How much do kangaroos of differing age and size eat relative to domestic stock?: implications for the arid rangelands

Terence J. Dawson and Adam J. Munn

School of Biological, Earth & Environmental Sciences.

University of New South Wales, Sydney, New South Wales 2052

Correspondence to: Professor T. J. Dawson, 10 Headland Ave, Austinmer 2515 NSW.

Email: t.dawson@unsw.edu.au

ABSTRACT

Over more than a century there has been debate about the interactions of kangaroos and introduced domestic stock, especially sheep, in the semi-arid and arid rangelands. The potential for competition between the species is still controversial, with pastoralists generally assuming that exploitative competition is a continuing feature of the rangelands, with competition by kangaroos leading to reduced stock production and carrying capacity. The current scientific consensus is that in the arid rangelands such competition is not common and occurs largely during dry periods when pasture is sparse. Competition is probably most persistent in more degraded environments.

There is still debate on the level of impact of kangaroos on sheep productivity in those situations where competition does occur. Departments of Agriculture consider that a kangaroo has the competitive impact equivalent to 0.7 sheep (in dry sheep equivalents or DSE); however, this value is not supported by most current data. A value for the competitive impact of kangaroos per kg body weight of approximately 0.6 DSE translates into 0.4 DSE when body size is taken into account, kangaroos being much smaller on average than sheep, particularly in harvested populations. There are still questions to be resolved about the appropriate DSE value in harvested populations because age reduction produces a population that is actively growing and which may have high metabolic costs (teenagers). Despite this complication we suggest that a DSE of 0.4 per individual kangaroo is still an appropriate assumption. Real competitive impacts of kangaroos on stock will depend on season and rangeland condition. If rangeland health is satisfactory competition will occur only in dry times.

Key words: kangaroos, sheep, competition, feed requirements, rangelends

Introduction

When, in the guise of a kangaroo biologist, one travels through the arid and semi-arid rangelands (particularly the sheep rangelands) of Australia, one gathers many opinions and words of advice and some are fascinating, if not to say hair-raising. The status of kangaroos in grazing country has been a fraught topic for more than a century (Lunney 1994). In the words of Gordon Grigg, the topic of 'what to do about kangaroos' is still perception-driven rather than information-driven (Grigg 2002). For an excellent insight into the current state of play in the kangaroo debate we refer readers to the paper that Gordon Grigg presented to one of the recent symposia of the Royal Zoological Society of NSW; it provides an insightful discussion of historical attitudes and current thinking by various "stakeholders" and additionally provides an excellent reference source on the subject.

Kangaroos in the context of this paper are the large species of the family Macropodidae and include the eastern and western grey kangaroos (*Macropus giganteus* and *M. fuliginosus*), the red kangaroo (*M. rufus*) and the euro (*M. robustus*). These species have broad distributions across the rangelands; in some areas of the eastern Australian sheep rangelands they all may occur, though there is some niche separation (Caughley 1987a; Dawson 1995; McCullough and McCullough 2000). Other macropodoids such as the smaller wallabies and rat kangaroos are not a "problem" in arid lands because most are largely extinct, in the main due to pastoralism – though foxes and cats may have been the end cause (Newsome 1971; Fisher *et al.* 2003).

It is now accepted that the arid and semi-arid rangelands have been badly degraded by pastoralism. Put very simply, the introduction of sheep and cattle to this environment has greatly reduced its productivity. This is well described by Caughley (1987a) and illustrated by the pattern of sheep numbers in western New South Wales in the years following settlement. However, a question often still posed today is: what is the place of kangaroos in the scheme of things, given the declining productivity and the declining financial returns from broad-fibre wool pastoralism? Can kangaroos be exploited to improve financial returns to the rangeland economy or are they just "pests" to be removed so that the pastoral industry can be propped up a little longer (Grigg 2002)? We provide information on the latter aspect and focus on two related questions that are often posed by graziers. How much do kangaroos eat and how

Pp 96 - 101 in the *Animals of Arid Australia: out on their own?* 2007, Edited by Chris Dickman, Daniel Lunney and Shelley Burgin. Royal Zoological Society of New South Wales, Mosman, NSW, Australia.

many extra sheep could be carried if we got the shooter in and harvested some kangaroos? Grigg (2002) suggested that a lot of kangaroos would have to be harvested to improve sheep productivity because kangaroos may take little vegetation relative to sheep, but this needs to be supported by more data.

