POPULATION MONITORING FOR KANGAROO MANAGEMENT

A.R. POPLE

Pople AR, 2004. Population monitoring for kangaroo management. *Australian Mammalogy* **26**: 37-44.

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*.

A.R. Pople, The Ecology Centre, Department of Zoology and Entomology, University of Queensland, Qld 4072, Australia. Email: tpople@zen.uq.edu.au.

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).

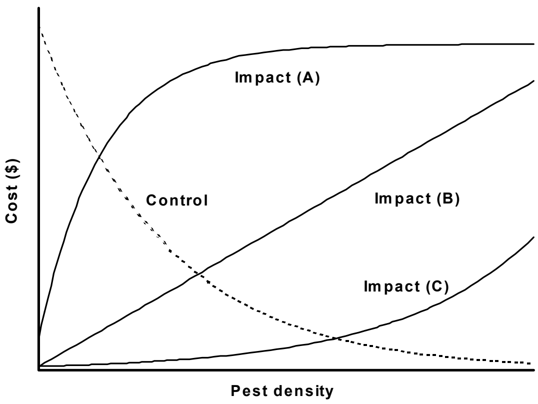

Fig. 1. Relationships between pest density and the *per capita* cost of control (dashed line) and the *per capita* cost of damage or impact (solid lines). A target density could be identified at the point of intersection. After Braysher (1993).

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-α 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.

ACKNOWLEDGEMENTS

Thanks to Mick McCarthy for suggesting ways of improving a draft of this manuscript. I would also like to thank Hugh Possingham for discussions on the use of decision theory and risk assessment.

REFERENCES

BAYLISS P, 1987. Kangaroo dynamics. Pp. 119-134 in *Kangaroos: their ecology and management in the sheep rangelands of Australia* ed by G. Caughley, N. Shepherd and J. Short. Cambridge University Press: Cambridge.

BORCHERS DL, ZUCCHINI W AND FEWSTER RM, 1998. Mark-recapture models for line transect surveys. *Biometrics* **54**: 1207-1220.

BRAYSHER M, 1993. *Managing vertebrate pests: principles and strategies.* Australian Government Publishing Service: Canberra.

CAIRNS SC AND GILROY J, 2001. *Re-appraisal and enhancement of the current methodology used in the estimation of kangaroo populations in western New South Wales*. Unpublished report to West 2000, Dubbo, NSW.

CAIRNS SC AND GRIGG GC, 1993. Population dynamics of red kangaroos (*Macropus rufus*) in relation to rainfall in the South Australian pastoral zone. *Journal of Applied Ecology* **30**: 444-458.

CAIRNS SC, GRIGG GC, BEARD LA, POPLE AR AND ALEXANDER P, 2000. Western grey kangaroos (*Macropus fuliginosus*) in the South Australian pastoral zone: the dynamics of populations at the edge of their range. *Wildlife Research* **27**: 309-318.

CAUGHLEY G, 1977. *Analysis of vertebrate populations*. Wiley and Sons: London.

CAUGHLEY GJ, 1979. Design for aerial censuses. Pp. 15-23 in *Aerial survey of fauna populations* ed by G.J. Caughley. Australian Government Publishing Service: Canberra.

CAUGHLEY G AND SINCLAIR ARE, 1994. *Wildlife ecology and management.* Blackwell Scientific Publications: London.

CLANCY TF, POPLE AR AND GIBSON LA, 1997. Comparison of helicopter line transects with walked line transects for estimating densities of kangaroos. *Wildlife Research* **24**: 397-409.

ENGEN S, LANDE R AND SAETHER B-E, 1997. Harvesting strategies for fluctuating populations based on uncertain population estimates. *Journal of Theoretical Biology* **186**: 201-212.

HILBORN R AND WALTERS CJ, 1992. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Chapman and Hall: New York.

HEDLEY SL, BUCKLAND ST AND BORCHERS DL, 1999. Spatial modelling from line transect data.

Journal of Cetacean Research and Management **1**: 255-264.

ISAAKS EH AND SRIVASTAVA RM, 1989. *Applied geostatistics*. Oxford University Press: New York.

LANCIA RA, NICHOLS JD AND POLLOCK KH, 1996. Estimating the number of animals in wildlife populations. Pp. 215-253 in *Research and management techniques for wildlife and habitats 5th edition* ed by T.A. Bookhout. The Wildlife Society: Bethesda, Md.

