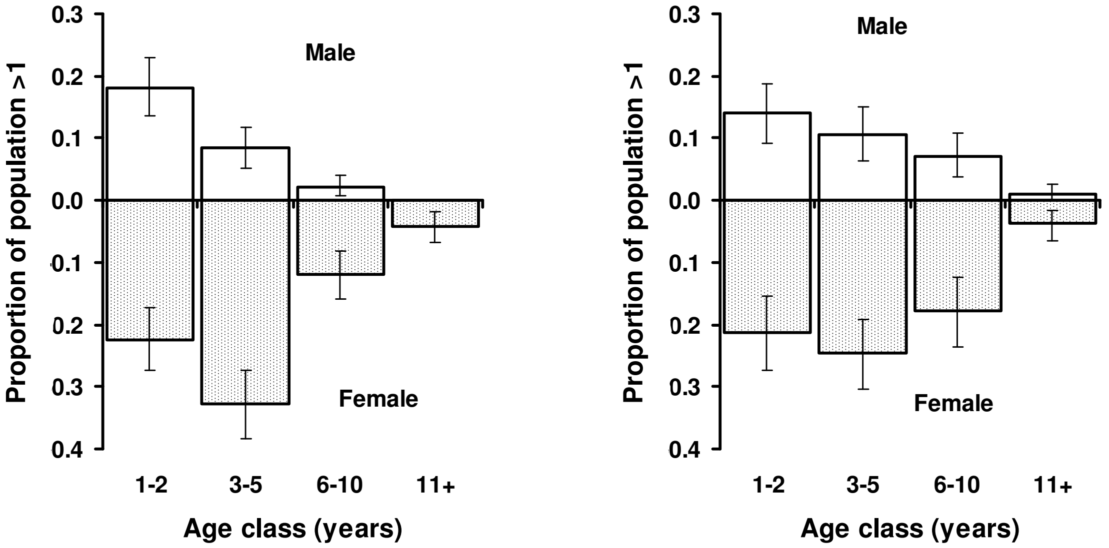
Kangaroos in the two unharvested populations are not surprisingly older on average and there is a higher proportion of females. The heavily harvested populations in central Queensland and eastern South Australia show marked contrasts with the other populations. The relative size of the sub-adult (1-2 years old) age class is partly a function of the adult sex ratio, but it is greatly influenced by past food supply. Good seasons result in high recruitment rates, contrasting with negligible recruitment in drought (Fig. 17.9*a*).



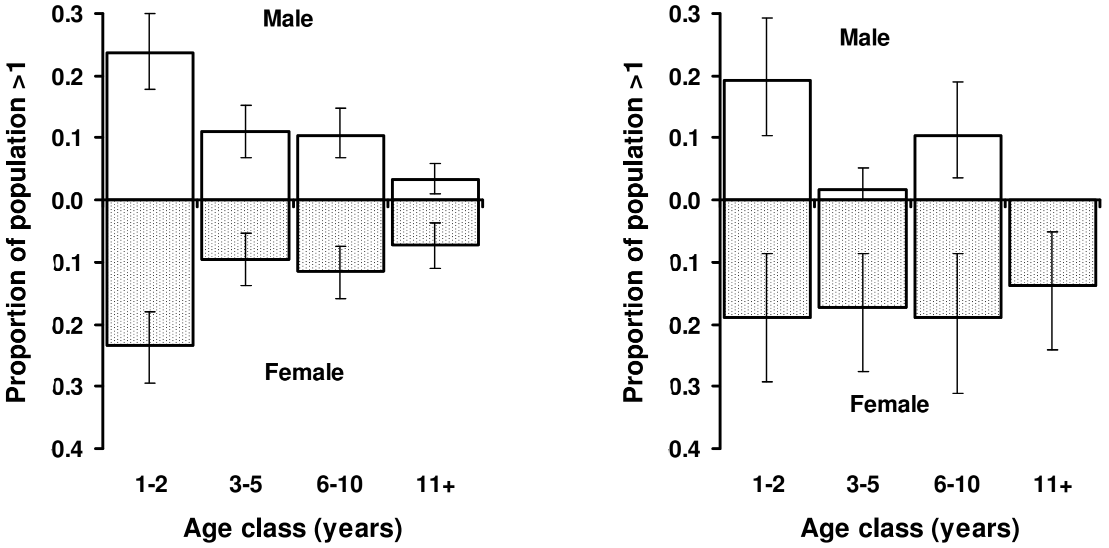
a. Currawinya (Southern Queensland) unharvested *b*. Boorara (Southern Queensland)