What do kangaroos eat?

In the rangelands, domestic stock and the various species of kangaroos focus their feed intakes on green grasses and palatable ephemeral dicotyledonous plants (forbs), though diets can move towards dry grasses, bushes and tree browse when rangeland conditions dry out and turn to drought (Barker 1987 (also for early references); Dawson 1989; Wilson 1991b; Dawson and Ellis 1994, 1996; Edwards *et al.* 1995; Dawson *et al.* 2004). The reason for the preference for green grasses and forbs by many herbivores is simple. Such plants are more fully and rapidly digested compared with other forages (Dawson 1989) (Table 1). Thus, from these plants energy can be assimilated quickly and additionally, nitrogen and other nutrient levels are high (Freudenberger *et al.* 1999). The bottom line is that less dry matter has to be harvested to meet maintenance needs and, additionally, harvest rates can be high enough to provide extra nutrients for growth, reproduction and other forms of production.

The importance of the green leaf of grasses and forbs to the well-being, growth and productivity of kangaroos, sheep and cattle is now well appreciated (see Ash *et al.* 1995; Freudenberger *et al.* 1999; Moss and Croft 1999). In the arid rangelands palatable perennial grasses are especially important in this regard because they persist during dry periods and respond with new growth after occasional small rains. Overgrazing removes these valuable species from the pasture and markedly reduces overall productivity (Freudenberger *et al.* 1999).

Does competition occur between kangaroos and stock?

Because kangaroo species and domestic stock overlap in diets it is often assumed that the two groups are always in dietary competition. This seems straight forward, but is it? Does competition actually occur? Competition in the rangelands can take two forms, interference competition and exploitive competition. In the former case a species physically interferes with another species' access to resources, while with exploitative competition harm, ultimately in the form of decreased reproductive fitness, comes to a species through the deprivation of a shared resource due to a competitor (Schoener 1983). Interference competition between native and introduced species appears not to be significant. Kangaroos can favour paddocks destocked of sheep (Edwards *et al.* 1996) but evidence that this is the result of interference competition is lacking. Where overlap in diet selection occurs (Dawson and Ellis 1994, 1996) we consider the possibility of exploitative competition. In the scenario of the artificial pastoral situation, exploitative competition due to kangaroos is thought to result in reduced livestock production that might take the form of:

a) a lowered carrying capacity of livestock,

b) a lowered production per head of stock, including lowered reproduction, or

c) a loss of drought reserves for livestock. In this situation, the idea has arisen that it is not possible to spell a block of country (i.e. destock to allow pasture recovery and a drought reserve) because the kangaroos will just move in and get the feed first.

Exploitative competition may be intermittent, i.e. seasonal, or related to cycles of drought. It can also be asymmetric, i.e. affect one species more than the others. Caughley (1987b) suggested that the effect of sheep on kangaroos in drought should be greater than the effect of kangaroos on sheep. Does an overlap in diet automatically result in competition? Although competition is notoriously hard to demonstrate in unmanipulated field studies (Edwards *et al.* 1996) it appears that "no" is the answer, even if herbivore species prefer to eat similar things. When there are ample feed resources competition is not seen. Several of our studies in the chenopod shrub rangelands at Fowlers Gap Research Station north of Broken Hill indicate that this is the usual situation. Much overlap in diet selection often occurs (Dawson and Ellis 1994; 1996; Edwards *et al.* 1995), but Edwards *et al.* (1996) and McLeod (1996) found competition only in very dry times when plant biomass was much reduced. McLeod (1997) basically showed that the large herbivores such as kangaroos cannot adjust their numbers fast enough to take advantage of good seasons and so must maintain numbers well below the effective carrying capacity for

Table 1. Rates of fermentative digestion of dry matter in principal forage types (a).

