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Whole-body fatness is a good predictor of phenotypic feed and liveweight efficiency in adult Merino ewes fed a poor-quality diet

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Abstract

Weight loss due to poor nutrition in adult ewes over summer–autumn is economically expensive due to immediate costs such as feed and labour but also due to ongoing costs to reproductive success and ewe health. We predicted that adult Merino ewes with a higher proportion of fat would be more efficient, both through lower intake and reduced weight loss. Four-year-old Merino ewes ($n = 64$) were held in single pens and fed a chaff-based diet either *ad libitum*, with the aim of achieving liveweight maintenance, or a restricted amount to achieve liveweight loss of 100 g/day. Liveweight change and feed intake were measured, and residual liveweight change and residual feed intake were used to indicate efficiency. There was a difference of 2 MJ of metabolisable energy per day between the most efficient and least efficient ewes for residual feed intake, and a difference of 90 g per day between the most efficient and least efficient ewes for residual liveweight change. There was a significant association between blood plasma concentrations of leptin and both liveweight and feed efficiency, so that ewes with high concentrations of leptin had a lower daily intake, and/or lost less weight than did those with low concentrations of leptin. Managing adult Merino ewes to maximise fat-tissue accretion during spring via genetics and/or nutritional management could be a useful

strategy to reduce feed requirements during summer–autumn because the ewes will be more efficient and have larger fat reserves to lose before achieving a lower critical limit.

Additional keywords: composition, intake, leptin, nutrition, resilience.

Introduction

Seasonal fluctuations in pasture supply and quality in Mediterranean climates, together with the varying energy needs for reproductive processes, mean that the nutritional requirements of the mature ewe flock are not always matched with available pasture. Where nutritional requirements for maintenance are not met ewes will lose weight, and it is well recognised that variations in liveweight and condition score have important repercussions for ewe fertility, reproductive rate and weaning rate. Ewes that are in poorer condition at joining have reduced fertility and reproductive rate and those in poorer condition at lambing have higher rates of mortality for both ewes (Edwards *et al*. 2011) and lambs (Kelly 1992;Behrendt *et al*. 2011; Oldham *et al*. 2011). Liveweight change in adult sheep can largely be explained by environmental and management differences and the varying demands of reproduction (Walkom *et al*. 2014). However, there is also evidence for variation among individual Merino sheep in their ability to maintain liveweight and condition when nutrition is poor (Blumer *et al*. 2016). It may be possible to select animals that are genetically more resilient to periods of poor nutrition (Rose *et al*. 2013). Resilient sheep could potentially be managed at higher stocking rates, have reduced dependence on supplementary feeding and require less labour to feed over summer and autumn. However, improvements in profitability from selecting animals that are genetically more resilient will be greater if the reduction in weight loss is achieved via improved efficiency rather than through increased intake of low-quality feed (Young *et al*. 2011). It is, therefore, important to investigate the biological drivers of liveweight change in adult Merino ewes when consuming suboptimal diets.

Efficiency is a function of intake and liveweight change, and differs for animals of different sizes and maturities. Koch *et al*. (1963) introduced the use of residuals to describe efficiency where these variables are accounted for in the model, and the error value then describes how the individual deviates from the population mean. Residual feed intake (RFI) has now been used to describe efficiency in most livestock species and is the difference between the actual feed intake of the individual and the expected feed intake (measured by the population mean), given a certain level of production, for example, liveweight gain, or milk yield. It has been shown to be independent from its component traits, liveweight and daily gain, although there is a positive correlation between RFI and dry matter intake (Arthur *et al*. 2001). Several studies have found that RFI is positively correlated with fat and have concluded that animals with more fat are less efficient (Arthur *et al*. 1996; Herd and Bishop 2000; Basarab *et al*. 2003). However, work by Blumer *et al*. (2016) demonstrated that sires with higher Australian sheep breeding values (ASBVs) for fat were associated with reduced liveweight loss in their adult ewe progeny during periods of poor nutrition, although the effect varied across environments. Most research concerning efficiency traits has focussed on young animals (Basarab *et al*. 2003; Knott *et al*. 2004; Kelly *et al*. 2010), or under conditions of increasing weight (Archer *et al*. 2002), rather than examining efficiency in adults at maintenance or when exposed to less than favourable nutrition.

