

Macropods, feral goats, sheep and cattle. 2. Equivalency in what and where they eat

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Abstract. The extent to which sheep, cattle, feral goats, red kangaroos, western grey kangaroos, euros and eastern grey kangaroos are equivalent in their use of the Australian southern rangelands is partly dependent on the extent to which their diets and foraging areas overlap. These herbivores all eat large amounts of green annual grasses, ephemeral forbs and the green leaf of perennial grasses when they are available. Overlap in use of these forages by all seven herbivores is concurrent and high. As the abundance of these preferred forages declines, sheep, cattle and feral goats consume increasing amounts of mature perennial grasses and chenopod and non-chenopod perennial forbs. Red kangaroos and western grey kangaroos continue to graze mature perennial grasses longer than sheep, cattle and feral goats, and only switch to perennial forbs when the quantity and quality of perennial grasses are poor. Consequently, overlap in use of perennial forbs by sheep, cattle, feral goats, red kangaroos and western grey kangaroos is sequential and moderately high. When palatable perennial forbs are eaten out, the diets of all herbivores except feral goats comprise predominantly dry perennial grass, and overlap is again concurrent and high. In comparison, feral goats have higher preferences for the browse of a wide range of shrubs and trees, and switch to these much earlier than the other herbivores. When perennial grasses and perennial forbs become scarce, sheep, feral goats and cattle browse large shrubs and trees, and overlap is sequential and high. If climatic conditions remain dry, then red and western grey kangaroos will also browse large shrubs and trees, but overlap between them, sheep, cattle and goats is sequential and low. In contrast to the other herbivores, the diets of euros and eastern grey kangaroos are comprised predominantly of perennial grasses, regardless of climatic conditions. As for diet composition, concurrent overlap in foraging distributions of sheep, cattle, feral goats and the four species of macropods is often low. However, over periods of several months to two or three years, as climatic conditions change, overlap in foraging distributions is sequential and high. While equivalency in what and where these herbivores eat is not quantifiable, it appears to be high overall. This is particularly so for perennial grass, which is the dominant forage for herbivores in the southern rangelands.

Additional keywords: diet composition, diet overlap, food preferences, grazing distribution.

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Introduction

A previous paper in this special issue (Pahl 2019) assessed the equivalency of sheep (*Ovis aries*), cattle (*Bos taurus* and *B. indicus*), feral goats (*Capra hircus*) and four large species of macropod, with regard to their daily dry matter intakes of low- and high-quality forages. On that basis, a 50 kg goat is 1 dry sheep equivalent (DSE), a 450 kg steer is 8 DSE, and a 50 kg macropod is 0.7–1 DSE. This DSE rating for macropods is considerably higher than the currently accepted rating of 0.45, based on the relative energy expenditures of same-sized macropods and sheep while grazing (Munn *et al.* 2009; Munn *et al.* 2013, 2016). Although the macropod DSE rating of 0.7–1 based on dry matter intakes doubles their contribution to total grazing pressure (TGP), it does not necessarily increase their potential to reduce whole-property livestock productivity. For the latter to occur, sheep, cattle, feral goats and the macropods would need to share both forages and foraging areas, as only then could one species reduce

the availability of forage for another. Diet composition of macropods and sheep can be significantly different at particular times (Munn *et al.* 2010; Munn *et al.* 2014), but dietary overlap over time is often high (Dawson and Ellis 1994; Edwards *et al.* 1996). Even so, Olsen and Braysher (2000) and Olsen and Low (2006), in their updates of the current state of scientific knowledge of kangaroos in the environment, concluded that macropods mostly do not reduce livestock productivity because they have different diets and forage in different areas.

An extensive body of literature describes the composition of the diets of Merino sheep, cattle, feral goats and macropods in the southern rangelands of Australia. These studies mostly report diet composition at the level of accepted broad plant groups, being annual grasses, perennial grasses, annual or ephemeral forbs, perennial forbs, and large shrubs and trees (McIntyre *et al.* 1999; Fensham *et al.* 2015). Annual grasses generally live for only a few months (Islam *et al.* 1999). Examples of annual grasses eaten by

these herbivores are *Chloris truncata* (windmill grass), *Iseilema membranaceum* (small Flinders grass), *Lolium rigidum* (annual ryegrass) *Sporobolus caroli* (fairy grass) and *Tripogon loliiformis* (fiveminute grass). In contrast, perennial grasses can live for many years, with species common to the southern rangelands including *Eragrostis setifolia* (bristly lovegrass), *Dichanthium sericeum* (Queensland bluegrass), and *Austrodanthonia bipartita* (wallaby grass). Forbs are sometimes described as herbaceous (non-woody) plants other than grasses, sedges and rushes (Dawson 1995; PlantNET 2019), but more often, they are regarded as both herbaceous plants and woody sub-shrubs or shrubs (Friedel 1984; Friedel *et al.* 1996; Landsberg *et al.* 1999; Fensham *et al.* 2010). Landsberg *et al.* (1999) used the classification of Raunkiaer (1934) to distinguish between herbaceous and woody forbs. Herbaceous forbs were defined as those with perennating buds <1 cm above ground level, whereas the perennating buds of woody forbs are >1 cm above ground level. Annual forbs are herbaceous, with examples including *Portulaca oleracea* (purslane), *Brachycome campylocarpa* (large white daisy), *Calotis inermis* (fluffy burr daisy), *Goodenia pusilliflora* (small-flower Goodenia), *Leontodon rhagadioloides* (cretan weed), *Rhodanthe floribundum* (common white sunray) and *Medicago polymorpha* (burr medic). Some herbaceous forbs are also perennial, with examples including *Calotis cuneifolia* (purple burr-daisy), *Evolvulus alsinoides* (slender dwarf morning-glory), *Goodenia pinnatifida* (cutleaf Goodenia) and *Solanum esuriale* (quena). Of the woody perennial forbs, some are chenopod shrubs, such as *Atriplex* (salt bushes), *Maireana* (blue bushes) and *Sclerolaena* (burrs) (Norbury *et al.* 1993; Friedel *et al.* 1996; Landsberg *et al.* 1999). Examples of non-chenopod perennial forbs are *Hibiscus sturtii* (Sturt's hibiscus), *Sida petrophila* (rock sida), *Eremophila glabra* (black fuchsia), *Senna artemisioides* (silver cassia), *Abutilon otocarpum* (desert Chinese lantern), *Roepera aurantiaca* (shrubby twinleaf) and *Jacksonia rhadinoclona* (Miles dogwood) (Friedel 1984; Friedel *et al.* 1996; Fensham *et al.* 2010). Consequently, where possible, perennial forbs in the diets of these herbivores were separated into chenopod and non-chenopod shrubs. The large shrubs and trees commonly eaten by these herbivores are *Acacia aneura* (mulga), *A. victoriae* (prickly wattle), *A. homalophylla* (yarran), *Dodonaea viscosa* (narrow-leaf hophbush), *Heterodendrum oleifolium* (rosewood), *Casuarina cristata* (belah), *Apophyllum anomalum* (warrior bush), *Eremophila longifolia* (Berrigan) and *Geijera parviflora* (wilga).

This paper reviews the equivalency of Merino sheep, cattle, feral goats, red kangaroos (*Osphranter rufus*), western grey kangaroos (*M. fuliginosus*), euros (*M. robustus erubescens*) and eastern grey kangaroos (*M. giganteus*) with regard to food preferences, diet composition and foraging distributions. In particular, equivalency is assessed in relation to the types and amounts of forages consumed by these herbivores in different vegetation types and over a range of climatic conditions in the southern rangelands of Australia.