c. Bulgunnia (Western South Australia) *d*. Mulyungarie (Eastern South Australia)

Figure 17.13. Age structures of harvested and unharvested red kangaroo populations in eastern Australia (Figure 17.11) sampled over 1993-95. Bars (stippled, female; open, male) represent the proportions (± 95% CI) of the non-juvenile population in each age class.



e. Terrick Terrick (Central Queensland) *f*. Bladensburg (North Queensland)



g. Toorak (Far north Queensland) unharvested *h*. Kulwin (Far north Queensland)

Figure 17.13. (cont.)

17.6 Determinants of female reproductive success and offspring sex ratio

There are now considerable reproductive data in addition to data on age and body condition from shot samples throughout eastern Australia for red kangaroos (Fig. 17.12) and the two species of grey kangaroos. The data have been collected by Tony Pople, Stuart Cairns, Steve McLeod and colleagues. These data allow a number of questions to be addressed. Firstly, Croft (2004) argued that older females are important to the overall reproductive success of a kangaroo population. Older red kangaroo females appear to have a higher probability of rearing young through to weaning (Bilton and Croft 2004). In addition, their daughters can learn habitat and diet selection from their mothers by being allowed to remain in the natal home range. Thus, if maternal age has a strong influence on breeding success, then a reduction in the average age of females in a population through harvesting, as described in Section 17.5, could alter a population's dynamics more than expected from simply increasing the proportion of mature animals.

A second set of questions involves the determinants of offspring sex ratio. It has been suggested that pouch young sex ratio in kangaroos varies geographically and with environmental conditions (Johnson and Jarman 1983). The data in this study broaden the geographic extent of that assessment. Furthermore, sex of offspring may vary with maternal age, social rank, and body condition as suggested for red deer (*Cervus elaphus*) (Clutton-Brock *et al.* 1982) and both red-necked wallabies (*Macropus rufogriseus*) and eastern grey kangaroos (Stuart-Dick and Higgenbottom 1989). These patterns can be explored, and their supporting theory tested (see Section 17.3), for red kangaroos on a broad geographic scale rather than in a longitudinal study at a single site (e.g. Section 17.3). Combining the two approaches should allow much stronger generalisations to be made.

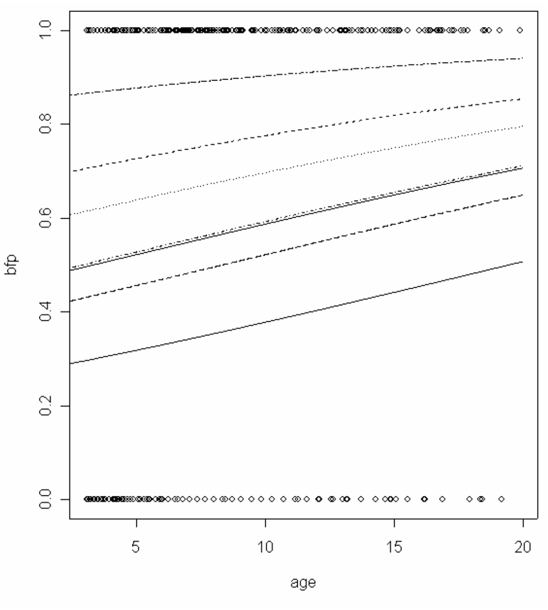
Breeding success in female red kangaroos has been measured elsewhere by the proportion of females with young-at-foot and by mean pouch young age (e.g. Newsome 1965, Shepherd 1987). These measures may be confounded by the fact that females with pouch young > 120 days old will have weaned their young-at-foot. Pouch young age and the proportion of females with young-at-foot therefore need to be considered together. One way of achieving this is to determine whether females are breeding to full potential (bfp). Females with pouch young < 120 days old and no young-at-foot are not breeding to full potential. Females with pouch young > 120 days old, or with pouch young and a young-at-foot, are breeding to full potential. The percentage of females breeding to full potential (%bfp) in a sample can then be used as a measure of breeding success. Only females ≥ 3 yo were considered in the statistic because younger females may have been rearing their first young.

