

# Macropods, feral goats, sheep and cattle. 1. Equivalency in how much they eat

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**Abstract.** The extent to which goats and cattle eat equivalent amounts of forage as sheep has been based on their maintenance energy requirements (MERs) relative to a 50 kg wether or dry ewe, known as a dry sheep equivalent (DSE). As such, a 50 kg goat was considered 1 DSE and a 450 kg steer as 7–8 DSE. In comparison, the DSE of macropods has been based on their basal metabolic rate (BMR) or energy expenditure of grazing ( $EE_g$ ) relative to those of sheep, with a 50 kg macropod thought to be 0.7 and 0.45 DSE respectively. Based on published energy requirements of goats, macropods and cattle relative to sheep, their DSE values are estimated to be 1.2, 1.0 and 7.6 respectively. However, relative energy requirements may not be the same as relative dry matter intakes (DMIs), due to differences in forage quality, the structure of digestive tracts and selective foraging capabilities. Allometric equations that predict DMI were developed from published liveweights and intakes of sheep, goats, macropods and cattle. Given DMIs when fed high-quality forage, a 50 kg goat was 1 DSE, a 50 kg macropod was 0.7 DSE and a 450 kg steer was 7.6 DSE. Their DMIs were depressed by 35–50% when fed low-quality forage, but a goat remained as 1 DSE, macropods increased to 1.0 DSE and cattle increased to 8.3 DSE. The capacity of macropods to maintain relatively higher DMIs of low-quality forage than sheep is probably due to their faster digesta passage rates and more expandable stomachs. These DMIs of animals provided ad-libitum quantities of similar forages in small pens are likely to differ from their DMIs when selectively grazing heterogeneous rangeland pastures. Under these conditions, sheep select higher-quality diets than cattle, and kangaroos select higher-quality diets than sheep, which increase the relative DMIs of the smaller herbivores. For this reason, a 50 kg macropod is likely to be 1 DSE and consume twice as much forage than previously assumed.

**Additional keywords:** allometric equations, diet quality, energy requirements, intake.

Received 4 July 2019, accepted 3 December 2019, published online 11 February 2020

## Introduction

Rangelands worldwide have been degraded through over-grazing by livestock and feral and native herbivores (Pickup *et al.* 1998; Tongway *et al.* 2003; McKeon *et al.* 2004; Han *et al.* 2008). The extent that macropods, the major native herbivores of the Australian rangelands, contribute to overgrazing and compete with sheep and cattle has been contested. Some authors believe this to be substantial (Wilson 1991; Norbury *et al.* 1993), whereas others propose it to be much less (Olsen and Braysher 2000; Grigg 2002; Olsen and Low 2006; Munn *et al.* 2009, 2010).

Sustainable use of rangelands requires that pastoralists budget the supply of pasture with the demand for forage of their livestock (Pahl *et al.* 2016; Stocktake 2017). In the Mitchell grasslands of south western Queensland, it is recommended that pastoralists estimate the amount of forage present at the beginning of the dry season then adjust numbers of livestock so that no more than 30% of that pasture is consumed over the following 12 months (Orr *et al.* 1993; Orr and Phelps 2013). Similar approaches are appropriate for non-seasonal or winter-dominant rainfall regions. In doing this, pastoralists tally their numbers of different classes

of livestock (e.g. weaners, dry cows, pregnant and lactating cows) and convert these to a total number of livestock units. These units tend to be a dry sheep equivalent (DSE) on sheep properties and an adult equivalent (AE) on cattle properties (Turner and Alcock 2000; McLean and Blakeley 2014). However, properties often run a combination of sheep and cattle, in which case AEs are converted to DSEs. Each animal unit requires a certain amount of forage daily to satisfy its maintenance energy requirements (Lambourne and Reardon 1963; McLennan 2015). In estimating livestock demand for forage, the total livestock units are multiplied by the amount of forage required daily, and then by the number of days of the forage budgeting period.

In undertaking a forage budget, pastoralists need to take into account the numbers of macropods and feral goats present, as on occasions these animals can be equally or more numerous than livestock (Bayliss 1985; Turner and Neagle 1997; Thompson *et al.* 2002; Jonzen *et al.* 2005; Hacker 2011). Although the exact number of these herbivores will be unknown, they also need to be converted to equivalent animal units. As has been the tradition for sheep and cattle, the extent that macropods and goats substitute

**Table 1. Frequently used terms and their acronyms and units**

Term	Acronym	Units
Adult equivalent	AE	450 kg steer/dry cow maintaining weight
Basal metabolic rate	BMR	kJ/kg <sup>0.75</sup> /day
Dry matter intake	DMI	kg dry matter/day
Dry sheep equivalent	DSE	50 kg wether/dry sheep maintaining weight
Energy expenditure of grazing	EE <sub>g</sub>	kJ/kg <sup>0.75</sup> /day
Field metabolic rate	FMR	kJ/kg <sup>0.75</sup> /day
Liveweight	LW	Total bodyweight of a living animal (kg)
Maintenance energy requirement	MER	kJ metabolisable energy/kg <sup>0.75</sup> /day
Mean retention time	MRT	hours
Neutral detergent fibre	NDF	g NDF/kg dry matter

for livestock has been based on their relative energy requirements (Dawson and Hulbert 1970; Munn *et al.* 2009; Smith *et al.* 2012). A 50 kg goat is accepted as 1 DSE (Partridge 1996; Milliar *et al.* 2003; Smith *et al.* 2012), but a range of DSE ratings have been proposed for macropods. Previously, based on the lower basal metabolic rates of marsupials compared with eutherian mammals (Dawson and Hulbert 1970), a kangaroo was rated as 0.7 DSE (Linton and Greenfield 1999; Gutteridge *et al.* 2001; Thompson *et al.* 2002; Fensham and Fairfax 2008; Russell 2009; Smith *et al.* 2012; Gordon *et al.* 2017). However, comparisons of the energy expenditure of sheep and kangaroos while grazing yielded a much lower rating of 0.45 DSE (Munn *et al.* 2009, 2013a, 2016a). Given that Grigg (2002), Munn *et al.* (2013a) and Munn *et al.* (2016a) propose to use energy requirements of macropods as an index of their forage requirements, using a DSE rating of 0.45 would substantially reduce their contribution to total grazing pressure (TGP) and their potential to decrease whole-property livestock productivity. However, energy requirements are not always synonymous with forage intake (Scarnecchia 1986), and as TGP is a ratio of forage intake to forage supply (The Forage and Grazing Terminology Committee 1992; Fisher *et al.* 2004; Allen *et al.* 2011), dry matter intake is a more appropriate measure of a herbivore's contribution to TGP. The purpose of this review is to determine the extent that sheep, goats, cattle and macropods are equivalent with regard to the amount of forage they consume daily. Another paper in this special issue, (Pahl 2019), examines equivalency with regard to what these species eat and where they eat it.

#### *Herbivore equivalents according to energy requirements*

The energy requirements of sheep (*Ovis aries*), goats (*Capra hircus*), macropods and cattle (*Bos taurus* and *B. indicus*) have traditionally been used to determine the extent they substitute for each other on grazing properties. Maintenance energy requirements (MERs) are commonly used for comparing the ruminants, where the common unit is a DSE. Less is known about the MERs of macropods, hence estimates of their DSE have been based on their basal metabolic rates (BMRs) and field metabolic rates (FMRs) relative to sheep. Field metabolic rate is commonly used in wildlife research publications to mean the energy expenditure of animals while grazing for short periods of time in paddocks of varying size. In the present paper, the energy expended while grazing is represented as EE<sub>g</sub>, which is substituted for FMR throughout. The acronyms and units of these and other terms frequently used in this paper are provided in Table 1.

#### *Energy requirements of sheep*

A DSE has been defined as a two-year old 50 kg wether or dry adult female, maintained at a constant liveweight (LW) (Turner and Alcock 2000; Making More from Sheep 2008; Bastin 2012; Evergraze 2013; NSW Department of Primary Industries 2015). However, less commonly, a DSE has been defined as a two-year-old 45 kg wether at maintenance (McLean and Blakeley 2014; Agriculture Victoria 2017). Given that Bastin (2012) reported the Australian Collaborative Rangelands Information System (ACRIS) used a 50 kg wether at maintenance as their DSE, and that in all pastoral bioregions numbers of livestock of various types and classes were converted to this unit of DSE, a 50 kg wether at maintenance is used as a DSE in this paper.