What do they prefer to eat?

Herbivores generally prefer plants or plant parts they can ingest quickly, which have high levels of nutrients such as protein, and which are readily digestible (Laredo and Minson 1973; McLeod

et al. 1990; Jalali *et al.* 2012). For example, the young leaves of herbaceous forbs and grasses, which are the preferred foods of both livestock and macropods (Dawson and Munn 2007), contain less fibre, more protein and are more digestible than mature leaves (Wilson and 't Mannelje 1978; Jung and Allen 1995; Archimède *et al.* 2000; Decruyenaere *et al.* 2009). Similarly, Dawson (1995), based on Short *et al.* (1974), compared the extent to which forages were digested by goats over a period of four hours. They digested, respectively, 87 and 39% of young and mature herbaceous forbs, 87 and 24% of new leaves and woody twigs of shrubs, and 75 and 15% of young grass leaves and mature dry grass.

The large differences in the quality of forages on offer in the southern rangelands will influence the preference hierarchies of sheep, cattle, feral goats and the four species of macropod for the broad plant groups. These preference hierarchies are described in the following sections. However, given that most studies did not compare the relative abundances of plants in the diets of herbivores with their relative abundances in the forage on offer, assessments of preference hierarchies are qualitative rather than quantitative.

Sheep

The most preferred forages of Merino sheep are fresh and green annual grasses and ephemeral forbs. When these are available, they are eaten in large quantities (Leigh and Mulham 1966a, 1966b; Leigh and Mulham 1967; Robards *et al.* 1967; Leigh *et al.* 1968; McMeniman *et al.* 1986; Wilson *et al.* 1969; Dawson *et al.* 1975; Ellis *et al.* 1977; Loremer 1978; Wilson 1979; Graetz and Wilson 1980; Downing 1986; Harrington 1986a; Wilson 1991a, 1991b; Dawson and Ellis 1994; Edwards *et al.* 1995).

When annual grasses and ephemeral forbs are dry or unavailable, sheep consume large amounts of perennial grasses if these are green (Leigh and Mulham 1966b; Robards *et al.* 1967; Leigh *et al.* 1968; McMeniman *et al.* 1986; Storr 1968; Ellis 1976; Ellis *et al.* 1977; Loremer 1978; Wilson 1979; Graetz and Wilson 1980; Squires 1980, 1982; Harrington 1986a; Dawson and Ellis 1994, 1996; Edwards *et al.* 1995).

As perennial grasses senesce and dry out, sheep switch to perennial forbs provided they have fresh growth. These include chenopods such as *Atriplex* (saltbush) and *Sclerolaena* (burrs), or non-chenopod perennial forbs such as *Calotis*, *Sida*, *Abutilon* and *Hibiscus* (Leigh and Mulham 1966a, 1966b, 1967; Robards *et al.* 1967; Wilson *et al.* 1969; Griffiths *et al.* 1974; Dawson *et al.* 1975; Ellis 1976; Ellis *et al.* 1977; Loremer 1978; Wilson 1979; Squires 1980; Wilson and Mulham 1980; Squires 1982; Harrington 1986a; Dawson and Ellis 1994, 1996; Edwards *et al.* 1995; Munn *et al.* 2010).

When the most palatable perennial forbs have stopped growing or are grazed out, sheep revert to dry perennial grasses providing they are still leafy (Squires 1980, 1982; Dawson and Ellis 1994; Edwards *et al.* 1995). They also consume less desirable perennial forbs at this time (Leigh and Mulham 1966b).

When it is very dry and the quantity and quality of perennial grasses and perennial forbs are low, sheep increasingly browse a narrow range of trees and shrubs, such as *Acacia*, *Dodonaea*, *Eremophila* and *Heterodendrum* (McMeniman *et al.* 1986; Storr 1968; Wilson *et al.* 1975; Harrington 1986a; Franco 2000; Munn *et al.* 2014). At this time, sheep also eat less palatable perennial

grasses such as *Aristida*, *Eragrostis* and *Amphipogon* (McMeniman *et al.* 1986; Wilson 1991a, 1991b).

When palatable shrub and tree species are not available or are eaten out, sheep increasingly eat dry burrs, dead grass stalks and other dead materials (tree leaves, twigs, fruits) lying on the ground (Leigh and Mulham 1966a, 1966b; Robards *et al.* 1967; Leigh *et al.* 1968; Wilson *et al.* 1969; Dawson and Ellis 1994).

Overall, it appears that Merino sheep most prefer the greenest and most digestible forage, comprising annual grasses and ephemeral forbs. When these are unavailable, they eat green perennial grasses. When the perennial grasses dry off, they switch to the new growth of perennial forbs, and when these are eaten out, they switch back to dry perennial grasses. Only when these more preferred forages are unavailable do sheep eat large amounts of browse from large shrubs and trees. When this last source of green material disappears, they eat dry materials lying on the ground.

Cattle

Although there are only a few studies of the diet composition of cattle in the southern rangelands, their preferred forage also appears to be ephemeral forbs, which make up the majority of the diet when readily available (Graetz and Wilson 1980; Squires and Low 1987; Coates and Dixon 2007).

When ephemeral forbs are scarce, green grass is the predominant forage of cattle if available (Graetz and Wilson 1980; Squires 1980, 1982; Squires and Siebert 1983; Downing 1986; Squires and Low 1987; Coates and Dixon 2007). As with sheep, cattle also prefer annual grasses to perennial grasses (Squires and Low 1987; Coates and Dixon 2007).

When the availability of green grass declines, cattle consume increasing quantities of perennial forbs such as saltbush when these were growing and available (Wilson 1979; Graetz and Wilson 1980; Squires 1980, 1982). When the perennial forb layer stops growing, or is grazed out, or not present, cattle eat large quantities of dry perennial grass if available and still leafy (Squires 1980, 1982; Squires and Siebert 1983).

When perennial grasses and perennial forbs such as saltbush are not available, cattle eat large amounts of browse from shrubs and trees, and particularly *A. aneura* (Chippendale 1962; Squires 1980, 1982; Downing 1986; Coates and Dixon 2007). At this time, cattle also increase their intake of less palatable grasses such as *Aristida* (Coates and Dixon 2007). When the supply of palatable browse runs out, they are forced to eat remaining dry grass stems and other dead materials on the ground (Chippendale 1962).

The diet preferences of cattle are thus similar to those of sheep. They most prefer ephemeral forbs and annual grasses, followed by green perennial grass, green and growing perennial forbs, dry perennial grass, browse, and finally, dry grass stalks and other dead materials lying on the ground.

Feral goats

Feral goats also most prefer green annual grasses and green ephemeral forbs, which make up the majority of their diet when available (Wilson *et al.* 1975; Downing 1986; Harrington 1986b). When these are unavailable, goats eat large amounts of perennial grasses providing they are green (Wilson and Mulham 1980; Squires 1980, 1982; Harrington 1986b).

As perennial grasses dry out, feral goats switch earlier than the other herbivores to non-chenopod perennial forbs such as *Ptilotus*, *Hibiscus*, *Senna*, *Euphorbia* and *Sida* providing they are green, and browse large shrubs and trees such as *Heterodendrum*, *Casuarina*, *Geijera*, *Dodonaea*, *Myoporum* and *Acacia* (Dawson *et al.* 1975; Squires 1980, 1982; Harrington 1986b). However, on occasions, chenopods such as *Sclerolaena*, are also consumed in moderate to large quantities (Wilson *et al.* 1975; Wilson and Mulham 1980; Harrington 1986b; Dawson and Ellis 1996).