Forage type	Maximum dry matter digestion (%)	Digestion of dry matter after 4 hours (%)
Forbs, young (b)	89	87
Forbs, mature	49	39
Grass, young	94	75
Grass, mature dry	57	15
Shrubs, new leaves	89	87
Shrubs, woody twigs	33	24

(a) These results were obtained from samples suspended in nylon bags inside a goat rumen. Rates of digestion are similar in kangaroos (Hume 1999).

(b) Forbs are small herbaceous plants.

most of the time. In contrast to this situation, Wilson (1991a) suggested that in the semi-arid acacia woodlands competition was more pervasive. However, in the study of Wilson (1991a), sheep and kangaroos were confined in pens and generally stocking rates were higher than the usual stocking levels in the district (McLeod 1996). The overall results of these studies indicate that competition occurs principally in droughts and then only in some circumstances.

In some situations competition is little evident even in moderate drought. This occurs if the stock and kangaroos eat different things. In the chenopod shrub rangelands sheep switch from grasses to saltbush as conditions become dry, while red kangaroos stay with grass and there is little overlap in diet (Dawson and Ellis 1994; Edwards *et al.* 1995). A similar situation occurs with goats and euros in the hilly country (Dawson and Ellis 1996). Goats mostly eat trees and shrubs whilst euros are grass specialists and very little competition occurs in dry times. However, if country has been severely degraded, with perennial grasses, shrubs and palatable browse eaten out, the situation is different. Overall productivity can be reduced but, significantly, livestock production may become dependent on annual forbs and grasses and these are what all herbivores will be focusing on. Additionally, such vegetation does not persist well into dry periods. The net effect in such degraded country is the likelihood of more severe competition, which persists for longer.

Possible levels of competition between stock and kangaroos

If direct competition occurred, what impact would it have? What effect could it have on production, or to turn the focus around, how much extra production would you expect if you removed kangaroos? In other words how much does a kangaroo eat relative to a sheep? Over the years we have heard many answers from graziers. Generally, the answer has been 'about the same', though we have been also told with a straight face that kangaroos eat twice as much as a sheep. Wilson (1991a) reported that, where it occurred, competition by a kangaroo had the effect on a sheep's wool growth or live weight gain of approximately 0.6 of a sheep (non breeding) of equivalent weight; a dry sheep equivalent (DSE) is used as a comparative measure of grazing pressures. The value long accepted by Departments of Agriculture is that the competitive grazing pressure of a kangaroo is 0.7 of a DSE (Hacker and McLeod 2003). This figure was derived from the fact that the resting or basal metabolic rate (BMR) of marsupials in the laboratory is about 70% of that of eutherian mammals (Dawson and Hulbert 1970). However, field circumstances are somewhat different from the conditions in which BMR is measured. Short (1985, 1986) deduced maximum feed intakes for sheep and red kangaroos from short term grazing trials in western New South Wales and concluded that they were not different when expressed in relation to metabolic body mass, $M^{0.75}$. So what is the real situation?

Equations have been developed that tell how much marsupial herbivores eat relative to eutherian herbivores in field situations. Equations also exist that give the values for field feed intakes of arid zone marsupials (of any feeding guild) versus those of mesic-zone marsupials. These equations are largely those derived by Nagy and co-workers using the doubly-labelled water technique, which measures field metabolic rate (FMR). The most recent appropriate references are Nagy *et al.* (1999) and Nagy and Bradshaw (2000). The predictions for daily energy turnover for free-living animals from these equations are given in Table 2. Feed requirements in g dry matter (DM) eaten per day (Table 2) also can be calculated from these data. This was done by assuming an appropriate digestible energy content of the feed of a particular feeding guild; for herbivores with a foregut fermenting digestive system 11.5 kJ/g dry matter was used (Nagy *et al.* 1999).