The BMR is the rate of energy expenditure of an inactive, post-absorptive (post-digestion), non-reproductive adult animal regulating its body temperature in its thermo-neutral zone, during its inactive circadian phase (McNab 1997). Published BMRs of adult Merino sheep accessed using Google Scholar ranged from 212 to 264 kJ/kg<sup>0.75</sup>/day for 11 studies reported in Marston (1948), Blaxter (1962), Langlands *et al.* (1963) and Shinde and Karim (2007). The mean BMR was 239 kJ/kg<sup>0.75</sup>/day.

The MERs of adult sheep are higher than BMRs due to the metabolisable energy requirements of ingestion, digestion, maintenance of LW and limited movement when confined. Thirteen published MERs of Merino sheep range from 285 to 388 kJ/kg<sup>0.75</sup>/day (Young and Corbett 1969; Young and Corbett 1972; Shinde and Karim 2007; Making More from Sheep 2008; Lifetimewool 2011; Bown *et al.* 2013). The average MER of Merino sheep for these studies is 345 kJ/kg<sup>0.75</sup>/day. The range in reported MERs is large and likely due to variation between studies in the physiological state of animals, the methods used and the quality of diets (Luo *et al.* 2004; Salah *et al.* 2014; Brassard *et al.* 2016).

A number of authors have also reported the EE<sub>g</sub>s of Merino sheep that were free to roam for several days in paddocks of various sizes. The EE<sub>g</sub>s reported for Merino sheep range from 363 to 598 kJ/kg<sup>0.75</sup>/day (Young and Corbett 1969; Young and Corbett 1972; Shinde and Karim 2007; Making More from Sheep 2008; Lodge 2011). The mean EE<sub>g</sub> of these studies is 495 kJ/kg<sup>0.75</sup>/day. In these individual studies, EE<sub>g</sub>s were 21–64% greater than the MERs of the same sheep. Other studies have also reported EE<sub>g</sub>s in excess of MERs, by 11–77% (Coop and Hill 1962; Lambourne and Reardon 1963; Blaxter 1967; Langlands *et al.* 1963; Osuji 1974). This wide variation in EE<sub>g</sub>s

recorded for grazing sheep is largely due to differences in levels of activity, and particularly the distances and elevations walked by sheep daily (Graham 1964; Wallach *et al.* 1984). However, most studies do not report activity levels, hence, the energetic costs of varying levels of activity are generally unavailable. Exceptions are Wallach *et al.* (1984) who reported the energy requirement of ewes walking 4.2 km and climbing 30 m daily to be 32% above their MER, and SCA (1990) which reported the energy expenditure of sheep walking 5 km and climbing 200 m daily to be 35–40% greater than their MER.

In comparison to the  $EE_g$ s of 363–598 kJ/kg<sup>0.75</sup>/day for Merino sheep reported above, considerably higher  $EE_g$ s were recorded for Merino sheep at Fowlers Gap in south western New South Wales. These were 884 kJ/kg<sup>0.75</sup>/day for sheep in a 16 ha enclosure (Munn *et al.* 2009), 858 kJ/kg<sup>0.75</sup>/day for sheep walking 7.9 km/day in a 560 ha paddock (Munn *et al.* 2013a), and 1126 kJ/kg<sup>0.75</sup>/day for sheep walking 4.3 km/day in a 16 ha enclosure (Munn *et al.* 2016a). The  $EE_g$ s for Merino sheep recorded in these three studies were 156, 149 and 226%, respectively, above the average MER of 345 kJ/kg<sup>0.75</sup>/day for Merino sheep reported above. The very high  $EE_g$ s recorded in these three studies are questionable, given SCA (1990) stated it is not possible to have  $EE_g$ s that are 2- to 3-fold higher than MERs. Also, they are much higher than the  $EE_g$ s of grazing Merino sheep recorded in other studies. Furthermore, these  $EE_g$ s contrast with a much lower  $EE_g$  of 461 kJ/kg<sup>0.75</sup>/day for Merino sheep in a 0.5 ha enclosure at Fowlers Gap recorded by Munn *et al.* (2016b).

#### Energy requirements of cattle

An AE has been defined by McLean and Blakeley (2014) as a 450 kg *B. taurus* steer of 2.25 years of age and maintaining liveweight (LW). Although there is variation within the literature as to the number of DSE that equal an AE, it is generally accepted that 1 AE equals 7–8 DSE (Partridge 1996; Milllear *et al.* 2003; Jonzen *et al.* 2005; NSW Department of Primary Industries 2006; Bastin 2008; Fensham and Fairfax 2008; Graham 2017). Six publications provided 15 estimates of the BMRs of cattle (Forbes *et al.* 1926; Blaxter and Wainman 1966; Vercoe 1970; Thonney *et al.* 1976; Hunter and Vercoe 1987; Yan *et al.* 1997). These BMRs ranged from 303 to 430 kJ/kg<sup>0.75</sup>/day, with a mean of 353 kJ/kg<sup>0.75</sup>/day.

Several authors provided 11 MERs of cattle (Patle and Mudgal 1975; Ferrell and Jenkins 1984; Castro Bulle *et al.* 2007; Chaokaur *et al.* 2015; McLennan 2015). These values range from 427 to 544 kJ/kg<sup>0.75</sup>/day, with a mean MER of 472 kJ/kg<sup>0.75</sup>/day.

When the demands of walking 7 km each day are added, McLennan (2015) determined that the  $EE_g$  of steers is 723 kJ/kg<sup>0.75</sup>/day, which was an increase of 33% above the MERs of these animals. In other studies, Havstad and Malechek (1982) reported that the  $EE_g$  of grazing cattle was 46% above their MER, Di Marco and Aello (2001) reported  $EE_g$ s of 16 to 52% above MERs, and Lachica and Aguilera (2003) reported studies which had found  $EE_g$ s to be 54, 74 and up to 107% greater than MERs. Based on an average increase of 55% above the mean MER of 493 kJ/kg<sup>0.75</sup>/day, the mean  $EE_g$  for cattle is 764 kJ/kg<sup>0.75</sup>/day.

#### Energy requirements of goats

The energy demands of goats have also been expressed in DSEs, where they are thought to be similar to sheep (Landsberg and

Stol 1996; Partridge 1996; Milllear *et al.* 2003; Smith *et al.* 2012). The BMRs reported by 17 studies for goats range from 236 to 386 kJ/kg<sup>0.75</sup>/day (Armstrong and Blaxter 1965; Prieto *et al.* 1990; Luo *et al.* 2004; Shinde and Karim 2007), with an average of 315 kJ/kg<sup>0.75</sup>/day.

Eight measurements of MERs for goats reported in the literature range from 385 to 443 kJ/kg<sup>0.75</sup>/day, with an average of 414 kJ/kg<sup>0.75</sup>/day (Oliveira 1987; Aguilera *et al.* 1990; Prieto *et al.* 1990; Lachica and Aguilera 2003; Luo *et al.* 2004; Shinde and Karim 2007; Brassard *et al.* 2016).

The  $EE_g$ s recorded for goats range from 490 to 693 kJ/kg<sup>0.75</sup>/day (Oliveira 1987; Herselman *et al.* 1999; Lachica *et al.* 1999; Lachica and Aguilera 2003; Shinde and Karim 2007), with an average of 554 kJ/kg<sup>0.75</sup>/day. These authors reported that these  $EE_g$ s were 32–68% higher than their associated MERs. For example, the  $EE_g$ s of goats walking between six and 15 km and climbing between 400 and 600 m daily were between 32 and 47% above their MERs. In relation to the energy requirements associated with grazing, Lachica *et al.* (1999) noted that the National Research Council (1981) recommended an increase of 25% above MER when activity was light, 50% in slightly hilly semiarid rangelands, and 75% in mountainous areas or when travelling long distances in sparse vegetation.