As the quantity and quality of perennial grasses and perennial forbs deteriorate, goats increasingly browse a wide range of large shrubs and trees (Wilson *et al.* 1975; Ellis 1976; Wilson and Mulham 1980; Squires 1980, 1982; Harrington 1986b; Dawson and Ellis 1996; Franco 2000). When it is particularly dry, these can include species not eaten by either sheep or cattle, and not browsed by goats under less severe conditions (Wilson *et al.* 1975; Squires 1980; Downing 1986). As the quantity and quality of browse falls to very low levels, goats then mostly consume dry grass, and when this becomes scarce, they mainly eat fallen leaves, seeds, flowers, dead grass stalks and other dry litter lying on the ground (Downing 1986; Squires 1980, 1982; Harrington 1986b).

Overall, feral goats also prefer green ephemeral forbs and green annual and perennial grasses, but have a higher preference for browse from a wide range of large shrubs and trees than the other herbivores.

Red kangaroo

As with sheep, feral goats and cattle, red kangaroos most prefer ephemeral forbs and annual grasses. During wet winters when ephemeral forbs are abundant, these can be more than 50% of their diet (Griffiths and Barker 1966; Storr 1968; Ellis *et al.* 1977; Barker 1987; Dawson and Ellis 1994). Similarly, green annual grasses appear to be preferred to green perennial grasses, and form high proportions of the diet of red kangaroos when they are available (Chippendale 1968; Storr 1968; Bailey *et al.* 1971; Barker 1987; Dawson and Ellis 1994).

When green annual grasses and ephemeral forbs are scarce, such as during wet summers, the diet of red kangaroos is predominantly green perennial grasses (Storr 1968; Ellis *et al.* 1977; Newsome 1980; Dawson and Ellis 1994; Edwards *et al.* 1995; Dawson *et al.* 2004). Red kangaroos appear to prefer smaller perennial grasses (Chippendale 1968), and consume more of these than do sheep (Dawson and Ellis 1994). Short grasses are likely to have a higher leaf to stem ratio and thus be of a higher quality than tall perennial grasses.

When seasons are dry, even when perennial forbs are available, perennial grasses are still often 70 to 90% of the diet of red kangaroos, provided they are abundant (Griffiths and Barker 1966; Chippendale 1968; Storr 1968; Bailey *et al.* 1971; Low *et al.* 1973; Griffiths *et al.* 1974; Dawson *et al.* 1975, 2004; Ellis 1976; Ellis *et al.* 1977; Newsome 1980; Dawson and Ellis 1994; Edwards *et al.* 1995). Only when it is very dry, when grass has become scarce, do chenopods such as *Atriplex*, *Maireana* and *Sclerolaena*, form a high proportion (up to 80%) of the diet of red kangaroos (Griffiths and Barker 1966; Bailey *et al.* 1971; Griffiths *et al.* 1974; Barker 1987; Dawson and Ellis 1994; Edwards *et al.* 1995; Munn *et al.* 2010).

During droughts, when the more palatable chenopods, other perennial forbs and perennial grasses have been eaten out, red kangaroos mainly consume the dry stems, butts and roots of perennial grasses, foliage from the less palatable perennial forbs such as *Chenopodium*, *Maireana* and *Senna*, and browse from *A. victoriae* (prickly wattle) and *Eremophila* spp. (Barker 1987; Short 1987; Dawson and Ellis 1994).

Overall, the forage preferences of red kangaroos are similar to those of sheep and cattle. They most prefer ephemeral forbs and annual grasses, followed by green perennial grass, dry perennial grass, perennial forbs, and when all else has been grazed out, the dead stalks of grasses and browse of shrubs and trees.

Western grey kangaroo

Only a small number of studies have recorded the dietary composition of western grey kangaroos, despite their abundance and wide distribution across the southern rangelands. Ephemeral forbs and annual grasses also appear to be their most preferred forages (Wilson 1991a, 1991b), and make up the majority of the diet when they were available (Barker 1987; Coulson and Norbury 1988). During wet summers, when ephemeral forbs and annual grasses are not available, but green perennial grasses are abundant, then perennial grass is almost the exclusive diet of western grey kangaroos (Coulson and Norbury 1988).

If autumn and winter are dry, and ephemeral forbs have disappeared and perennial grasses are mature, perennial grasses are still the dominant forage of western greys (Wilson 1991a, 1991b). When it is particularly dry and perennial grass quantity and quality are low, western greys eat increasing amounts of perennial forbs, particularly chenopods such as *Atriplex* and *Maireana* (Barker 1987; Munn *et al.* 2014).

Under prolonged dry conditions, when perennial grasses and the palatable perennial forbs have been eaten out, western grey kangaroos consume predominantly the browse of shrubs such as *A. victoriae*, *Dodonea viscosa* and *Eremophila* spp. (Barker 1987).

Overall, western grey kangaroos appear to have similar dietary preferences to red kangaroos, sheep and cattle. As is the case with red kangaroos, western greys generally consume less ephemeral and perennial forbs than sheep. However, western grey kangaroos appear to have higher preferences for perennial forbs than red kangaroos (Short 1986).

Euro

A few studies have recorded the dietary composition of euros, showing they regularly consume more grass than livestock, feral goats and the red and western grey kangaroos (Ellis *et al.* 1977; Dawson and Ellis 1996; Franco 2000). In wet winters, when both annual grasses and ephemeral forbs are available, ephemeral forbs are at most 25% of the diet of euros (Storr 1968; Ellis *et al.* 1977; Dawson and Ellis 1996). As with the other herbivores, euros appear to have a high preference for annual grasses, which dominate their diet when they were abundant (Dawson *et al.* 1975).

During wet summers when perennial grasses are green and plentiful, these are almost the exclusive diet of euros (Storr 1968; Ellis *et al.* 1977; Dawson and Ellis 1996; Franco 2000). Even when perennial grasses are drying out and senescing, and their quality has appreciably declined, they are still the dominant

forage of euros even when perennial forbs and other shrubs are still available (Storr 1968; Ellis *et al.* 1977; Dawson and Ellis 1996; Franco 2000). Even species of *Aristida*, generally regarded as poor quality grasses, are often a substantial component of their diet (Franco 2000).

However, euros increase their intake of chenopods and other perennial forbs to between 20–40% of their diet during very dry seasons when perennial grass quantity and quality are very poor (Storr 1968; Dawson *et al.* 1975; Ellis *et al.* 1977; Dawson and Ellis 1996). During very dry periods and droughts, in contrast to sheep, cattle, feral goats, red kangaroos and western grey kangaroos, browse from large shrubs and trees is usually less than 5% of the diet of euros (Dawson *et al.* 1975; Ellis *et al.* 1977; Dawson and Ellis 1996).

Overall, although annual grasses appear to be the most preferred forage of euros, perennial grasses are their dominant forage in all seasons. They maintain a high proportion of grasses in their diet even when these are scarce, and when chenopods and other perennial forbs are available.

Eastern grey kangaroo

Eastern grey kangaroos are widespread and abundant in the north-east of the southern rangelands, but their food preferences and diet composition in that region are the least well known of the large macropods. However, it appears that eastern grey kangaroos have a high preference for annual grasses and ephemeral forbs, as these are eaten in moderate to large amounts when available (Griffiths and Barker 1966; Dawson *et al.* 2004). When these are not available, eastern greys eat very large amounts of perennial grasses, and only small amounts of perennial forbs and large shrubs and trees (Kirkpatrick 1965; Griffiths and Barker 1966; Griffiths *et al.* 1974; Franco 2000; Dawson *et al.* 2004). Even under very dry, or drought conditions, eastern grey kangaroos eat very small amounts of browse from large shrubs and trees (Griffiths and Barker 1966; Griffiths *et al.* 1974). The forage preferences of eastern grey kangaroos thus appear similar to those of euros, although eastern greys may consume more ephemeral forbs and less perennial forbs than euros.