The FMRs and feed intakes in Table 2 are those predicted for an average sheep, and for female eastern grey kangaroos (mesic) and red kangaroos (arid). They suggest that kangaroos take little from arid zone pastures relative to sheep. Grigg (2002) used these equations to suggest low feed intakes for kangaroos compared with sheep. However, if the 95% confidence intervals are considered, these predictions are really loose and of limited value in regard to kangaroos. The reason is partially that insufficient data are available on larger animals. No doubly-labelled water measurements have been made for *M. rufus*. The only measured FMRs for kangaroos are for 2 male *M. giganteus* (one a juvenile) obtained in a small enclosure at Monash University, Melbourne. The mean FMR was 8170

Table 2. Predicted field metabolic rates and feed requirements of sheep and kangaroos from mesic and arid environments from the equations of Nagy et al. (1999) and Nagy and Bradshaw (2000). Note the large 95% confidence intervals.

	Units	Pred. Mean	95% CI
Field Metabolic Rate			
Sheep (40kg)	kJ day^{-1}	15030	5500 - 41120
Kangaroo (25kg) - (mesic)	kJ day^{-1}	3970	2400 - 6560
Kangaroo (25kg) - (arid)	kJ day^{-1}	2250	1010 - 4980
Feed Requirements			
Sheep (40kg)	g DM* day^{-1}	1310	480 - 3580
Kangaroo (25kg) - (mesic)	g DM day^{-1}	350	210 - 570
Kangaroo (25kg) - (arid)	g DM day^{-1}	200	90 - 430

*DM = dry matter.

kJ/d (range 5610 – 10730 kJ/d), which translated into an estimated feed intake of 710 g of DM/d for an 'average' male of 44 kg (Nagy *et al.* 1990).

Additional equations are available to calculate field energy needs. Using an expanded data set, Cooper *et al.* (2003) suggested that BMR was a more accurate indicator of FMR for marsupials than was mass because of a tight correlation between BMR and FMR. Of note, Cooper *et al.* (2003) confirmed for marsupials that FMR is not a simple ratio of BMR; in the past a factor of 2 times BMR has been used to estimate feed requirements in the field. From the equations of Cooper *et al.* (2003), a 25-kg kangaroo was predicted to have an FMR 1.85 times BMR, which would represent an intake of 382 g DM/d; however, confidence intervals for their predictions were not provided.

Field energy use by kangaroos has also been obtained using heart rate telemetry, where heart rate is calibrated against metabolic rate; the technique is well validated (Fanning and Dawson 1989). Such studies have given values of 1.5 – 2.3 BMR for female red kangaroos in cool conditions (Fanning and Dawson 1989) and 1.5 -1.6 BMR for red and eastern grey kangaroos during a hot summer (McCarron *et al.* 2001). Estimates of feed intake from such measurements only represent snapshots of the feed needs of the kangaroos since FMR may vary significantly, due to factors such as climate and differing levels of activity. Additionally, use of a single presumed level of the digestible energy content of feed (i.e. 11.5 kJ /g DM) is an oversimplification.

Actual patterns and levels of feed intake for red kangaroos and sheep have been assessed by Steve McLeod (McLeod 1996). From detailed observations he determined the plants, and which parts of those plants, were eaten. By matching what was taken from plants in each bite by animals with similar-sized 'bites' he was able to build up a more precise picture of foraging by red kangaroos and sheep during different seasons. Knowledge was gained on which parts of plants were eaten; for these 'bites' water content and digestibility were determined. This information, together with the rates at which the different plants were harvested, enabled digestible dry matter intake to be estimated for various seasonal diets. Probable maximal feed intakes over different seasons by red kangaroos and sheep in the wild were: for kangaroo females (25 kg), 430 g DM/d; kangaroo males (60 kg), 910 g DM/d; sheep (female 40kg), 940 g DM/d (S. McLeod pers. com.). Thus, when these data are examined on a per kg basis, an adult kangaroo is 0.6 – 0.7 of a sheep, similar to the competitive effect equivalence of Wilson (1991a). However, given that females and juveniles (the smaller sized animals) make up the bulk of kangaroo populations it would be reasonable to suggest from overall data that an 'average' kangaroo in the rangeland would have a competitive impact of something less than 0.6, probably about 0.4 DSE, that is, if competition occurred.