#### Energy requirements of macropods

The energy requirements of macropods are less studied than livestock. The BMRs of marsupials are known to be, on average, around 70% those of an equivalent-sized eutherian mammal (Dawson and Hulbert 1970; Nagy 1987). Consequently, the energy requirements of macropods have been assumed to be between 0.6 and 0.8 of a DSE, regardless of species or LW (Landsberg and Stol 1996; Partridge 1996; Linton and Greenfield 1999; Gutteridge *et al.* 2001; Thompson *et al.* 2002; Fensham and Fairfax 2008; Russell 2009; Smith *et al.* 2012; Gordon *et al.* 2017). However, when individual species were examined, Dawson and Hulbert (1970) reported a BMR of 197 kJ/kg<sup>0.75</sup>/day for red kangaroos (*Osphranter rufus*), and Dawson *et al.* (2000) reported BMRs of 209 kJ/kg<sup>0.75</sup>/day for red kangaroos and 234 kJ/kg<sup>0.75</sup>/day for eastern grey kangaroos (*Macropus giganteus*). The mean BMR of these is 213 kJ/kg<sup>0.75</sup>/day.

Similarly, Dawson and Munn (2007) noted that only three studies had recorded the MERs of macropods. These were 385 kJ/kg<sup>0.75</sup>/day for an adult female red kangaroo (Munn and Dawson 2003) and 387 kJ/kg<sup>0.75</sup>/day for an adult male red kangaroo (McIntosh 1966), and 456 and 412 kJ/kg<sup>0.75</sup>/day for red kangaroos and euros (*Macropus robustus erubescens*) respectively (Hume 1974). The average MER over all these measurements for red kangaroos and euros is 411 kJ/kg<sup>0.75</sup>/day. It is noted that Hume (1974), at the same time as he measured the MERs of red kangaroos and euros, recorded a MER of 569 kJ/kg<sup>0.75</sup>/day for Merino sheep, considerably above the average of 345 kJ/kg<sup>0.75</sup>/day noted above.

Also, only a small number of studies have recorded the  $EE_g$ s of macropods, although they were reported as FMRs. The  $EE_g$ s were 474 and 531 kJ/kg<sup>0.75</sup>/day for two eastern grey kangaroos (Nagy 1987), 478 kJ/kg<sup>0.75</sup>/day for eastern grey kangaroos in a small enclosure in Melbourne (Nagy *et al.* 1990), 455 kJ/kg<sup>0.75</sup>/day for red kangaroos in a 16 ha enclosure at Fowlers Gap (Munn *et al.* 2009), 413 kJ/kg<sup>0.75</sup>/day for red kangaroos hopping 3.6 km/day in

**Table 2.** Mean basal metabolic rate (BMR), maintenance energy requirement (MER) and energy expenditure while grazing (EE<sub>g</sub>) of sheep, goats, cattle and macropods

Figures in brackets are the ratios of the energy requirements of a species relative to that of sheep. Columns two to four show the mean BMR, MER and EE<sub>g</sub> derived from the studies referenced in the sections above on energy requirements of sheep, cattle, goats and macropods. Column five shows mean EE<sub>g</sub>s at Fowlers Gap of sheep and macropods from three studies (Munn *et al.* 2009, 2013a, 2016b), which do not contribute to the means in column four

Species	BMR	MER (kJ/kg <sup>0.75</sup> /day)	EE <sub>g</sub>	EE <sub>g</sub> Fowlers Gap
Merino sheep	239	345	495	956
Goat	315 (1.32)	414 (1.20)	554 (1.12)	–
Cattle	353 (1.48)	472 (1.37)	764 (1.54)	–
Macropods	213 (0.89)	411 (1.19)	494 (1.00)	473 (0.49)

a large paddock at Fowlers Gap (Munn *et al.* 2013a), and 765 kJ/kg<sup>0.75</sup>/day for western grey kangaroos (*Macropus fuliginosus*) hopping 2 to 4 km/day in a 16 ha enclosure at Fowlers Gap (Munn *et al.* 2016a). However, when Munn *et al.* (2016a) excluded three western grey kangaroos which hopped around 3.5 km/day due to repetitive movements along fence lines, they reported a lower average EE<sub>g</sub> of 552 kJ/kg<sup>0.75</sup>/day. The mean EE<sub>g</sub> for the three eastern grey kangaroos measured by Nagy (1987) and Nagy *et al.* (1990) is 494 kJ/kg<sup>0.75</sup>/day, and the mean EE<sub>g</sub> for the red and western grey kangaroos recorded by Munn *et al.* (2009), Munn *et al.* (2013a) and Munn *et al.* (2016a) is 473 kJ/kg<sup>0.75</sup>/day. These individual EE<sub>g</sub>s were 1–34% higher than the mean MER of red kangaroos and euros of 411 kJ/kg<sup>0.75</sup>/day.

#### Equivalency based on energy requirements

The mean BMRs, MERs and EE<sub>g</sub>s in kJ/kg<sup>0.75</sup>/day for sheep, goats, cattle and macropods are presented in Table 2. Based on the means from numerous studies, the BMR of goats, cattle and macropods, respectively, are 1.32, 1.48 and 0.89 that of Merino sheep. Hence, a 50 kg goat is 1.3 DSE, a 450 kg steer is 7.7 DSE, and a 50 kg macropod is 0.9 DSE. When mean MERs are compared, goats are 1.20, cattle are 1.37 and macropods are 1.19 that of Merino sheep. Based on MERs, a 50 kg goat is 1.2 DSE, a 450 kg steer is 7.1 DSE, and a 50 kg macropod is 1.2 DSE. Although this DSE of 1.2 or 1.3 for goats is higher than the generally accepted value of 1 DSE (Partridge 1996; Millier *et al.* 2003; Smith *et al.* 2012), a number of authors have reported that goats have higher MERs and EE<sub>g</sub>s than sheep (Mohammed and Owen 1982; Oliveira 1987; AFRC 1998; National Research Council 2007; Shinde and Karim 2007). Similarly, the DSE of 0.9 or 1.2 for macropods is considerably higher than previously published values of between 0.6 and 0.8 (Linton and Greenfield 1999; Gutteridge *et al.* 2001; Thompson *et al.* 2002; Fensham and Fairfax 2008; Russell 2009; Smith *et al.* 2012; Gordon *et al.* 2017). In comparison, the DSE of 7.7 or 7.1 for a 450 kg steer is similar to published values of 7–8 DSE (Partridge 1996; Millier *et al.* 2003; Jonzen *et al.* 2005; NSW Department of Primary Industries 2006; Bastin 2008; Fensham and Fairfax 2008; Graham 2017).

In relation to mean EE<sub>g</sub>s, goats were 1.12, cattle were 1.54 and macropods were 1.00 that of Merino sheep (Table 2). As such, a 50 kg goat is 1.1 DSE, a 450 kg steer is 8.0 DSE, and a 50 kg macropod is 1.0 DSE. These DSE ratings are similar to

those based on BMRs and MERs, even though recorded EE<sub>g</sub>s are likely to be more variable due to substantial differences in the horizontal and vertical distances traversed daily by animals in individual studies. Even when studies provide distances traversed, it is unknown whether these are typical of the species studied. For example, Munn *et al.* (2009) compared the EE<sub>g</sub>s of red kangaroos and sheep in a 16 ha enclosure at Fowlers Gap but did not report activity levels. In comparison, when Munn *et al.* (2013a) compared the EE<sub>g</sub>s of red kangaroos and sheep in a large paddock at Fowlers Gap, sheep walked 7.9 km daily and red kangaroos hopped 3.6 km daily. Similarly, when Munn *et al.* (2016a) compared EE<sub>g</sub>s of sheep and western grey kangaroos in a 16 ha enclosure, sheep walked 4.3 km daily and the western greys hopped 2.4 km daily (after excluding grey kangaroos exhibiting abnormally high levels of movement).