What do they actually eat?

Each species of herbivore has a hierarchy of preferences for particular groups of plants, but there are often discrepancies between forage preferences and diet composition due to variation in forage availability at any given place or time (Wilson 1991a). Hence, diet composition is a function of both forage preferences and forage availability. Most studies of diet composition did not measure the relative abundances of the broad plant groups, and these no doubt varied extensively between vegetation types. For example, the relative abundance of chenopod perennial forbs in chenopod shrublands is much higher than in poplar box-mulga woodlands, whereas the opposite is the case for the browse of large shrubs and trees. Similarly, the relative abundance of perennial grasses in Mitchell grasslands is much higher than in chenopod shrublands. Hence, more insights into similarities and differences in diet composition of these herbivores are provided by comparisons of their diets in vegetation types with very different relative abundances of the main

Table 1. Diet composition based on several studies^A of sheep, cattle, feral goats, red kangaroos, euros, western grey kangaroos (W. grey) and eastern grey kangaroos (E. grey) in poplar box-mulga woodlands in New South Wales and Queensland

AG = annual grasses, EF = ephemeral forbs, PG = perennial grasses, CH = chenopod perennial forbs, N-CH = non-chenopod perennial forbs, BR = browse from large shrubs and trees, DM = dry materials lying on the ground; ▏ = very small, ■ = small, ■ = moderate, ■ = large, ■ = very large

Species	Season	AG	EF	PG	CH	N-CH	BR	DM
Sheep	Wet autumn		■	■		■	■	
	Wet winter		■	■	■	■		
	Wet spring	■	■	■	■	■		■
	Wet summer	■	■	■	■	■		■
	Dry autumn		■	■	■	■	■	
	Dry winter		■	■	■	■	■	▏
	Dry spring		■	■	■	■	■	▏
	Dry summer		■	■	■	■	■	▏
	Drought			■	■	■	■	■
Cattle	Wet autumn		■	■			■	
	Wet winter	■	■	■				
	Wet spring		■	■		■	■	■
	Wet summer		▏	■	■	■	■	■
	Dry winter			■	▏	▏	■	▏
	Dry spring			■	▏	▏	■	▏
	Dry summer			■			■	
	Drought			■			■	■
	Goat	Wet autumn		■	■			■
Wet winter		■	■			■		
Wet spring		■	■		■	■	▏	
Wet summer		■	■			■		
Dry autumn			■		■	■	■	
Dry winter			■	■		■	■	
Dry spring			■	■		■	■	
Dry summer			■	■		■	■	
Drought			■			■	■	
Red	Wet autumn		■	■			▏	
	Wet winter		■	■	■			
	Wet spring		■	■	■		▏	
	Wet summer		■	■	■	■		
	Dry spring			■	■	■		
Euro	Wet autumn		■	■			▏	
	Wet winter		■	■			▏	
	Wet spring		■	■			▏	
	Wet summer		▏	■			▏	
W. grey	Wet winter		■	■	■	▏		
	Wet summer		■	■			▏	
E. grey	Wet autumn		■	■			■	
	Wet winter		■	■	■			
	Wet spring		■	■			▏	
	Wet summer		■	■				
	Drought		■	■	■	■		

^AGriffiths and Barker (1966); Griffiths *et al.* (1974); Squires (1980), (1982); Downing (1986); Harrington (1986a), (1986b); McMeniman *et al.* (1986); Squires and Low (1987); Wilson (1991a), (1991b); Franco (2000); Coates and Dixon (2007).

plant groups, and then as these change with season and climate variability. Also, availability of forage types varies with species of herbivore due to differences in body size, daily intake requirements and selective foraging abilities. Consequently, small and sparsely distributed high-quality components of pastures tend to be more available to the smaller herbivores.

Poplar box-mulga woodlands

Numerous studies have recorded the composition of diets of sheep, cattle, feral goats and macropods in poplar box-mulga woodlands in the rangelands of New South Wales and southern

Queensland (Table 1). In Table 1, wet seasons were regarded as those with average- to above-average rainfall, whereas dry seasons were those with below- to well-below-average rainfall. Droughts were characterised by very low rainfall over an extended period of time, as well as a depleted pasture layer. Diet composition in this paper is described at the level of broad plant groups, being annual grasses, ephemeral forbs, perennial grasses, chenopod perennial forbs, non-chenopod perennial forbs, browse from large shrubs and trees and dead materials lying on the ground. Many authors have recorded the proportions of these plant groups in the diets of sheep, cattle, feral goats

and macropods in the southern rangelands. The most common method used was histological examination of fragments of plants present in stomach or faecal samples, where diet composition was based on the percentage of identifiable fragments that belonged to each plant group. Much less commonly, diet composition was based on the percentage of total grazing time that animals spent eating each plant group, or a combination of the percentage utilisation and abundance of each plant group. The percentages of plant groups in the diets of these herbivores reported by authors were ranked according to a five-category scale – very small (<5%), small (5–19%), moderate (20–39%), large (40–65%) and very large (>65%), which are represented by bars of increasing width in Table 1.

Perennial grasses were by far the dominant forage of herbivores in the poplar box-mulga woodlands (Table 1). It is also apparent that in this vegetation type the diet of sheep, cattle and feral goats was much more diverse than that of the four species of large macropod. Diet composition of the macropod species was mostly recorded during wet seasons, but it consisted of large to very large amounts of perennial grasses and small to moderate amounts of ephemeral forbs. In comparison, during wet seasons, the diet of sheep contained less perennial grass and more ephemeral forbs, chenopod perennial forbs and non-chenopod perennial forbs than macropods. During dry seasons, sheep increased their intake of perennial grasses and non-chenopod perennial forbs, and during drought, their diet was predominantly foliage from chenopods, non-chenopods and browse from large shrubs and trees. Diet composition of the macropods was recorded in only two dry seasons and one drought compared with 13 wet seasons, and it consistently comprised very large amounts of perennial grasses and only small amounts of chenopod perennial forbs.

Cattle, over all seasons, ate more perennial grass than sheep and feral goats, but less than the macropods. The amount of ephemeral forbs eaten by cattle was lower than sheep, goats and red kangaroos, but similar to western and eastern grey kangaroos and euros. The amounts of chenopod and non-chenopod perennial forbs in the diet of cattle were similar to those of goats and the four species of macropods, but much less than sheep. Cattle also ate more browse than the other herbivores except feral goats.

Goats ate less perennial grass than all other herbivores. During wet seasons, they ate large amounts of ephemeral forbs, similar to sheep. Goats also differed from the other herbivores in that they ate moderate to large amounts of browse in all seasons. This appears due to their acceptance of a wider range of large shrub and tree species, ability to browse at greater heights than sheep, forage in areas inaccessible to sheep and cattle, and their greater ability to pluck leaves from stems (Wilson *et al.* 1975; Squires 1980, 1982; Wilson and Mulham 1980; Wilson and Harrington 1984; Downing 1986). Also, feral goats ate more dead materials on the ground (leaves, flowers, seeds, burrs), particularly during dry seasons and drought. Hence, over time, feral goats ate more shrub and tree browse, dead materials and non-chenopod perennial forbs, and less perennial grass, than the other herbivores.