The influence of size and age on kangaroo feed requirements

There is, however, an issue that has been generally overlooked. What happens to feed intake if you change the age structure of kangaroo populations, as occurs with heavy harvesting (Figure 1) (Dawson 1995)? With the change in age structure comes a decrease in average size. Grigg (2002) indicated a range of 16 – 19 kg for the average weights of kangaroos in such populations. What impact does this have on foraging competition? It is important to note that the feed requirements of kangaroos do not vary directly with mass. The intake of adults varies in proportion to metabolic body mass (i.e. $M^{0.75}$); however, the situation with juveniles is complicated by the cost of growth (Munn and Dawson 2003). Kangaroos, like other marsupials, continue to grow for longer than eutherians; this is particularly so for males because of the sexual dimorphism of kangaroos. The costs of growth have often been overlooked when considering feed requirements. Much of the variability seen throughout comparative studies between kangaroos and ruminants (see Hume 1999, p 13) apparently occurs because some young and juvenile kangaroos have been included in the studies.

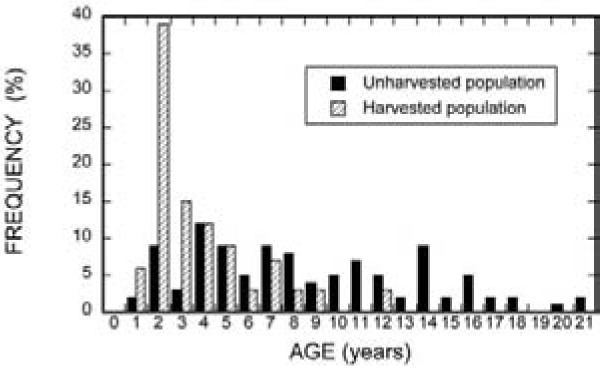

Figure 1. Differences in the age structures of populations of wallaroos (*M. robustus*) where they were unharvested (Fowlers Gap Station, NSW) as against where significant harvesting occurred (Coolatai, NSW) (Dawson 1995).

We have addressed this matter by re-examining the relative dry matter intakes and energy use of adult and juvenile red kangaroos (Munn and Dawson 2003). We used tame animals, with six animals of similar mass and age in each group. The adults were mature, non-lactating females and the juveniles were young at foot and just-weaned juveniles. The measurements were made in metabolism cages in temperature controlled (25°C) rooms. Thus they might be expected to be lower than field values, since thermal and activity inputs are not equivalent; however, the maintenance digestible energy requirements (MER) of our adults was 1.9 BMR. This is similar to FMR values and consequently such studies may be used as a guide to field requirements; they also show much less variability.

Relative energy and feed requirements of red kangaroos of differing ages and sexes and ruminants on a good quality diet of chopped lucerne hay are shown in Table 3. The maintenance energy requirements (MER) of non-lactating females and mature males are similar at near 385 kJ/kg$^{0.75}$, which is approximately 55% of MER values for sheep. The values for adult kangaroos relative to feral goats were, interestingly, 70% i.e. the same as the difference in BMR. The basic point is that if intakes are adjusted to usually

Table 3. Comparison of maintenance energy requirements and voluntary dry matter intakes of red kangaroos of differing ages and sexes and ruminants on a diet of chopped lucerne hay