Although these EE<sub>g</sub>s suggest a DSE rating of 1 for macropods, a much smaller DSE for macropods was obtained by comparing the EE<sub>g</sub>s of Merino sheep and kangaroos recorded at the same time at Fowlers Gap (Table 2). This was due to the very high EE<sub>g</sub>s of Merino sheep of 884, 858 and 1126 kJ/kg<sup>0.75</sup>/day recorded by Munn *et al.* (2009), Munn *et al.* (2013a) and Munn *et al.* (2016a) respectively. Relative to the mean EE<sub>g</sub> of 956 kJ/kg<sup>0.75</sup>/day of sheep in these three studies, the EE<sub>g</sub> of macropods is 0.49 that of Merino sheep. However, instead of scaling the EE<sub>g</sub>s of both kangaroos and sheep with LW<sup>0.75</sup>, as is traditionally used, these authors used LW<sup>0.60</sup> for kangaroos and LW<sup>0.73</sup> for sheep, following the findings of Nagy (1994), Capellini *et al.* (2010) and Munn *et al.* (2013b). Based on these energetic scaling exponents, the EE<sub>g</sub> of macropods was 0.45 that of sheep. The EE<sub>g</sub>s of Merino sheep at Fowlers Gap were much higher than those recorded by other studies, including the EE<sub>g</sub> of 461 kJ/kg<sup>0.75</sup>/day recorded by Munn *et al.* (2016b) for Merino sheep in a 0.5 ha enclosure at the same location, but the results were similar to those predicted by other authors. For example, Nagy (1987) developed allometric equations to show that the ratio of marsupial to eutherian EE<sub>g</sub> was 0.44. Similarly, Fanning and Dawson (1989), presumably using the same equations, obtained a ratio of 0.45

Munn *et al.* (2009), Munn *et al.* (2013a) and Munn *et al.* (2016a) found the EE<sub>g</sub>s of kangaroos to be 0.45 those of sheep. These and other authors (Grigg 2002; Ampt and Baumber 2006; Olsen and Low 2006; Dawson and Munn 2007) have proposed that a kangaroo DSE is much less than the traditionally accepted 0.7. For example, Grigg (2002) suggested that a DSE rating for a typical macropod in harvested populations could be as low as

0.15, taking into account their lower  $EE_g$  compared with sheep and their lower average LW of 16–19 kg compared with 45 kg for sheep.

The DSE ratings reported above based on the various energy requirements of sheep, goats cattle and macropods have been proposed as an index of their forage requirements and hence their contribution to TGP (Grigg 2002; Munn *et al.* 2009, 2012). This assumes that the energy requirement of herbivores is the primary determinant of their daily intake of forage (Nagy 1987; Hume 1999). However, the amount of forage consumed daily can vary substantially with differences in diet quality (Edouard *et al.* 2008; Meyer *et al.* 2010), diet selectivity (Clauss *et al.* 2013; Müller *et al.* 2013) and the structure of the digestive tract (Clauss *et al.* 2007a; Müller *et al.* 2013).

*Herbivore equivalents according to dry matter intakes*

This paper compares the daily forage intakes of sheep, goats, cattle and macropods in two ways. The first is based on nine publications that recorded the intakes of sheep and macropods during the same feeding trials, using exactly the same high-quality lucerne and low-quality cereal straw forages. The second is based on a large number of publications which mostly recorded intakes of a single species. Hence, there was more variation in the types of high- and low-quality forages fed to animals.

*Comparison of intakes when the same forage was fed to sheep and macropods*

Nine publications reported LWs and intakes of sheep and macropods when fed the same lucerne chaff or hay (Table 3). These macropods were the red kangaroo, eastern grey kangaroo, euro and wallaroo (*Macropus robustus robustus*). Of these nine studies, four also recorded intakes when animals were fed the same cereal straw. In most cases, the authors reported intakes in kg dry matter per kg of LW per day (kg/kg LW/day) and kg dry matter per kg of metabolic LW per day (kg/kg  $LW^{0.75}$ /day). For each of these studies, the intakes of macropods were divided by the intakes of sheep fed the same lucerne or straw diets (Table 3). This provided a ratio of macropod intake to sheep intake, which was then used as a macropod DSE.

On average, on a kg/kg LW/day basis, macropods consumed 0.89 of the same lucerne diet as sheep, and 1.14 of the same straw forage as sheep. On a kg/kg  $LW^{0.75}$ /day basis, macropods consumed 0.76 of the same lucerne forage as sheep, and 0.96 of the same straw forage as sheep. This indicates a macropod is 0.76 of a DSE when fed a high-quality forage such as lucerne, and 0.96 of a DSE when fed poor quality forage such as straw. However, the ratios of macropod to sheep intakes across studies varied from 0.57 to 0.99 when fed lucerne, and from 0.55 to 1.53 when fed straw. This is likely due to differences in the LWs and levels of maturity of macropods and sheep used in these studies, as well as differences in the composition of forages and in the responses of small numbers of animals to experimental conditions and treatments.

*Scaling of intake with liveweight*

The studies referenced in Table 3 assumed that the scaling of intake with  $LW^{0.75}$  accounted for declines in mass-specific dry matter intake as LW increases, as is the case for energy requirements. This is consistent with the observations of

**Table 3. Ratios of the daily dry matter intakes of lucerne and straw by macropods relative to sheep, in kg/kg LW/day and in kg/kg  $LW^{0.75}$ /day, as recorded during nine studies**  
LW = liveweight

Species	Ratio of macropods : sheep		Reference
	(kg/kg LW/day)	(kg/kg $LW^{0.75}$ /day)	
<i>Lucerne</i>			
Red kangaroo	1.12	0.83	Foot and Romberg (1965)
Red kangaroo	0.58	0.59	McIntosh (1966)
Red kangaroo	0.90	0.87	Griffiths and Barker (1966)
Eastern grey	0.83	0.74	Griffiths and Barker (1966)
Red kangaroo	1.16	0.95	Forbes and Tribe (1970)
Eastern grey	0.84	0.69	Forbes and Tribe (1970)
Eastern grey	1.09	0.99	Kempton <i>et al.</i> (1976)
Eastern grey	1.15	0.93	Dellow and Hume (1982)
Red kangaroo	0.64	0.58	Hume (1974)
Euro	0.63	0.57	Hume (1974)
Euro	0.81	0.62	Dellow (1982)
Eastern grey	1.01	0.81	Dellow (1982)
Wallaroo	0.86	0.73	Hume (1984)
Mean of ratios	0.89	0.76	
<i>Straw</i>			
Red kangaroo	1.79	1.37	Foot and Romberg (1965)
Red kangaroo	0.84	0.71	Forbes and Tribe (1970)
Eastern grey	1.00	0.87	Forbes and Tribe (1970)
Red kangaroo	0.59	0.55	Hume (1974)
Euro	0.77	0.71	Hume (1974)
Wallaroo	1.82	1.53	Hume (1984)
Mean of ratios	1.14	0.96	

Meissner and Paulsmeier (1995) and Müller *et al.* (2013), who both noted that metabolic LW (i.e.  $LW^{0.75}$ ) is often used to compare intakes of species, where it is assumed that intake is driven by energy demand. In support of this, analyses of a number of empirical datasets containing large numbers of herbivorous species with several-fold differences in LWs, showed that intake scaled with LW according to  $LW^{0.75}$  (Shipley *et al.* 1994; Clauss *et al.* 2007b; Meyer *et al.* 2010; Müller *et al.* 2013).

However, Müller *et al.* (2013) observed that the scaling of intake with LW varied with gut architecture. Intake of hindgut-fermenting herbivores (e.g. horses) scaled with  $LW^{0.85-0.91}$ , non-ruminant foregut fermenters (e.g. macropods) scaled with  $LW^{0.76-0.81}$ , and ruminants (e.g. sheep, cattle) scaled with  $LW^{0.75-0.77}$ . Ruminants, due to selective retention of large fibrous particles in the forestomach, tend to have longer mean retention times (MRTs) than hind-gut and non-ruminant foregut fermenters (Demment and Van Soest 1985). Clauss and Hummel (2005) noted that large particles which increase MRTs can substantially limit intake, and most herbivores, with the exception of ruminants, selectively expel large particles from their gut. Foose (1982) and Steuer *et al.* (2011) observed that ruminants on average had MRTs, which were 1.5- to 1.6-fold longer than

hindgut fermenters, which resulted in DMIs of hindgut fermenters being around 1.6-fold higher than those of ruminants.

Müller *et al.* (2013) also found that intake scaling exponents varied with mature LW. Intake scaled with  $LW^{0.62-0.72}$  for species which weighed <10 kg, and  $LW^{0.84-0.89}$  for species weighing >10 kg. Clauss *et al.* (2013) and Riaz *et al.* (2014) also reported higher scaling exponents for intake of larger compared with smaller species. For example, Riaz *et al.* (2014) found that the intakes of sheep and goats scaled with  $LW^{0.64-0.71}$  while intakes of cattle and buffalo scaled with  $LW^{0.82-0.88}$ . Additionally, it appears that within species, young growing animals have lower scaling exponents than larger mature animals (Graham *et al.* 1974; Forbes 2007; Almeida *et al.* 2019).