Chenopod shrublands

As with the poplar box-mulga woodlands, perennial grasses were the dominant forage of herbivores in the chenopod

shrublands of New South Wales (Table 2). The possible exception was feral goats whose diet was dominated by chenopod and non-chenopod perennial forbs and browse. However, two of the three observations for feral goats were recorded under dry conditions (dry spring and drought) when it is expected these forages would be dominant. After perennial grasses, chenopods were the next dominant forage of herbivores in the chenopod shrublands, and were often eaten in moderate to very large amounts by sheep, cattle, goats, red kangaroos and western grey kangaroos.

As with the poplar box-mulga woodlands, sheep ate moderate to large amounts of ephemeral forbs during wet seasons. During dry seasons when these were scarce and perennial grasses were mature and dry, they ate large amounts of chenopods. Diet composition of cattle showed a similar pattern.

The diet of red kangaroos was very similar to sheep and cattle during wet seasons in that it was predominantly perennial grasses and ephemeral forbs. However, their diets differed during dry seasons as red kangaroos ate much more perennial grass than sheep and cattle, and generally less chenopods. Diets of red kangaroos, sheep, cattle and goats were also similar during drought in that perennial grasses declined to moderate amounts, and foliage of chenopod and non-chenopod perennial forbs and large shrubs and trees became the dominant forage.

The diet of western grey kangaroos in the chenopod shrublands was also similar to those of sheep, cattle and red kangaroos during wet seasons, when it consisted predominantly of perennial grasses and ephemeral forbs. Also, the diet of western grey kangaroos was similar to sheep, cattle, goats and red kangaroos during dry seasons and drought, in that the foliage of chenopod and non-chenopod perennial forbs and large shrubs and trees became their dominant forage. Western greys appeared to consume more annual grasses than the other herbivores during some wet seasons, but this may be an artefact of a small number of studies.

While the diet composition of euros in chenopod shrublands was more diverse than in poplar box-mulga woodlands, perennial grasses were by far the dominant component, setting them apart from sheep, cattle, goats, red kangaroos and western grey kangaroos. Only small amounts of ephemeral forbs, chenopod and non-chenopod perennial forbs and large shrubs and trees were eaten by euros.

Only one study – Dawson *et al.* (2004) – recorded the diet composition of eastern grey kangaroos in chenopod shrublands. During a wet summer, wet winter and wet autumn, eastern greys ate very large amounts of perennial grasses, small amounts of ephemeral forbs and chenopod perennial forbs, and very small amounts of non-chenopod perennial forbs and browse. Hence, their diet was similar to that of euros.

Eucalypt and Acacia woodland with spinifex

The diets of sheep, red kangaroos and euros in the eucalypt and *Acacia* woodlands containing spinifex were less diverse than those in other vegetation types, but the trends were similar (Table 3). Again, perennial grasses dominated the diets of all three species. The diets of sheep and red kangaroos were very similar during wet seasons, being dominated by perennial grasses, followed by ephemeral forbs and then annual grasses. During the same wet seasons, euros ate more perennial grass,

Table 2. Diet composition based on several studies^A of sheep, cattle, feral goats, red kangaroos, euros, western grey kangaroos (W. grey) and eastern grey kangaroos (E. grey) in chenopod shrublands of New South Wales

AG = annual grasses, EF = ephemeral forbs, PG = perennial grasses, CH = chenopod perennial forbs, N-CH = non-chenopod perennial forbs, BR = browse from large shrubs and trees, DM = dry materials lying on the ground; ▏ = very small, ■ = small, ■■■ = moderate, ■■■■■ = large, ■■■■■■■ = very large

Species	Season	AG	EF	PG	CH	N-CH	BR	DM
Sheep	Wet autumn		■	■■■■■	■	▏		
	Wet winter	■	■■■■	■■■	■	■		
	Wet spring	■	■■■■	■■■	■	▏		
	Wet summer		■	■■■■■	■	■		
	Dry autumn			■■■	■■■■■			■
	Dry winter		■	■■■	■■■■■		■	
	Dry spring	■	■	■	■■■■■			
	Dry summer		■	■■■	■■■■■		■	
	Drought			■■■	■■■			■
Cattle	Wet autumn		▏	■■■■■	■■■			
	Wet winter		■	■■■■■	■	▏	▏	
	Wet spring		■■■■■	■■■				
	Dry winter		▏	■	■■■■■		▏	
Goat	Wet winter		■	▏	■■■■■	■	■■■■■	
	Dry spring			■	■■■	■■■	■■■	
	Drought		▏	■■■	■■■■■	▏	■■■	
Red	Wet autumn		■	■■■■■	▏			
	Wet winter	■■■■■	■■■■	■		▏		
	Wet spring	▏	■■■	■■■■■	▏	■		
	Wet summer	▏	■	■■■■■	▏	▏		
	Dry autumn		▏	■	■■■■■	▏	▏	
	Dry winter		■	■■■■■	■■■			
	Dry spring			■■■■■	■	■		
	Dry summer		▏	■■■■■	■■■■■	■		
	Drought		▏	■	■■■■■	■■■		■■■
Euro	Wet winter		■■■	■■■■■	■	▏	▏	
	Wet summer		▏	■■■■■	■	■	▏	
	Dry winter		■	■■■■■	■	■	■	
	Dry spring			■■■■■	■			
	Dry summer		▏	■■■■■	■■■	▏	▏	
	Drought		▏	■■■■■	■	▏	■	
	Drought			■■■■■	■■■			■
W. grey	Wet winter	■■■■■	■■■	■		■■■		
	Wet spring	■■■	■	■■■■■		▏		
	Wet summer		■	■■■■■	▏	▏		
	Dry spring		■■■	■		■■■		
	Dry summer			■■■	■■■■■	■	■	
	Drought			■	■■■■■	■■■		■■■
	Drought			■■■■■	■■■	▏	▏	
E. grey	Wet winter	■■■■■	■	■■■■■	■			
	Wet summer		■	■■■■■	▏			
	Wet autumn		▏	■■■■■	■	▏	▏	

^ALeigh and Mulham (1966a); (1966b), (1967); Robards *et al.* (1967); Leigh *et al.* (1968); Wilson *et al.* (1969); Bailey *et al.* (1971); Ellis (1976); Dawson *et al.* (1975), (2004); Ellis *et al.* (1977); Graetz and Wilson (1980); Short (1985); Barker (1987); Dawson and Ellis (1994), (1996); Edwards *et al.* (1995); Munn *et al.* (2010), (2014).

less ephemeral forbs and no annual grasses. During the dry seasons, sheep replaced ephemeral forbs with browse, red kangaroos replaced ephemeral forbs with more perennial grasses, and euros continued to eat very large amounts of perennial grasses.

Mixed vegetation of central Australia

In the grasslands, shrublands and woodlands of central Australia (Table 4), perennial grasses were again the dominant forage of cattle and red kangaroos. In all seasons, cattle ate large to very large amounts of perennial grasses and only small amounts of

ephemeral forbs and browse. In comparison, although the diet of red kangaroos always contained moderate to very large amounts of perennial grasses, they also consumed moderate to large amounts of annual grasses.