	Energy requirement	Dry matter intake
	kJ $kg^{-0.75}$ day^{-1}	g DM day^{-1}
Red kangaroos		
Adult Female (26 kg)[a]	385 ± 37	414 ± 38
Adult male (62 kg)[b]	387 ± 5	834 ± 7
Juvenile (11 kg)[a]	677 ± 26	370 ± 14
Young at foot (6 kg)[a]	641 ± 27	233 ± 23
Young male (30 kg)[c]	527	685
Ruminants		
Sheep (51 kg)[b]	680 ± 8	1233 ± 10
Goat (32 kg)[d]	531 ± 78	660 ± 120

References: [a]Munn and Dawson (2003); [b]McIntosh (1966), for 3 large animals; [c]Hume (1974), no error terms; [d] Freudenberger et al. (1993).

accepted masses, then a female kangaroo of 25 kg would represent a DSE of 0.4 in comparison with a 40 kg dry sheep, if diets and digestibilities were similar. Even large adult male kangaroos do not reach the dry matter intakes of most adult sheep.

The situation with growing animals complicates things. Growth is expensive in terms of energy and nutrients (as those of us who have had teenage children, notably males, know). Energy needs, as seen from Table 3, are markedly higher in terms of metabolic body size (kg $^{0.75}$) and these translate into the measured daily dry matter intakes in Table 3. Recently weaned juveniles (11 kg) at about 12 months had dry matter intakes that were not statistically different from those of the adult females, with a young at foot (6 kg) needing about 60% of adult female requirements, if it is reliant on forage alone (Munn and Dawson 2003). A young male of the same size as the adult female would require in excess of 50% more feed than the adult to maintain growth.

What is the net effect of these differences in metabolic rates and feed requirements on potential competition with sheep and goats? A point to be made initially is that, during drought, young animals (that is animals with high metabolic rates) are likely to be rare or absent from the population (Shepherd 1987) and breeding would have ceased (Newsome 1966). Consequently, this situation involves adults only (probably of a lower size if harvesting is significant). A DSE of approximately 0.4 per kangaroo therefore would be a good estimate of the potential competitive impact.

Conclusion

This review suggests that competitive impacts of kangaroos on stock in good vegetation conditions are normally not an issue in the arid rangelands; there is adequate feed for all in undegraded land not in drought (Edwards *et al.* 1996; McLeod 1996). When pasture conditions are 'poor' we have complex situations. The level of degradation of the vegetation will be important in determining potential competitive dietary overlap (Barker 1987; Dawson and Ellis 1994). Also in these conditions there is the complexity associated with the survivability of juveniles and their contribution to kangaroo populations in the rangelands. Bilton and Croft (2004) give considerable insight into the vagaries of the survival of young in this environment. We have estimated the average DSEs of some kangaroo populations that may pertain in 'poor' seasonal conditions. Values of around 0.4 DSE seem to apply, but further research is needed to give more certainty to our assumptions.

References

Ash, A. J., McIvor, J. G., Corfield, J. P. and Winter, W. H. 1995. How land conditions alter plant-animal relationships in Australian's tropical rangelands. *Agricultural Ecosystems and Environments*. **56**:77-92.

Barker, R. D. 1987. The diet of herbivores in the sheep rangelands In "Kangaroos: their ecology and management in the sheep rangelands of Australia" (Eds G. Caughley, N. Shepherd and J. Short). Pp. 69-83. Cambridge University Press, Cambridge.

Bilton, A. D. and Croft, D. B. 2004. Lifetime reproductive success in a population of female red kangaroos *Macropus rufus* in the sheep rangelands of western New South Wales: Environmental effects and population dynamics. *Australian Mammalogy* **26**:45-60.

Caughley, G. 1987a. Introduction to the sheep rangelands. In "Kangaroos: their ecology and management in the sheep rangelands of Australia". (Eds G. Caughley, N. Shepherd and J. Short). Pp. 1-13. Cambridge University Press, Cambridge.