Evidence that intake scales more highly with LW than energy requirement (for which the usual scaling exponent is 0.75) is provided by a number of authors. Meyer *et al.* (2010) reported that the intakes of 84 species of mammalian herbivore scaled with  $LW^{0.78}$ , and Bourlière (1975) found that intakes of 12 species of herbivore scaled to  $LW^{0.84}$ . Likewise, Meissner and Paulsmeier (1995), who compared the intakes of seven species of domestic and wild ruminants, found that intakes scaled to  $LW^{0.89}$ . Müller *et al.* (2013) also reported that several authors had found a scaling exponent of 0.9 was appropriate for domestic and wild ruminants (Minson 1990; Reid *et al.* 1990; Hackmann and Spain 2010), and an exponent of 1.0 has been used to compare intakes of sheep and cattle in North America (Riaz *et al.* 2014). According to Riaz *et al.* (2014), it was Graham (1972) who first proposed the use of 0.90 as a scaling exponent for comparisons of intakes of sheep and cattle. Subsequently, a number of authors have scaled intakes of sheep and cattle to  $LW^{0.9}$  (Bird 1974; Playne 1978; Poppi *et al.* 1981a). Munn *et al.* (2015) used a scaling exponent of 0.85 for sheep, which is close to the average of the scaling exponents provided by the studies above.

Meissner and Paulsmeier (1995) argued that the scaling of intake with LW also varied with differences in forage quality. They explained that intake of low-quality forage is controlled more by the capacity and characteristics of the gut, whereas intake of high-quality forage is controlled more by physiological mechanisms such as energy requirements. The same conclusions were reached by Fonseca *et al.* (1998), Lu *et al.* (2005), Hackmann and Spain (2010) and Müller *et al.* (2013). Given that gut capacity scales with  $LW^{0.9-1.0}$  (Demment and Van Soest 1985; Müller *et al.* 2013), Meissner and Paulsmeier (1995) concluded that, depending on forage quality, the exponent used to scale intake with LW could range between 0.75 and 1.0.

Meissner and Paulsmeier (1995) also proposed that exponents for scaling of intake with LW varied not only with forage quality but also with the age, LW, sex and physiological state of animals. Hence, they recommended that the scaling exponent used to compare intakes among herbivore species should be determined in each study. Similarly, Riaz *et al.* (2014) proposed that intake scaling exponents were likely to be species specific. This is also consistent with the conclusions of Munn *et al.* (2012), who found that a species-specific (feral goat) FMR was 40% lower than that predicted by multi-species allometric equations.

The extent to which the relative intakes of herbivore species differ due to the scaling exponent used is apparent when the range of potential exponents (0.6–1.0) is applied to the intakes of sheep and macropods presented in Table 3. Depending on the

exponent used, the ratio of macropod to sheep intakes of lucerne differed by up to 29%, whereas that for straw differed by up to 33%.

#### *Species-specific allometric equations for intake*

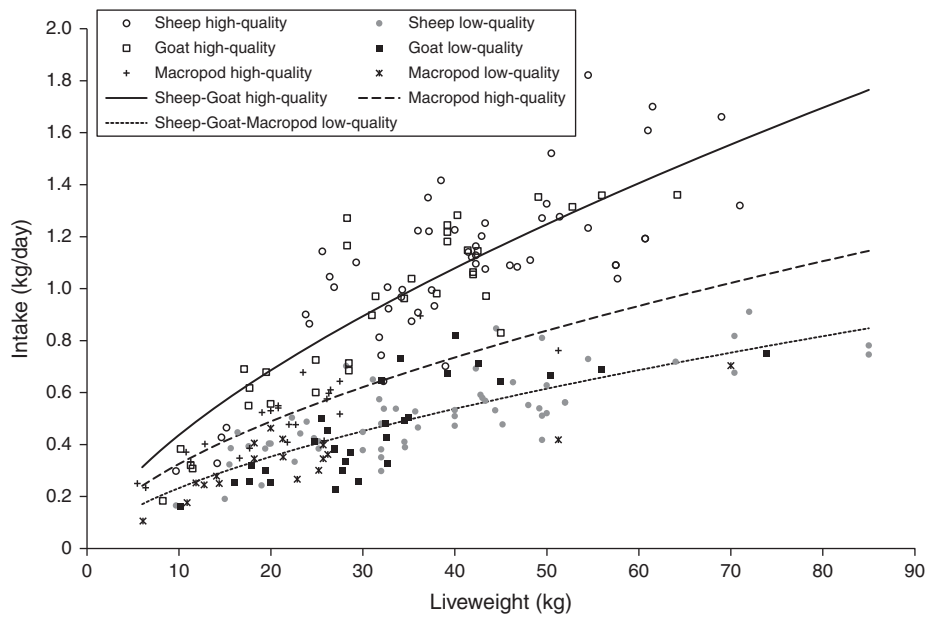
Robust species-specific allometric equations that described the relationship between intake and LW could not be developed from the nine studies which fed the same forages to sheep and macropods (Table 3). Consequently, Google Scholar was used to access additional literature which reported intakes of either sheep or macropods, the second approach referred to above. Likewise, literature was accessed which reported the intakes of goats and cattle. Studies were chosen that recorded intakes of both high- and low-quality forages. The quality of the forages fed to animals was judged, as much as possible, on their content of neutral detergent fibre (NDF). According to Edouard *et al.* (2008), the NDF content of forages is the component most consistently related to intake. The high-quality forages, mostly lucerne hay or lucerne chaff but occasionally rye grass/clover hay, had NDF levels of 300–550 g/kg dry matter. These were predominantly fed without supplements. The low quality forages were mostly cereal straws (wheat, oats, barely) with NDF levels of 700–850 g/kg dry matter, or occasionally mature grass hays or cereal hays with NDF levels of 600–800 g/kg dry matter. Liveweights and intakes of low-quality forages were sourced only from studies in which the forage comprised cereal straw only, or was predominantly cereal straw. Studies which modified straws through alkali or nitrogen treatments, or which added substantial amounts of energy and protein supplements to improve forage quality, were rejected. The publications that provided LW and intake data points used in Figs 1 and 2, and not used elsewhere in this paper, are listed in Appendix 1.

The publications of Appendix 1 plus those listed in Table 3 provided 53 records for sheep on a high-quality forage and 60 on a low-quality forage. The corresponding figures for goats, cattle and macropods were 34 and 31, 78 and 78, and 23 and 18 respectively. Datasets for red and eastern grey kangaroos, euros and wallaroos, were pooled, as sample sizes for individual species were small and the intakes relative to LWs of individual species were not significantly different (nonlinear regression,  $P > 0.05$ ).

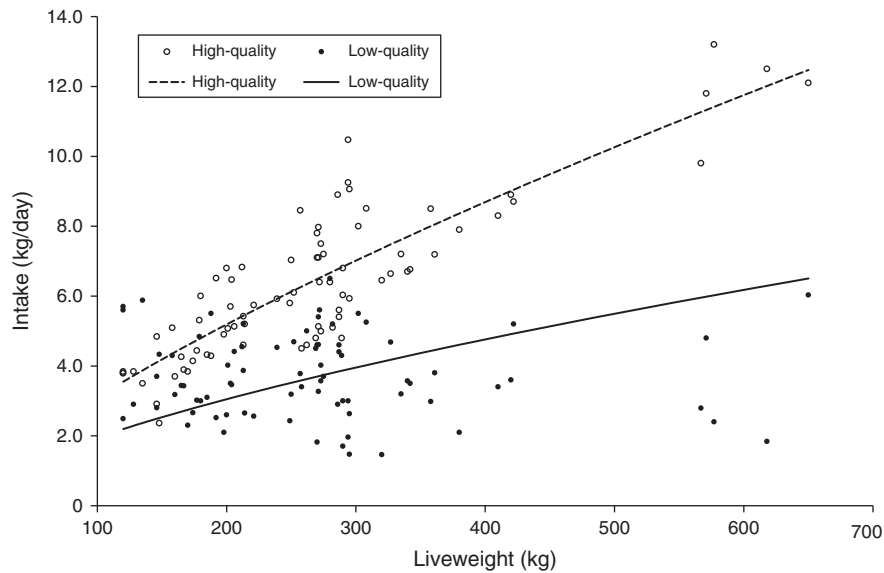
The procedure 'Fitnonlinear' in GENSTAT (2017) was used to fit the power curves to individual species datasets under a nonlinear regression framework, testing differences between the design factors (species and feed types). Three-parameter curves were initially utilised, however the intercept parameter was typically close to zero, and was not significant for any regression, so was omitted. Hence, the two-parameter power curve was adopted throughout. The general allometric equation used in this paper to represent the relationship between dry matter intake (DMI) and LW was:

$$Y = aX^b,$$

where  $Y$  is DMI and  $X$  is LW. The parameters  $a$  and  $b$  specify the position and curvature of the regression and are also the  $y$ -intercept and slope, respectively, of the linearised regression. The allometric equations and associated  $R^2$  values for sheep, goats, macropods and cattle when fed high and low-quality forages are shown in Table 4.