Belah-rosewood woodlands

In contrast to the other vegetation types, chenopods and browse were as dominant as perennial grasses in the diets of sheep and feral goats in the belah-rosewood woodlands of New South Wales (Table 5). Trends in diet composition of sheep and feral goats observed in other vegetation types were also observed in

Table 3. Diet composition based on Storr (1968) of sheep, red kangaroos and euros in eucalypt and *Acacia* woodlands with spinifex in Western Australia

AG = annual grasses, EF = ephemeral forbs, PG = perennial grasses, CH = chenopod perennial forbs, N-CH = non-chenopod perennial forbs, BR = browse from large shrubs and trees, DM = dry materials lying on the ground; | = very small, ■ = small, ■■■ = moderate, ■■■■■ = large, ■■■■■■■ = very large

Species	Season	AG	EF	PG	CH	N-CH	BR	DM
Sheep	Wet autumn		■■■■■	■■■■■				
	Wet summer	■■■	■	■■■■■				
	Dry winter		■■■	■■■■■				
	Dry spring			■■■■■			■■■	
Red	Wet autumn		■■■	■■■■■				
	Wet summer	■■■	■	■■■■■				
	Dry winter		■	■■■■■				
	Dry spring		■	■■■■■				
Euro	Wet autumn		■	■■■■■				
	Wet summer			■■■■■				
	Dry winter		■	■■■■■				
	Dry spring		■	■■■■■				

Table 4. Diet composition based on several studies^A of cattle and sheep in central Australia mixed plant communities, including Mitchell grasslands, open woodlands with eucalypts and acacias, *Acacia* shrublands and mulga grasslands

AG = annual grasses, EF = ephemeral forbs, PG = perennial grasses, CH = chenopod perennial forbs, N-CH = non-chenopod perennial forbs, BR = browse from large shrubs and trees, DM = dry materials lying on the ground; | = very small, ■ = small, ■■■ = moderate, ■■■■■ = large, ■■■■■■■ = very large

Species	Season	AG	EF	PG	CH	N-CH	BR	DM
Cattle	Wet spring			■■■■■			■■■	
	Wet summer		■	■■■■■			■	
	Dry autumn		■	■■■■■			■	
	Dry spring			■■■■■				
	Dry summer			■■■■■			■	
Red	Wet autumn	■■■■■		■■■				
	Wet winter	■		■■■■■				
	Wet spring	■■■		■■■■■			■	
	Wet summer	■■■		■■■■■				
	Dry autumn	■■■■■		■■■				
	Dry summer			■■■■■			■	

^AChippendale (1962, 1968); Newsome (1980); Squires and Siebert (1983).

Table 5. Diet composition based on several studies^A of sheep and feral goats in belah-rosewood woodlands with a shrub understorey in New South Wales

AG = annual grasses, EF = ephemeral forbs, PG = perennial grasses, CH = chenopod perennial forbs, N-CH = non-chenopod perennial forbs, BR = browse from large shrubs and trees, DM = dry materials lying on the ground; | = very small, ■ = small, ■■■ = moderate, ■■■■■ = large, ■■■■■■■ = very large

Species	Season	AG	EF	PG	CH	N-CH	BR	DM
Sheep	Wet winter		■	■■■■■	■■■■■		■	
	Wet summer			■■■■■	■■■■■		■	
	Dry winter			■■■■■	■■■■■		■	
	Dry spring			■■■■■	■■■■■			
	Drought			■	■■■		■■■■■	
Goat	Wet winter		■	■■■■■	■■■■■		■	
	Wet summer			■■■■■	■		■	
	Dry winter			■	■■■		■■■■■	
	Dry spring			■	■■■		■■■■■	
	Drought				■		■■■■■	

^AWilson *et al.* (1975), Wilson and Mulham (1980), Downing (1986).

Table 6. Diet composition based on several studies^A of sheep and cattle in Mitchell grasslands in Queensland and Northern Territory

AG = annual grasses, EF = ephemeral forbs, PG = perennial grasses, CH = chenopod perennial forbs, N-CH = non-chenopod perennial forbs, BR = browse from large shrubs and trees, DM = dry materials lying on the ground; ▏ = very small, ■ = small, ■■■ = moderate, ■■■■■ = large, ■■■■■■■ = very large

Species	Season	AG	EF	PG	CH	N-CH	BR	DM
Sheep	Wet autumn	■■■	■■■	■■■		■■■		
	Wet winter	▏	■	■■■■■		■		
	Wet summer	■	■	■■■■■		▏		
Cattle	Wet autumn	■		■■■■■		■		
	Wet winter	■	■	■■■■■		■		
	Wet spring		■	■■■■■		■		
	Wet summer	■	■	■■■■■		■■■		
	Dry spring		■	■■■■■		■		

^ALoremer (1978); McMeniman *et al.* (1986); Squires and Low (1987); Coates and Dixon (2007).

the belah-rosewood woodlands. Their diets were the same during wet seasons, being predominantly perennial grasses and chenopods with small amounts of ephemeral forbs and browse. During dry seasons, sheep still consumed large amounts of perennial grasses and chenopods, while goats consumed large amounts of browse, moderate amounts of chenopods and only small amounts of perennial grasses. Although both sheep and goats increased their intake of browse during drought, goats ate more browse than sheep.

Mitchell grasslands

Not surprisingly, perennial grasses were the dominant forages of sheep and cattle in the Mitchell grasslands of Queensland and the Northern Territory (Table 6). Except possibly for a wet autumn, where sheep ate less perennial grass and more ephemeral forbs and annual grasses than cattle, their diets were predominantly perennial grasses and small amounts of non-chenopod perennial forbs.

Overlap in what they eat

The diet composition of sheep, cattle, feral goats and the four species of macropod is a function of their forage preferences and forage availability. Dawson (1995) reported a hierarchy of forage preferences for red kangaroos, sheep and euros in chenopod shrublands at Fowlers Gap. The most preferred forage of red kangaroos was young grass, followed by green herbaceous forbs, mature grass, saltbush, dry grass, browse and bluebush. For sheep, the hierarchy was green herbaceous forbs, young grass, saltbush, mature grass, browse, dry grass and bluebush. Hence, sheep had higher preferences for green forbs, saltbush and browse, whereas red kangaroos had higher preferences for young grass, mature grass and dry grass. Euros had even higher preferences for grass, with their hierarchy being young grass, mature grass, green forbs, dry grass, bluebush, saltbush and browse.

These hierarchies of forage preferences identified by Dawson (1995) were based on the abundance of plants in the diets of herbivores relative to their abundance in their habitat. However, the availability of forage is also a function of herbivore body size, daily intake requirements and selective foraging abilities. Minor components of pastures can be available to small herbivores such as euros, but not to larger herbivores such as sheep. For example, green leaves of perennial grasses are

available to macropods longer than they are available to sheep and cattle (Chippendale 1962; Griffiths and Barker 1966), and even though sheep and cattle may have the same preference for green grass leaf, they switch to saltbush earlier than macropods. Consequently, hierarchies of forage preferences may be more similar than reported by Dawson (1995).

Ephemeral forbs and annual grasses, the highest quality forages present in the southern rangelands, are highly preferred by sheep, cattle, goats and the four species of macropod (Dawson and Munn 2007). These are eaten in large quantities by all herbivores when they are available, and thus diet overlap is concurrent and high. However, annual grasses and ephemeral forbs are often small plants, and thus their proportions in the diets of herbivores are likely to increase with decreasing body size.

Wet summers facilitate the growth of perennial grasses. The newly grown leaves of perennial grasses, which are also highly preferred by these herbivores, dominate their diets at this time. Again, diet overlap is concurrent and high. The exception is often feral goats, which may consume moderate to large amounts of browse from large shrubs and trees even when green perennial grasses are available.