Caughley, G. 1987b. Ecological relationships. In "Kangaroos: their ecology and management in the sheep rangelands of Australia". (Eds G. Caughley, N. Shepherd and J. Short). Pp. 159-187. Cambridge University Press, Cambridge.

Cooper, C. E., Withers, P. C. and Bradshaw, S. D. 2003. Field metabolic rate and water turnover of the numbat (*Myrmecobius fasciatus*). *Journal of Comparative Physiology B* **173**:687-693.

Dawson, T. J. 1989. Diets of macropodoid marsupials: General patterns and environmental influences. In "Kangaroos, Wallabies and Rat Kangaroos" (Eds G. Grigg, P. Jarman and I. Hume). Pp. 129-142. Surrey Beatty and Sons, Chipping Norton, Australia.

Dawson, T. J. 1995. "Kangaroos: Biology of the largest marsupials". University of New South Wales Press, Sydney.

Dawson, T. J. and Ellis, B. A. 1994. Diets of mammalian herbivores in Australian arid shrublands: seasonal effects on overlap between red kangaroos, sheep and rabbits on dietary niche breadths and electivities. *Journal of Arid Environments* **26**:257-271.

Dawson, T. J. and Ellis, B. A. 1996. Diets of mammalian herbivores in Australian arid hilly shrublands: seasonal effects on overlap between euros (hill kangaroos), sheep and feral goats, and on dietary niche breadths and electivities. *Journal of Arid Environments* **34**:491-506.

Dawson, T. J. and Hulbert, A. J. 1970. Standard metabolism, body temperature, and surface areas of Australian marsupials. *American Journal of Physiology* **218**:1233-1238.

Dawson, T. J., McTavish, K. J. and Ellis, B. A. 2004. Diets and foraging behaviour of red and eastern grey kangaroos in arid shrub land: is feeding behaviour involved in the range expansion of the eastern grey kangaroo into the arid zone? *Australian Mammalogy* **26**:169-178.

Edwards, G. P., Croft, D. B. and Dawson, T. J. 1996. Competition between red kangaroos (*Macropus rufus*) and sheep (*Ovis aries*) in the arid rangelands of Australia. *Australian Journal of Ecology* **21:**165-172.

Edwards, G. P., Dawson, T. J. and Croft, D. B. 1995. The dietary overlap between red kangaroos (*Macropus rufus*) and sheep (*Ovis aries*) in the arid rangelands of Australia. *Australian Journal of Ecology* **20:**324-334.

Fanning, F. D., and Dawson, T. J. 1989. The use of heart rate telemetry in the measurement of energy expenditure in free-ranging red kangaroos. In "Kangaroos, Wallabies and Rat Kangaroos" (Eds G. Caughley, N. Shepherd and J. Short). Pp. 129-142. Surrey Beatty and Sons, Chipping Norton, Australia.

Fisher, D. O., Blomberg, S. P. and Owens, I. P. F. 2003. Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proceedings of the Royal Society, London* B **270**: 1801-1808.

Freudenberger, D. O. and Hume, I. D. 1993. Effects of water restriction on digestive function in two macropodid marsupials from divergent habitats and the feral goat. *Journal of Comparative Physiology* B **163**:247-257.

Freudenberger, D. O., Wilson, A. D. and Palmer, R. 1999. The importance of perennial grasses for sheep production in the semi-arid woodlands of eastern Australia. *The Rangeland Journal* **21**:199-219.

Grigg, G. 2002. Conservation benefit from harvesting kangaroos: status report at the start of a new millennium. A paper to stimulate discussion and research. In "A zoological revolution. Using native fauna to assist in its own survival." (Eds D. Lunney and C. Dickman) Pp. 53-76. Royal Zoological Society of New South Wales, Mosman 2088 and Australian Museum.

Hacker, R. and McLeod, S. 2003. "Living with kangaroos: A guide to kangaroos and their management in the Murray-Darling Basin". ISBN 07347 1505 6. New South Wales Agriculture, Sydney

Hume, I. D. 1974. Nitrogen and sulphur retention and fibre digestion by euros, red kangaroos and sheep. *Australian Journal of Zoology* **22**:13-23.