**Fig. 1.** Dry matter intake (DMI) and liveweight (LW) data points for sheep, goats and macropods fed high- and low-quality forages, and fitted lines for sheep-goats fed high-quality forage ( $DMI = 0.084 \times LW^{0.588}$ ), macropods fed high-quality forage ( $DMI = 0.097 \times LW^{0.653}$ ), and sheep-goats-macropods fed low-quality forage ( $DMI = 0.058 \times LW^{0.604}$ ). (Data points sourced from references listed in Appendix 1.)



**Fig. 2.** Dry matter intake (DMI) and liveweight (LW) data points for cattle, and the fitted lines for high-quality forages ( $DMI = 0.101 \times LW^{0.744}$ ) and low-quality forages ( $DMI = 0.101 \times LW^{0.643}$ ). (Data points sourced from references listed in Appendix 1.)

The relationships between DMIs and LWs of sheep and goats when fed a high-quality forage were very similar and not significantly different (non-linear regression,  $P > 0.05$ ), and hence were represented by a single fitted line (Fig. 1). The allometric equation for sheep and goats pooled when fed a high-quality forage has a scaling exponent of  $LW^{0.65}$  (Table 5). Both sheep and goats ate significantly more of the high-quality forages than macropods (non-linear regression,  $P < 0.001$ ), and hence the

intake of these forages by macropods is represented by a separate fitted line as per the allometric equation of Table 4.

The DMIs of low-quality forages by sheep and goats were almost identical (non-linear regression,  $P > 0.05$ ), and although this was approximately 14% higher than the intake of macropods on these forages, the difference was not significant (non-linear regression,  $P = 0.254$ ). Consequently, the relationship between DMI of low-quality forage and LW of sheep, goats and

**Table 4.** The allometric equations and associated  $R^2$  values for intakes of high- and low-quality forages by sheep, goats, macropods and cattle

Species	High quality	$R^2$	Low quality	$R^2$
Sheep	$0.116 \times LW^{0.606}$	0.62	$0.075 \times LW^{0.538}$	0.62
Goat	$0.077 \times LW^{0.716}$	0.80	$0.033 \times LW^{0.773}$	0.62
Macropods	$0.084 \times LW^{0.588}$	0.61	$0.065 \times LW^{0.537}$	0.73
Cattle	$0.101 \times LW^{0.744}$	0.74	$0.101 \times LW^{0.643}$	0.62

**Table 5.** The allometric equations for intakes of high- and low-quality forages by combinations of sheep, goats, macropods and cattle and the  $R^2$  values of the fitted lines in Fig. 1

Species	High quality	$R^2$	Low quality	$R^2$
Sheep-goat	$0.097 \times LW^{0.653}$	0.71	$0.060 \times LW^{0.597}$	0.75
Sheep-goat-macropods	$0.065 \times LW^{0.752}$	0.75	$0.058 \times LW^{0.604}$	0.65
Sheep-goat-macropods-cattle	$0.057 \times LW^{0.841}$	0.94	$0.035 \times LW^{0.825}$	0.91

**Table 6.** Daily dry matter intakes (kg) of sheep-goats and macropods of three liveweights (LW) when consuming high- or low-quality forage and the ratios of macropod intakes to sheep-goat intakes

Species	High quality			Low quality		
	LW (kg)			LW (kg)		
	20	35	50	20	35	50
Sheep-goat	0.686	0.989	1.248	0.353	0.496	0.615
Macropods	0.490	0.680	0.839	0.353	0.496	0.615
Ratio	0.71	0.69	0.67	1.00	1.00	1.00

**Table 7.** Daily dry matter intakes (kg) of cattle of four liveweights (LW) when fed high- and low-quality forages

	High quality				Low quality			
	LW (kg)				LW (kg)			
	200	300	450	600	200	300	450	600
5.209	7.044	9.524	11.798	3.045	3.952	5.129	6.172	

macropods is represented by a single fitted line (Fig. 1), using an allometric equation with a scaling exponent of  $LW^{0.60}$  (Table 5).

The equations for macropod intake of high-quality forage (Table 4) and sheep-goat intake of high-quality forage (Table 5) were used to compare the DMIs of sheep-goats and macropods of three different LWs (Table 6). When averaged across these three LWs, macropods consumed 0.69 the amount of high-quality forage consumed by sheep and goats daily. As a single equation was used to calculate DMIs of low-quality forage by all three species, the DMI of macropods in this instance was the same as sheep and goats.

The DMIs of high-quality forage by sheep, goats and macropods were all higher than their intakes of low-quality forage ( $P < 0.001$ ). However, the DMI of low-quality forage by sheep and goats was only 51% that of high-quality forage, whereas that for macropods was 65% (Table 6).

The relationship between LW and intake of cattle was analysed separately as the range of LWs did not overlap with

the LWs of sheep, goats and macropods. The allometric equations for cattle fed high and low-quality forages (Table 4) were used to calculate the DMIs of these forages by cattle varying in LW from 200 to 600 kg (Table 7).

The DMI of high-quality forage by cattle was significantly higher than for low-quality forage ( $P < 0.001$ ; Fig. 2). When averaged across these four LWs, the DMI of low-quality forage was 55% that of high-quality forage, which is intermediate between sheep/goats and macropods.

Given the DMIs of high-quality forage by sheep, goats and macropods presented in Table 6 and those of cattle in Table 7, a 450 kg steer is equivalent to 7.6 sheep or goats and 11.4 macropods, when the latter animals all weigh 50 kg. When fed a low-quality forage, a 450 kg steer is equivalent to 8.3 sheep, goats or macropods, again where the latter animals all weigh 50 kg.

The high intake scaling exponents of between 0.8 and 1.0 observed and/or recommended by a number of authors (Graham 1972; Bourlière 1975; Minson 1990; Meissner and Paulsmeier



**Table 8.** Dry sheep equivalent ratings for 50 kg goats, 450 kg cattle and 50 kg macropods based on their basal metabolic rates (BMRs), maintenance energy requirements (MERs) and energy expenditures of grazing ( $EE_g$ ) from Table 2, and the dry matter intakes (DMIs) when fed high-quality forage and low-quality forage relative to those of 50 kg Merino sheep (Tables 6, 7)

	BMR	MER	$EE_g$	DMI high quality	DMI low quality
Goat	1.3	1.2	1.1	1.0	1.0
Cattle	7.7	7.1	8.0	7.6	8.3
Macropod	0.9	1.2	1.0	0.7	1.0

1995; Hackmann and Spain 2010; Riaz *et al.* 2014) were not consistent with the scaling exponents derived for the intakes of high and low-quality forages in this study. The highest scaling exponents observed in this study occurred when animals consumed a high-quality forage. For sheep, intake scaled with  $LW^{0.61}$ , for goats it was  $LW^{0.72}$  and for cattle it was  $LW^{0.74}$ . These are similar to the exponents derived by Riaz *et al.* (2014), who found that intake of sheep scaled with  $LW^{0.64}$ , goats scaled with  $LW^{0.71}$  and cattle scaled with  $LW^{0.88}$ . However, the authors who reported higher intake scaling exponents obtained these when they pooled several species of herbivore of varying LWs. Interestingly, higher intake scaling exponents were also found in this study when herbivores were pooled. For example, intake of the high-quality forage scaled with  $LW^{0.84}$  for sheep, goats, macropods and cattle combined (Table 5). However, the scaling exponent is only one part of the allometric equation, and on its own cannot be reliably used to show differences in intakes between species.