As climatic conditions deteriorate, ephemeral forbs and annual grasses disappear and the availability of green perennial grass declines, sheep and cattle turn at different times to perennial forbs, dry grass and browse from large shrubs and trees. Consequently, diet overlap tends to be sequential. Cattle, the largest of these herbivores, need to consume large amounts of forage daily and have neither the ability nor the time to search for and selectively eat sparsely distributed high quality forages, such as annual grasses, ephemeral forbs and the green parts of perennial grasses. For example, as the availability of ephemeral forbs and green grasses decline, sheep and cattle switch to more readily available but poorer quality forages. However, cattle switch to the next preferred plant group earlier than sheep, with the sequence for both herbivores being ephemeral forbs and annual grasses, green perennial grass, new growth of perennial forbs, dry perennial grass, large shrubs and trees and finally, dead materials on the ground (Graetz and Wilson 1980; Squires 1980, 1982; Wilson and Harrington 1984). In another instance (Downing 1986), sheep were able to maintain a high proportion of green *Eragrostis lacunaria* (purple lovegrass) in their diet whereas cattle switched to dry *Stipa variabilis* (spargrass).

Consequently, over time, the diets of sheep contained more ephemeral forbs and green grasses, and less dry grass, perennial forbs and browse from shrubs and trees than cattle (Wilson 1979; Downing 1986; Squires 1980, 1982; Squires and Low 1987). Even so, sequential diet overlap in the use of the broad forage groups by sheep and cattle is high.

In contrast to sheep and cattle, red kangaroos and western grey kangaroos take much longer to switch to perennial forbs. These kangaroos have much greater selective foraging abilities than sheep and cattle, due to their smaller body size, narrower jaws and crouching posture (Taylor 1983; Jarman and Phillips 1989). This enables them to maintain a diet with a high proportion of green perennial grass much longer than sheep (Chippendale 1962; Griffiths and Barker 1966) and probably enables them to consume more of the higher-quality parts of drier perennial grasses than sheep. Hence, sheep switch to perennial forbs such as chenopods much earlier than macropods (Ellis *et al.* 1977; Munn *et al.* 2010). At such times, as pastures dry out or are grazed out, the diet of sheep can be predominantly chenopods, while that of red kangaroos is predominantly perennial grasses (Dawson *et al.* 1975; Ellis *et al.* 1977; Barker 1987; Dawson and Ellis 1994; Edwards *et al.* 1995). Barker (1987) reported a similar trend for sheep and western grey kangaroos in chenopod shrublands near Kinchega National Park, in south-western New South Wales. During good seasons, sheep and western greys ate similar proportions of grasses and ephemeral forbs, but sheep switched earlier to chenopod shrubs as conditions deteriorated. Storr (1968) also noted that as pastures dried out in woodlands containing soft and hard spinifex in Western Australia, perennial grasses still dominated the diet of red kangaroos whereas sheep reduced their intake of perennial grasses in favour of browse. Similarly, near Alice Springs in central Australia, after good rainfall in December 1970, Low *et al.* (1973) observed that the diet of red kangaroos was mainly grasses whereas that of cattle was mainly browse. Red kangaroos almost immediately switched to grass after rain, whereas grass was not dominant in the diet of cattle until February 1971. It is likely that cattle could not efficiently harvest the newly grown grasses soon after rain when their height and biomass were low. In comparison, euros and eastern grey kangaroos are much more reluctant to switch to perennial forbs, and maintain diets that are predominantly perennial grasses.

As climatic conditions deteriorate further, and palatable perennial forbs are defoliated but dry perennial grass is still available, sheep and cattle will switch back to perennial grasses. Under these conditions, dry perennial grasses can dominate the diets of sheep, cattle and the four species of macropod (Squires 1980, 1982; Dawson and Ellis 1994, 1996; Edwards *et al.* 1995). However, cattle may consume more browse and less grass than sheep and the macropods (Chippendale 1962; Squires 1980, 1982; Downing 1986), and browse will be a large if not dominant component of the diet of feral goats (Wilson *et al.* 1975; Downing 1986).

During droughts, when the pasture layer has been exhausted, the diets of sheep, feral goats, cattle, red kangaroos and western grey kangaroos are comprised largely of less preferred chenopod and non-chenopod shrubs, browse from large shrubs and trees and dry materials lying on the ground (McMeniman *et al.* 1986; Harrington 1986a, 1986b; Barker

1987; Dawson 1989; Coates and Dixon 2007). In contrast, the diets of euros and eastern grey kangaroos remain dominated by the remnants of perennial grasses (Storr 1968; Griffiths *et al.* 1974; Dawson and Ellis 1996).

Where do they forage?

At bio-regional scales across the southern rangelands, the highest densities of macropods and feral goats tend to coincide with the highest densities of sheep and cattle (Storr 1968; Caughley *et al.* 1980; Short *et al.* 1983; Calaby and Grigg 1989; Cairns *et al.* 1991; Pople and Froese 2012; Department of Environment and Heritage Protection Queensland 2017). This is likely due to differences in the productivity or carrying capacity of bio-regions, with the more productive lands supporting larger numbers of herbivores (Jonzen *et al.* 2005). Additionally, it is due to changes associated with pastoral development including provision of permanent waters, control of wild dogs, tree-clearing and pasture improvement (Department of Environment and Heritage Protection 2013; Department of Environment and Heritage Protection Queensland 2017; Lavery *et al.* 2018). It may also indicate that these herbivores prefer similar environments. However, at a smaller scale, within paddocks, species of herbivore may graze or browse different areas due to differential preferences for forage species or vegetation structures, and constraints imposed by the distribution of water sources. Or, they may simply choose to avoid each other.

Sheep and cattle often prefer to graze in more open landscapes such as plains, clay-pans and lake-beds, particularly during plant growing seasons when ephemeral forbs and green grasses are readily available (Low *et al.* 1973; Dudzinski *et al.* 1982; Wilson and Harrington 1984; Terpstra and Wilson 1989). As grasses dry out and both quantity and quality decline, sheep and cattle venture into more wooded areas in search of browse and remaining grasses (Low *et al.* 1973; Dudzinski *et al.* 1982).

Feral goats eat more browse than sheep and macropods and prefer to forage in wooded landscapes (Landsberg and Stol 1996). Also, more densely timbered areas, especially rocky hills, provide feral goats with shelter and afford them protection from predators, such as wild dogs, and from mustering by pastoralists. When forage is plentiful, and when drinking water is nearby or the weather is cool, feral goats are likely to remain in densely timbered and hilly areas, and thus have distributions that overlap little with sheep or cattle. However, when forage supplies become scarce in the timbered and hilly landscapes, feral goats will move to parts of paddocks or to other paddocks which still contain forage. Like macropods, the dispersion of feral goats is generally not constrained by fences. Even so, as forage resources become increasingly limited in both quantity and dispersion, the foraging distributions of feral goats are likely to increasingly overlap with those of livestock (Landsberg and Stol 1996; Witte 2002).

The foraging distributions of macropods appear to follow a similar trend to that of feral goats. For example, eastern grey kangaroos prefer wooded landscapes, possibly because they are less visible to predators (Caughley 1964). They remain in wooded areas while pasture quantity and quality are adequate, but as conditions deteriorate, they forage in open areas where pasture is available (Hill 1982; Terpstra and Wilson 1989).

Similarly, western grey kangaroos prefer mixes of open and dense vegetation types, as these provide their requirements for both shelter and grazing (Short *et al.* 1983). For example, at Hattah-Kulkyne National Park in semiarid north-western Victoria, the foraging distribution of western grey kangaroos varied over time in response to changes in combinations of forage conditions and shelter provided by a range of vegetation types (Coulson 1993). Similarly, eastern grey kangaroos in poplar box-mulga woodlands in south-west Queensland preferred mixtures of vegetation offering high cover and high forage availability (Hill 1981; McAlpine *et al.* 1999). Even on a daily time scale, eastern greys, western greys and euros will shelter during the day in dense shrublands and woodlands which provide cover, then move to open vegetation at night where grasses and forbs are available (Terpstra and Wilson 1989; Coulson 1993; Arnold *et al.* 1994). However, these species are largely absent from large expanses of open vegetation (Terpstra and Wilson 1989; Arnold *et al.* 1995).