Hume, I. D. 1999. "Marsupial Nutrition". Cambridge University Press, Cambridge.

Lunney, D. 1994. Review of official attitudes to western New South Wales 1901 – 1993 with particular reference to the fauna. In "Future of the fauna of western New South Wales". (Eds. D. Lunney, S. Hand, P. Reed and D Butcher). Pp. 1-26. Royal Zoological Society of New South Wales, Mosman 2088.

McCullough, D. R. and McCullough, Y., 2000. "Kangaroos in outback Australia: comparative ecology and behavior of three coexisting species". Columbia University Press, New York.

McCarron, H. C. K., Buffenstein, R., Fanning, F. D. and Dawson, T. J. 2001. Free-ranging heart rate, body temperature and energy metabolism in eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Macropus rufus*) in the arid regions of south east Australia. *Journal of Comparative Physiology* B **171**: 401-411.

McIntosh, D. L. 1966. The digestibility of two roughages and the rates of passage of their residues by red kangaroos, *Megaleia rufa* (Desmerest) and the merino sheep. *CSIRO Wildlife Research* **11**:125-135.

McLeod, S. R. 1996. The foraging behaviour of the arid zone herbivores, the red kangaroo (*Macropus rufus*) and the sheep (*Ovis aries*) and its role in their competitive interactions, population dynamics and life-history strategies. PhD Thesis, University of New South Wales, Sydney.

McLeod, S. R. 1997. Is the concept of carrying capacity useful in variable environments? *Oikos*. **79**:529-542.

Moss, G. L. and Croft, D. B. 1999. Body condition of the red kangaroo (*Macropus rufus*) in arid Australia: The effect of environmental condition, sex and reproduction. *Australian Journal of Ecology* **24(2)**:97-109.

Munn, A. J. and Dawson, T. J. 2003. Energy requirements of the red kangaroo (*Macropus rufus*): impacts of age, growth and body size in a large desert-dwelling herbivore. *Journal of Comparative Physiology* B **173**:575-582.

Nagy, K. A. and Bradshaw, S. D. 2000. Scaling of energy and water fluxes in free-living arid-zone Australian marsupials. *Journal of Mammalogy* **81**:962-970.

Nagy, K. A., Girard, I. A. and Brown, T. K. 1999. Energetics of free-ranging mammals, reptiles and birds. *Annual Review of Nutrition* **19**:247-27.

Nagy, K. A., Sanson, G. A. and Jacobsen, N. K. 1990. Comparative field energetics of two macropod marsupials and a ruminant. *Australian Wildlife Research* **17**:591-599.

Newsome, A. E. 1966. The influence of food on breeding in the red kangaroo in Central Australia. *CSIRO Wildlife Research* **11:**187-196.

Newsome, A. E. 1971. Competition between wildlife and domestic livestock. *Australian Veterinary Journal* **47**:577-586.

Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240-285.

Shepherd, N. 1987. Condition and recruitment of kangaroos. In "Kangaroos: their ecology and management in the sheep rangelands of Australia". (Eds G. Caughley, N. Shepherd and J. Short). Pp. 135-158. Cambridge University Press, Cambridge.

Short, J. 1985. The functional response of kangaroos, sheep and rabbits in an arid grazing system. *Journal of Applied Ecology* **22**: 435-447.

Short, J. 1986. The effect of pasture availability on food intake, species selection and grazing behaviour of kangaroos. *Journal of Applied Ecology* **23**:559-571.

Wilson, A. D. 1991*a*. The influence of kangaroos and forage supply on sheep productivity in the semi-arid woodlands. *Rangeland Journal,* **13**:69-80.

Wilson, A. D. (1991*b*). Forage utilization by sheep and kangaroos in a semi-arid woodland. *Rangeland Journal* **13**:81-90.