LANDE R, ENGEN S AND SAETHER B-E, 1995. Optimal harvesting of fluctuating populations with a risk of extinction. *The American Naturalist* **145**: 728-745.

MCCALLUM HI, 1999. How to count kangaroos. *Australian Zoologist* **31**: 309-316.

MCCALLUM H, 2000. *Population parameters*. Blackwell Science: London.

MCCARTHY MA, 1996. Red kangaroo (*Macropus rufus*) dynamics: effects of rainfall, density dependence, harvesting and environmental stochasticity. *Journal of Applied Ecology* **33**: 45-53.

MCLEOD S AND POPLE T, 1998. Optimal exploitation strategies for kangaroo populations in variable environments. Pp. 375-380 in *Proceedings of the 11th Australian veterbrate pest conference.* May 1998, Bunbury Western Australia.

MILNER-GULLAND EJ, SHEA K, POSSINGHAM H, COULSON T AND WILCOX C, 2001. Competing harvesting strategies in a simulated population under uncertainty. *Animal Conservation* **4**: 157-67.

NEWSOME AE, 1965. The distribution of red kangaroos, *Megaleia rufa* (Desmarest), about sources of persistent food and water in central Australia. *Australian Journal of Zoology* **13**: 289-299.

POPLE AR, 1996. Effects of harvesting upon the demography of red kangaroos in western Queensland. Ph.D. thesis, University of Queensland, Brisbane.

POPLE AR, 1999a. Repeatability of aerial surveys. *Australian Zoologist* **31**: 280-286.

POPLE AR (ED), 1999b. Aerial surveys for kangaroo management. *Australian Zoologist* **31**: 266-320.

POPLE AR AND GRIGG GC, 1998. *Commercial harvesting of kangaroos in Australia*. Environment Australia: Canberra. (http://www.ea.gov.au/biodiversitytrade-use/wild-harvest/kangaroo/harvesting/index.html).

POPLE AR, CAIRNS SC, CLANCY TF, GRIGG GC, BEARD LA AND SOUTHWELL CJ, 1998. Comparison of surveys of kangaroos in Queensland using helicopters and fixed-wing aircraft. *The Rangeland Journal* **20**: 92-103.

POPLE AR AND MCLEOD SR, 2000. Kangaroo management and the sustainable use of rangelands. Pp. 78-86 in *Management for sustainable ecosystems* ed P.T. Hale, A. Petrie, D. Moloney and P. Sattler. Centre for Conservation Biology, University of Queensland: Brisbane.

POSSINGHAM HP, 2001. *The business of biodiversity*. Australian Conservation Foundation: Melbourne.

PRINCE RIT, 1984. *Exploitation of kangaroos and wallabies in Western Australia. I. Exploitation and management of the red kangaroo: 1970-1979.* Department of Fisheries and Wildlife: Perth.

SEBER GAF, 1982. *The estimation of animal abundance and related parameters*. Griffen: London.

SHEA K, AMARASEKARE P, KAREIVA P, MANGEL M, MOORE J, MURDOCH WW, NOONBURG E, PARMA AM, PASCUAL MA, POSSINGHAM HP, WILCOX C AND YU D, 1998. Management of populations in conservation, harvesting and control. *Trends in Ecology and Evolution* **13**: 371-375.

SHEPHERD N AND CAUGHLEY G, 1987. Options for management of kangaroos. Pp. 188-219 in *Kangaroos: their ecology and management in the sheep rangelands of Australia* ed by G. Caughley, N. Shepherd and J. Short. Cambridge University Press: Cambridge.

SOUTHWELL C, 1989. Techniques for monitoring the abundance of kangaroo and wallaby populations. Pp. 659-693 in *Kangaroos, wallabies and rat-kangaroos* ed by G. Grigg, P. Jarman and I. Hume. Surrey Beatty and Sons: Sydney.

THOMAS L, BUCKLAND ST, BURNHAM KP, ANDERSON DA, LAAKE JL, BORCHERS DL AND STRINBERG S, 2002. Distance sampling. Pp. 544-552 in *Encyclopedia of environmetrics* ed by A.H. El-Shaarawi and W.W. Piegorsch. John Wiley and Sons: Chichester, UK.