The maintenance requirements for immature *versus* mature animals are different and this has been demonstrated byGraham (1980) who showed that basal metabolism is higher in younger animals. Roux (2013) showed that maintenance requirements can be largely explained by differences in body composition and the energetic efficiency of protein *versus* fat synthesis, and Ball and Thompson (1995) showed that, at maturity, sheep selected to have more carcass fat had a lower intake requirement to maintain weight than did sheep from a random line. Richardson and Herd (2004) suggested that the combination of protein metabolism and stress accounted for 37% of the variation in RFI in beef cattle. Work in adult mice has shown that selection for lower heat production produced animals that consumed less, and had higher proportions of fat (Nielsen *et al*. 1997). Fatness in sheep is routinely measured on farms using condition scoring, a subjective measure of

subcutaneous fat (Jefferies 1961), to provide an indication of the animal energy balance. Subcutaneous fat depth is also routinely measured objectively using ultrasound at the c-site (Gilmour *et al*. 1994). Another objective measure of fatness is the concentration of the hormone leptin, which has been demonstrated to be a good indicator of whole-body fatness in sheep (Blache *et al*. 2000). We, therefore, hypothesise that when adult Merino ewes are managed to maintain or lose weight, animals with higher measures of fatness will be more efficient, through both lower intake and reduced weight loss per unit of intake. In addition, the opposite will be true; animals with proportionally less fat will have higher maintenance costs and increased intake.

Materials and methods

Feed intake, liveweight change, condition score, ultrasound fat depth and plasma leptin concentration were measured for 64 adult Merino ewes held in single pens and fed a poor-quality chaff-based diet either *ad libitum* or below maintenance. All experimental work involving animals was conducted under the authority of the *Animal Welfare Act of Australia* and the experimental schedule received prior approval from the animal-ethics committees of the Department of Agriculture and Food Western Australia (DAFWA; Approval number 4-11-21) and Murdoch University (Approval number R2433/11).

Experimental animals

The ewes were sourced from the Information Nucleus Flocks based at Armidale, New South Wales, Turretfield, South Australia, and Katanning, Western Australia (Fogarty *et al*. 2007; van der Werf *et al*. 2010), and from the Maternal Efficiency Flock established in 2009 by DAFWA. Dams for the Maternal Efficiency Flock were sourced from two Merino studs in south-western Australia and industry sires were used, with a focus on increased growth, fat and muscle. The flock has been maintained at ~700 ewes as a self-replacing resource flock at Pingelly, Western Australia. Forty ewes were sourced from each of the four sites.

All ewes in the current study were born in 2007 and, at the time of the experiment (2011–2012), were approaching 5 years old. The ewes had full pedigree information, including ASBVs, and recorded measurements for a wide range of wool, meat and reproductive traits. Ewes had been managed through at least two reproductive cycles and liveweight measurements were collected at regular intervals throughout. The ewes were by sires that encompassed a range of ASBVs for fat and muscle (Sheep Genetics) and, of the 35 Merino sires represented, 11 had progeny in both experimental treatment groups.

The ewes (160) were transported to the Department of Agriculture and Food Western Australia research station at Medina, Perth (32°13′S, 115°48′E). They initially grazed as a group on poor-quality winter pasture and were supplemented with pellets to maintain average liveweight for 30 days. Prior to allocation, ewes were treated with a broad-spectrum anthelmintic (Triton®; Merial, Sydney, NSW, Australia). Sixty-four ewes were then allocated into one of two groups and moved to an animal house. Selection for the experiment was balanced for ewe source, liveweight and condition score, and included a range of sire ASBVs for fat and muscle (Table 1). Ewes were maintained in individual pens (1.8×0.9 m) with a slatted concrete floor. The experiment was conducted during summer in an animal house with natural lighting and open ventilation, so as to resemble temperatures and daylengths experienced on farms when liveweight loss is common in Mediterranean climates.