Logistic regression was used to model the influence of maternal body condition and age, and the study site as a proxy for local environmental conditions, on %bfp. An index of maternal body condition was calculated from the residuals of the multiple regression of log(body weight) as a function of log(age), log(hind foot length) and a dummy variable representing the study site. This relationship accounted for the non-linear relationship between body weight and a one-dimensional quantity such as length and the known variation in growth patterns between geographically separated study sites (e.g. Section 13, Fig. 13.3).

The most parsimonious model predicting %bfp included all three terms: maternal age, body condition and study site. Their relative influences can be seen graphically by comparing how much each variable affects %bfp (Figure 17.14). Depending on the value of age and condition, study site is responsible for variation in %bfp of roughly 50-60%. Holding condition constant, maternal age changes %bfp by 10-20% (Figure 17.14*a*). Finally, holding age constant, condition changes %bfp by roughly 30-40% (Figure 17.14*b*). Environmental conditions are clearly the major determinant of reproductive success, although within a site there will be variation in body condition among individuals. Maternal age is a lesser influence.

These results could be incorporated into population models to examine the extent to which changes in age structure reduce rates of recruitment. The indications here are that it would be slight, as Bilton and Croft (2004) similarly suggested for the influence of maternal age on a female red kangaroo's lifetime reproductive success. Nevertheless, studies of the population dynamics of harvested populations suggest these populations are not experiencing long-term decline through depressed recruitment following the removal of older, more reproductively successful animals that are 'educators' of new recruits. A likely explanation is that female reproductive success and juvenile survival is enhanced in harvested populations with a reduction in density and subsequent greater availability of resources. Comparisons of breeding success and juvenile survival in harvested and unharvested population have provided supporting data for this explanation (Pople 1996).

Pouch young sex ratio (proportion male) ranged 0.46-0.55, with no obvious geographic pattern. Environmental and maternal correlates of this variation now need to be assessed.



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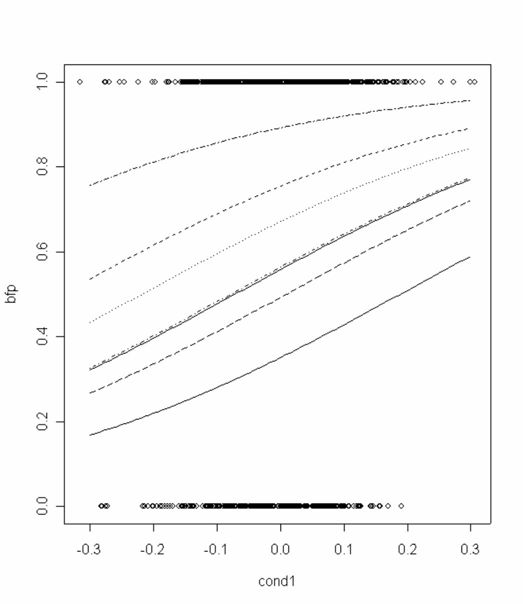

(*b*)

Figure 17.14. Fitted logistic regression model predicting reproductive success (bfp) in red kangaroos. Lines represent separate sites across eastern Australia (Fig. 17.11). The influence of maternal age is shown in (a) and the influence of body condition is shown in (b).

17.7. Acknowledgements

Norbert Menke is thanked for again providing the maps in this Section. Data in this section have been gratefully provided by a number of people including Stuart Cairns and Steve McLeod. Gordon Maag is also thanked for collecting many of the shot samples in Queensland.

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