## Discussion

The equivalencies of sheep, goats, cattle and macropods with regard to their contributions to TGP have been based on their energy requirements, where these were assumed the main predictor of their DMIs. Although there is considerable intra-species variability in BMRs, MERs and  $EE_g$ s recorded by individual studies, the means of multiple studies are a more reliable basis for inter-species comparisons of energy requirements. The published mass-specific energy requirements of goats are 1.1–1.3 times those of Merino sheep (Tables 2, 8), whereas published DMIs of high- and low-quality forages are the same as those of sheep (Fig. 1; Table 8). Therefore, the energy requirements of goats appear to overestimate their DMIs relative to sheep. However, this could be due to the ability of goats to digest more dry matter than sheep (Francoise Domingue *et al.* 1991; Molina Alcaide *et al.* 1997), particularly for forages with high fibre and lignin contents and low levels of nitrogen (Gihad *et al.* 1980; Doyle *et al.* 1984; Howe *et al.* 1988). Given that this review found that the DMIs of goats and sheep were the same, a 50 kg goat is regarded as 1 DSE.

Cattle also have higher mass-specific energy requirements than sheep (Table 2). Given their BMRs, MERs and  $EE_g$ s, a 450 kg steer is 7.1–8.0 DSE. These are quite similar to the DSE predicted from comparison of DMIs, being 7.6 and 8.3 for high- and low-quality forage respectively (Table 8). Consequently, a 450 kg steer, or 1 AE, is regarded as 8 DSE.

With regard to macropods, the mean BMR of marsupials is known to be 0.7 that of eutherian mammals (Dawson and Hulbert 1970), which has given rise to the view that a 50 kg macropod is 0.7 DSE. However, comparison of the BMRs of red kangaroos, eastern grey kangaroos and sheep indicated that

kangaroos are 0.9 DSE (Table 2). Furthermore, when published MERs and  $EE_g$ s of kangaroos were compared with the corresponding mean values of Merino sheep, then a kangaroo is 1.2 or 1.0 DSE (Table 8). These DSE ratings for kangaroos are much higher than the 0.45 DSE determined by Munn *et al.* (2009), Munn *et al.* (2013a) and Munn *et al.* (2016a). Similarly, Hume (1974) recorded a comparatively high MER of 569 kJ/kg<sup>0.75</sup>/day for Merino sheep, and when compared with the MERs of red kangaroos and euros recorded at the same time, red kangaroos were 0.80 and euros were 0.73 that of Merino sheep. Although these are the only studies that have compared the  $EE_g$ s and MERs of kangaroos and sheep at the same location at the same time, the high MERs and  $EE_g$ s recorded for sheep suggest these were atypical of sheep generally. Consequently, the mean energy requirements of kangaroos and sheep from multiple studies have been used here to provide a DSE for kangaroos of between 0.9 and 1.2 (Table 8). Given that the published energy requirements of kangaroos range from considerably lower to considerably higher than those of sheep, and that DMI is a more relevant measure of a species contribution to TGP, a 50 kg kangaroo is considered to be 0.7 DSE when consuming high-quality forage and 1.0 DSE when consuming low-quality forage.

These kangaroo DSE values are consistent with the findings of Wilson (1991). Based on a field trial at Lake Mere in western New South Wales, where sheep and western grey kangaroos grazed native pastures together or separately at a range of densities, this author concluded that the amount of forage consumed by kangaroos was 0.75 that of same-sized sheep.

The DMIs of kangaroos and sheep observed in this review are also consistent with the findings of Short (1985), who compared the intakes of red kangaroos and sheep grazing native pastures in small yards at Kinchega National Park, in south west New South Wales. The DMI of red kangaroos was 0.0623 kg/LW<sup>0.75</sup>/day, whereas that of sheep was 0.0611 kg/LW<sup>0.75</sup>/day, and the ratio of macropod to sheep intake was 1.02. Short (1985) concluded that the feed intakes of sheep and kangaroos were similar, in spite of the 30% lower BMRs of marsupials compared with eutherian mammals.

In a similar way, Short (1986) compared the intakes of red kangaroos and western grey kangaroos at Kinchega National Park. The intake of red kangaroos was 0.066 kg/LW<sup>0.75</sup>/day, which is similar to the earlier study, whereas that of western greys was 0.087 kg/LW<sup>0.75</sup>/day. The ratio of western grey kangaroo to red kangaroo intake was 1.32.

The relatively high DMI of the western grey kangaroo was also reported by Powell and Arnold (1984). On a metabolic LW basis (presumably LW<sup>0.75</sup>), the intake of oat chaff (NDF 585 g/kg) by western greys was 1.2 that of Merino wethers.

In comparison, when fed less fibrous forages, the ratios of western grey kangaroo to sheep intakes were 0.65 to 0.80.

A key finding of this review of DMIs is that the DMI of high-quality forage by macropods is 0.7 that of sheep and goats of the same LW. This suggests that macropods have lower energy requirements than sheep and goats. The findings that the DMI of low-quality forage by macropods is the same as that of sheep and goats, and that their DMI of low-quality forage is suppressed (relative to high-quality forage) less than that of sheep and goats, are consistent with the literature which shows declining DMI with declining forage quality, and variable responses to this due to differences in the structure of digestive tracts.

#### *Variation in intake with forage quality*

The much lower DMI of straw compared with lucerne observed in this review is consistent with the trend of declining intakes as protein levels decrease and fibre and lignin concentrations increase (Jung and Allen 1995; Weston 1996; Edouard *et al.* 2008; Decruyenaere *et al.* 2009; Meyer *et al.* 2010). Similarly, a number of livestock feeding trials have recorded decreases in DMIs as the dry matter digestibility of forages decrease and MRTs increase (Laredo and Minson 1973; Thornton and Minson 1973; Poppi *et al.* 1981a, 1981b, 1981c; Hendricksen *et al.* 1981; Lechner-Doll *et al.* 1990). As intake of low-quality forage is limited by slow passage rates, it is expected that the scaling of intake with LW would decline as forage quality declines.

This review found that the scaling of intake with LW declined with a decline in forage quality. The intake of sheep eating lucerne scaled with  $LW^{0.61}$  whereas the intake of straw scaled with  $LW^{0.54}$ . In the same way, the scaling of intake fell from  $LW^{0.59}$  to  $LW^{0.54}$  for macropods, and from  $LW^{0.74}$  to  $LW^{0.64}$  for cattle. The exception was goats, where the scaling exponent of  $LW^{0.77}$  when fed straw was higher than  $LW^{0.72}$  when fed lucerne. The lower scaling exponents for sheep, macropods and cattle eating straw is opposite to the trend predicted by Meissner and Paulsmeier (1995), who proposed that intake will scale more highly with LW than energy requirements when herbivores consume low-quality forage.

#### *Variation in intake with digestive tracts*

When DSE ratings based on DMIs of low-quality forages were compared with those based on DMIs of high-quality forages they were almost identical for goats, only 9% higher for cattle, but around 50% higher for macropods (Table 8). This appears related to differences in the extent to which the DMIs of these herbivores declined when fed a low-quality forage. The DMI of low-quality forage by sheep and goats was only 51% that of high-quality forage, for cattle it was 55%, and for macropods it was 65%.

The difference between the ruminants and the macropods in their intakes of low-quality forage is likely due to differences in the capacity and characteristics of their digestive tracts. As is the case for ruminants versus hindgut fermenters (Foote 1982; Steuer *et al.* 2011), the MRTs of sheep fed lucerne hay and cereal straws were around 1.5 times greater than for kangaroos fed the same forages (Foot and Romberg 1965; McIntosh 1966; Forbes and Tribe 1970; Powell and Arnold 1984). Munn *et al.* (2010) also noted that the flow of material from the forestomach of ruminants

was restricted by particle size more so than in macropods, and that this had potential to limit food intake due to bulky plant material filling the rumen. As with hindgut fermenters such as equids, Hume (1999) noted that kangaroos, because of their tubiform foregut, have an advantage over ruminants that have a sacciform foregut. The tubiform gut of kangaroos enables faster rates of passage of fluid and particles compared with ruminants, and thus food intake of kangaroos declines less with increases in the fibre content of forage than it does in ruminants (Hume 1984, 1999). However, the faster passage rates of macropods results in digestion of less fibre compared with sheep (Foot and Romberg 1965; McIntosh 1966; Forbes and Tribe 1970).