Diets and treatments

During an introductory period (16 days), the ewes were fed a base ration consisting of *ad libitum* barley straw chaff. This was supplemented with whole lupins and a commercial mineral supplement (shipping mix, Macco Feeds, Williams, Western Australia) plus an additional 5 g of vitamin A (Advanced Feeds, Midland, Western Australia) given once weekly. The straw was mixed with urea to increase protein concentration, and with molasses to increase palatability (dry matter 92.8%, metabolisable energy 5.1 MJ/kg dry matter). On Day 17 (6 January 2012), feeding was restricted in Group 2 to result in weight loss of ~100 g/day in a 50 kg sheep, or ~0.75 of a condition score (CS) over 54 days (1 CS = 7.5 kg in a 50 kg sheep; Freer *et al*. 1997). Grazfeed (Freer *et al*.

1997) was used to calculate maintenance requirements for a 50 kg ewe and the feed deficit required to lose weight was then applied on an individual basis according to ewe liveweight, resulting in constant weight loss for the group across 54 days. Group 1 continued with *ad libitum* feeding of the base diet. Ewes were supplemented with lupins (8–20 g/kg metabolic liveweight per day) when required to maintain the expected average-liveweight profiles for each group until Day 71. During the course of the study, four ewes were removed, including one ewe due to poor adaptation to the concrete floor, one due to inappetence, and two ewes that were healthy and maintaining weight but had low intakes. An additional ewe had data excluded at analysis.

Measurements

Ewes were weighed twice weekly before feeding, and condition scored (on a subjective scale, where CS of 1 is very thin and 5 is very fat; Jefferies 1961) once weekly. Sheep were fed each day a weighed amount of feed according to treatment group. Sheep in Group 1 received the previous day's intake of the chaff diet plus 30%, to ensure that *ad libitum* feeding levels were maintained. Chaff refusals were measured daily before re-feeding (no lupin seed or mineral powder was recovered for the 60 ewes remaining in the experiment). Ewes were measured for muscle and fat depth at the 12/13th rib by using ultrasound by an accredited operator, before entry to the animal house (Day 0) and following their exit from the animal house (Day 73).

Blood collection and plasma analysis

Blood was collected (10 mL) via jugular venipuncture on the day before housing (Day –1), and on Days 35 and 71, 2 h after feeding. Blood samples were collected into heparinised blood tubes before being centrifuged and the plasma was stored at -20°C before it was assayed for leptin. Leptin was measured using the double-antibody RIA technique previously described in detail by Blache *et al*. (2000). The intra-assay coefficient of variation was 4.87%. Three control samples were included in the assay to determine the inter-assay CVs of 2.7%, 3.2% and 4.3% (low, medium and high respectively). The minimum detectable concentration was 0.079 ng/mL.

Liveweight traits

Liveweights were adjusted for wool weight, based on greasy fleece weights collected at shearing after the experiment and assuming linear wool growth. A linear regression of liveweight against time was used to eliminate noise in the weight data, and to predict weights at the start and finish of the measurement period (Days 18–71; SAS 2002). Daily liveweight change was derived from the predictions. Liveweight was also expressed as metabolic liveweight (liveweight$^{0.75}$). Intake of metabolisable energy (ME) was calculated as the average of daily dry matter intake for each ewe over the 53-day treatment period and multiplied by the ME content of each feed. ME intake was also expressed as a percentage of liveweight (average dry matter intake/average liveweight), and as gross feed conversion efficiency (daily liveweight change/daily dry matter intake).