In contrast, Caughley (1964) found that the distribution of red kangaroos, unlike that of eastern greys, did not correlate with a visibility index, and Low *et al.* (1973) concluded that changes in the foraging distribution of red kangaroos were primarily influenced by pasture conditions. Similarly, McAlpine *et al.* (1999) concluded that it was forage quality and not tree cover which influenced the abundance of red kangaroos. However, several studies have observed that red kangaroos forage in woodlands after rainfall when forage quantity and quality are high, but as these deteriorate, they move into open areas (Newsome 1965a, 1965b; Low *et al.* 1973; Dudzinski *et al.* 1982). At the same locations, cattle foraged in open areas after rain and then moved into woodlands when pasture conditions deteriorated, the reverse of the response by red kangaroos (Low *et al.* 1973; Dudzinski *et al.* 1982).

Overall then, in relation to vegetation types, concurrent overlap in foraging distributions of sheep, cattle, feral goats and macropods is often small. However, over periods of several months to two or three years, as forage conditions invariably change from good to poor, overlap in foraging distributions is high and mostly sequential. The exception is large expanses of open vegetation which are highly acceptable to sheep and cattle, but which are largely avoided by macropods and feral goats.

The foraging distributions of livestock and macropods are also focussed, to varying degrees, around water points. Sheep, and to a lesser extent, cattle, appear to forage closer to water sources than do macropods. When it is hot and dry, sheep mostly graze within 1 km of waters (Squires 1974), and much of their time may be spent within 200 m of water (Andrew and Lange 1986). However, generally, sheep forage within 3 km of water (Wilson and Harrington 1984; James *et al.* 1999; Fensham and Fairfax 2008). Cattle may graze only 4 km from water in good seasons, but under drier conditions when forage supplies around waters are low, they will graze out to 10 km (James *et al.* 1999). After reviewing several studies, Fensham and Fairfax (2008) concluded that cattle mainly graze up to 6 km from water. However, given that the water requirements of cattle are around 50% higher than sheep when compared on a metabolic body-weight basis (Wilson and Graetz 1980; Wilson and Harrington 1984; Schlink *et al.* 2010), it is likely they will need to visit waters more often than sheep.

Using the same methodology, Fensham and Fairfax (2008) reported that red kangaroos generally graze within 7 km of water. In comparison, Lavery *et al.* (2018) found that the largest numbers of red kangaroos were observed within 2 km of water points in Idalia National Park and on a pastoral property in central western Queensland. However, the relationship between density and distance from water was not significant. Similarly, Fukuda *et al.* (2009) found that fencing off water points previously available to red kangaroos did not change their density and distribution during a drought.

Lavery *et al.* (2018) also found that the densities of euros were highest between 2 and 3 km from water. Euro densities were between 50 and 190/km² at distances of 2 to 3 km from artificial water points, and less than 50/km² closer to or further away from waters. Lavery *et al.* (2018) concluded that densities of red kangaroos and euros were not influenced by distance to water, but instead were dictated by pasture quality. This could be expected given that several studies have shown that macropods have much lower daily water requirements than livestock and hence do not show the same water-focussed grazing patterns as livestock (Dawson *et al.* 1975; Munn *et al.* 2013, 2014).

Similarly, in three conservation areas in the rangelands of north-western New South Wales, Russell *et al.* (2011) reported that the erection of goat-proof fences that forced red, eastern and western grey kangaroos and euros to travel more than 4 km to water did not change their grazing distributions during periods of below- and above-average rainfall.

In contrast to this, in the absence of livestock, Gibson (1994) and Gibson (1995) observed that eastern grey kangaroos, red kangaroos and euros appeared to spend more time much closer to water points within a National Park in south-west Queensland. Macropod faecal pellet density was highest at the bores, declined sharply out to 200 m and then remained constant with distance up to at least 1 km from the bore. In addition to this, Gibson (1994) tracked the movements of radio-collared red and eastern grey kangaroos at these bores. On average, eastern grey kangaroos travelled up to 2.25 km from one bore, and red kangaroos travelled up to 1.98 km from the same bore. At a second bore, red kangaroos travelled 2.39 km on average from the water point. Possibly, the absence of livestock and increased forage availability near water points made it more attractive for these macropods to remain closer to bores.

Only one study was found that reported the distances that feral goats graze from water. At two locations in the rangelands of north-western New South Wales, Russell *et al.* (2011) reported that goat activity was rarely observed more than 4 km from waters. Through the construction of goat-proof fences, these authors demonstrated that there was little goat activity at 3 km from waters, and virtually not activity further than 4 km from waters. However, given that feral goats have much lower daily water requirements than sheep (Dawson *et al.* 1975; Munn *et al.* 2012) and thus need to drink less frequently, it is likely they are able to forage further from water than sheep.

In relation to foraging distributions around water points, those of sheep are likely to be more constrained than those of cattle, macropods and feral goats. Hence, sheep mainly forage within 2–3 km of waters, resulting in high pasture utilisation rates in these parts of paddocks. Cattle regularly forage at distances up to 6 km from water, and hence biosphere effects

extend much further into paddocks. The foraging distributions of macropods, and to a lesser extent feral goats, with their much lower water requirements and ability to pass through fences, are less constrained by water points. Consequently, they are able to access parts of paddocks least utilised by livestock, where forage quantity and quality are higher. This is possibly the reason why Lavery *et al.* (2018) observed the highest densities of euros and red kangaroos at distances of between 2 and 3 km from waters. This is consistent with several studies that have recorded concentrations of macropods on areas from which sheep have been excluded (Andrew and Lange 1986; Watson *et al.* 1988; Terpstra and Wilson 1989; Norbury and Norbury 1993; Edwards *et al.* 1996).

Conclusions – equivalency in what and where they eat

Based on the preceding discussion, the following conclusions may be drawn regarding overlap in the use of the broad forage groups by herbivores in the southern rangelands.

- When annual grasses, ephemeral forbs and green perennial grasses are abundant, overlap in their use by sheep, cattle, feral goats and the four species of macropod is concurrent and high.
- Overlap in the use of dry perennial grasses by sheep, cattle and the four species of macropod is high and mostly sequential. Overlap between these herbivores and feral goats is sequential and low.
- Overlap in the use of chenopod and non-chenopod perennial forbs by sheep, cattle, feral goats and red and western grey kangaroos is sequential and moderately high. Overlap between these herbivores and euros and eastern grey kangaroos is sequential and low.
- Overlap in the use of browse by sheep, goats and cattle is sequential and high. Overlap between these herbivores and red kangaroos and western grey kangaroos is sequential and low, and very low for eastern grey kangaroos and euros.

Concurrent overlap in the foraging distributions of sheep, cattle, feral goats and the macropods is often small. However, over periods of several months to a few years, as climatic conditions change, overlap in foraging distributions is high and mostly sequential. This tends to occur where there are mosaics of vegetation types that vary substantially in their shrub and tree cover. This is not the case in large expanses of open vegetation which are highly acceptable to sheep and cattle, but which are mostly avoided by macropods and feral goats.

Although equivalency in what and where these herbivores eat is not quantifiable, it appears to be high overall. This is particularly so for perennial grass, which is the dominant forage for herbivores in the southern rangelands.

Conflicts of interest

The author declares no conflict of interest.

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