Additionally, Munn *et al.* (2010) also referred to the numerous haustrations of the macropod forestomach which enable it to expand considerably (Munn and Dawson 2006), and that this was likely to assist them maintain food intakes during long feeding bouts. Clauss *et al.* (2007a) noted that macropods were similar to equids in that they were able to substantially expand their gastrointestinal tract and thereby markedly increase their DMI. In comparison, ruminant sheep and cattle appear to have less ability to increase DMI by this mechanism (Clauss *et al.* 2007a).

These differences in the capacity and functioning of the digestive systems of macropods and ruminants appear to explain why the DMI of low-quality forage by macropods was less restricted than for sheep, goats and cattle. They also explain how intakes of low-quality forages can be influenced significantly by the capacity and characteristics of the gut, and thus correlate less well with energy requirements.

The DMIs of sheep, goats, cattle and macropods in this review were compared when they consumed forage of the same or similar quality. This rarely occurs within the rangelands, where herbivores with very different selective foraging capacities graze heterogeneous pastures.

#### *Variation in intake with capacity for selective foraging*

The DMI of herbivores is likely to vary with their capacity to select the higher-quality plants and plant parts present in pastures. Green grass leaves have less fibre, more protein and are more digestible than old grass leaves and grass stems (Laredo and Minson 1973; Wilson and 't Mannetje 1978; Poppi *et al.* 1981a; Dawson 1989; Archimède *et al.* 2000). Therefore, DMIs of young green leaf by sheep and cattle are considerably higher than mature leaf and stems (Laredo and Minson 1973; Poppi *et al.* 1981a, 1981b, 1981c; McLeod *et al.* 1990; Archimède *et al.* 2000; Drescher *et al.* 2006). However, the extent to which green and growing material contributes to total diet composition varies between species, due largely to differences in LW.

According to Müller *et al.* (2013), larger species of herbivores regularly ingest diets of lower quality than smaller species. These authors considered this a consequence of their higher absolute daily food requirement that constrains the time they can allocate to searching for higher-quality forages. In most environments, the proportion of pasture that is low-quality tends to increase with increases in pasture biomass, and thus the supply of high-quality plants and plant parts tend to be low and sparsely distributed (Demment and Van Soest 1985). Müller *et al.* (2013) also reported that the lower diet quality of large herbivores is a consequence of their larger and blunter feeding apparatus that again prevents them from foraging selectively.

The greater ability of sheep to maintain higher proportions of green grass in their diets compared with cattle was observed by Squires (1982). In all six sampling periods, the diets of sheep contained higher proportions of green variable speargrass (*Stipa variabilis*) than did cattle diets which always contained higher proportions of dry variable speargrass. Similarly, Mulholland *et al.* (1977) observed that sheep consistently selected a diet with a higher proportion of green material than did cattle when grazing together on stubbles of wheat, oats or barley.

Both Taylor (1983) and Jarman and Phillips (1989) noted the highly developed capacity of eastern grey kangaroos, whiptail wallabies (*Macropus parryi*) and the wallaroo to select leaf in preference to the sheaf and stems of grasses. Jarman and Phillips (1989) proposed that their narrower incisor arcade and ability to crouch low contributed to their far greater capacity compared with livestock to select the higher quality parts of grasses. This is likely to be the reason why macropods are often able to maintain a higher green component in their diet than sheep. At Gilruth Plains in south west Queensland, Griffiths and Barker (1966) observed that the stomach contents of eastern grey and red kangaroos were green, whereas that of sheep consisted of yellow dried-off stalks of grass. At Fowlers Gap, Ellis *et al.* (1977) also noted that the stomach contents of sheep was mostly stems of forbs, whereas the finely-chewed contents of the stomachs of red kangaroos did not appear to contain woody stem material. Similarly, Chippendale (1962) reported that the dried bases of perennial grasses were the predominant diet of cattle, whereas green leaf was the main component of red kangaroos grazing at the same location in central Australia.

Given the propensity of smaller herbivores to harvest higher quality forage than larger herbivores, it is likely that their mass-specific DMIs will be higher than those of larger herbivores grazing at the same location. For example, if the diet of kangaroos was considered equivalent in quality to lucerne and that of sheep equivalent to straw at Gilruth Plains, then the ratio of kangaroo to sheep DMI at that location would be 1.36 for animals of equal weight.

## Conclusions

The extent sheep, goats, cattle and macropods are equivalent to each other on pastoral properties has been based on their relative energy requirements. Although there is considerable variation in the energy requirements of these herbivores recorded by individual studies, and particularly for sheep, mean BMRs, MERs and  $EE_{g,s}$  provided a more consistent basis for inter-species comparisons of energy requirements. For example, Munn *et al.* (2009), Munn *et al.* (2013a) and Munn *et al.* (2016a) reported that a kangaroo was 0.45 DSE, based on comparisons of the  $EE_{g,s}$  of kangaroos and sheep at the same times and locations. However, the  $EE_{g,s}$  of Merino sheep recorded in these three studies were 43 to 88% higher than the highest  $EE_g$  recorded for Merino sheep by other studies. When the mean BMRs, MERs and  $EE_{g,s}$  of multiple studies of macropods and Merino sheep were compared (Table 8), the respective DSE values for macropods were 0.9, 1.2 and 1.0. These are similar to the DSE values of 0.7 and 1.0 derived from comparisons of the DMIs of high- and low-quality forages by macropods and sheep. However, the lower DMI of macropods when fed high-quality forage suggests they

have lower energy requirements than ruminant livestock. The similar DMIs of macropods and ruminant livestock when fed low-quality forage occurs because macropods have faster digesta passage rates and more expandable stomachs.

The DMIs of sheep and goats are very similar in spite of the higher energy requirements of goats. This possibly occurs because goats digest more dry matter than sheep. Hence, on the basis of DMI, a 50 kg goat is regarded as 1 DSE. Cattle have higher mass-specific and absolute energy requirements than sheep, goats and macropods. Based on relative energy requirements, a 450 kg steer is 7.1–8.0 DSE, and based on DMI it is 7.6–8.3 DSE. Hence, the relative energy requirements and DMIs of cattle are very similar. When cattle were fed high-quality forage, a 450 kg steer or AE equalled 7.6 sheep or goats weighing 50 kg, and 11.4 macropods that weigh 50 kg. When fed low-quality forage, an AE equalled 8.3 50 kg sheep, goats or macropods.

However, the relative DMIs of these species when grazing in large paddocks with heterogeneous pasture quality are likely to differ from those observed when fed ad-libitum quantities of the same or similar forages in small pens. Goats and sheep, due to their much smaller LWs and mouths, will consume more high-quality forages than cattle when foraging in the same paddocks, and hence a 450 kg steer is likely to be equivalent to fewer than 8 DSE. Similarly, given the greater capacity of macropods to select high-quality forages compared with sheep, it is expected that a 50 kg macropod will often be equivalent to one DSE. Larger-scale versions of the field grazing trials conducted by Short (1985) are required to determine the relative DMIs of free-ranging sheep, goats, macropods and cattle when they can select from a wide range of forages.

## Conflicts of interest

The author declares no conflicts of interest.

## Acknowledgements

The research undertaken for this paper occurred within a project managed by NSW Department of Primary Industries and was partly funded by MLA. Dennis Poppi provided definitions of different forms of energy requirements and suggestions for inter-species comparisons of intake. David Mayer promptly and expertly provided statistical analyses. Steven Bray and Debra Corbet provided valuable comments on the manuscript prior to submission to The Rangeland Journal, and the suggestions provided by two anonymous reviewers and the Associate Editor greatly improved this paper.

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**Appendix 1. References that provided the liveweight and intake data points shown in Figs 1 and 2, but were not used in any other part of this paper**

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