Statistical analyses

The restricted and *ad libitum* dietary groups were analysed separately (*ad libitum*, $n = 29$; restricted, $n = 30$) by using linear mixed-effects models in SAS (SAS 2002). For both groups, daily liveweight change was analysed as the dependent variable, with ewe source (flock of origin) tested as a fixed effect, starting liveweight and ME intake as covariates, and sire as a random term. All first-order interactions were included, and removed in a stepwise fashion if not significant ($P > 0.05$). ME intake was also modelled, but only for the *ad libitum* group. Intake was not analysed for the restricted group, as the animals consumed all feed available; hence, intake was determined by the amount offered. These models are described as the base models. The residuals from the base models represent efficiency. When intake is the dependent variable, the error term is described as RFI and animals with lower or negative residuals are more efficient, requiring lower intake for similar liveweight performance. When liveweight change is the dependent variable, animals with higher or positive residual errors are more efficient, gaining more (or losing less) weight at similar intakes. This will be defined as residual liveweight change (RLWC).

The residual efficiency indicators were then analysed as dependent variables in a combined dataset (i.e. ewes in both dietary groups). Covariates were starting CS, mean C-site fat (over the loin) and

mean eye muscle depth, and sire ASBVs for fat, muscle and growth. The first-order interactions between each covariate and the fixed effects of diet and ewe source were tested, and removed in a stepwise fashion if not significant ($P > 0.05$).

For leptin, the combined dataset was used, with fixed effects including diet, ewe source and bleed number (Day –1, Day 35 or Day 71). Sire and ID were included as random terms to account for repeated sires within groups and repeated samplings of the same animal. Following the establishment of the fixed-effect model, covariates were then included in separate models. Covariates tested were starting liveweight, and sire ASBVs for fat, muscle and growth. Sire ASBVs were tested both in separate models and as interacting terms, and with and without starting liveweight as an independent term.

Finally, the residual efficiency indicators were analysed as dependent variables in a combined dataset to examine the effect of leptin. The first-order interactions between leptin and the fixed effects of diet and ewe source were also tested, and removed in a stepwise fashion if not significant ($P > 0.05$).

Pearson correlation coefficients between the residual efficiency indicators, as well as gross-feed conversion, dry matter intake and intake as a percentage of liveweight were determined using the multivariate analysis of variance (MANOVA) procedure in SAS. Diet and ewe source were included in the multivariate model as fixed effects.

Results

Daily liveweight change and intake – base models

At the start of the differential feeding period (Day 17), the ewes were on average 57.7 kg (s.e.m. 0.85) and had a CS of 2.8 (s.e.m. 0.04). The average liveweight of the restricted and *ad libitum* group is shown in Fig. 1. On average, ewes in the restricted group lost 95 g/day (±18 g s.d.) and this varied

from 51 g/day (±12 g s.e.) for 40 kg ewes to 131 g/day (±10 g s.e.) for 70 kg ewes. Starting liveweight explained 34% of the variation in liveweight change.

For ewes in the *ad libitum* group, liveweight change was predicted from both starting liveweight and ME intake. Ewes performed better than maintenance, gaining a predicted 21 g/day, with a standard deviation of 21 g. Ewes with a starting liveweight of 40 kg gained weight at 67 g/day (±19 g) and 70 kg ewes lost weight at 25 g/day (±19 g; $P = 0.06$). For each 1 MJ increase in ME intake, there was a predicted 24 g/day increase in liveweight gain (or decrease in liveweight loss; $P < 0.05$). The base model for liveweight change in the *ad libitum* group described 42% of the variance for liveweight change.

For ewes in the *ad libitum* group, ME intake was significantly affected by starting liveweight and liveweight change (Table 2). Ewes averaged 6.2 MJ of ME/day, with a standard deviation of 0.89 MJ/day. Ewes with a starting liveweight of 40 kg consumed 4.9 MJ of ME/day (±0.35 MJ) and ewes at 70 kg consumed 7.5 MJ of ME/day (±0.34 MJ; $P < 0.05$). For each 10 g increase in daily liveweight change, there was a predicted 0.1 MJ/day increase in ME intake ($P < 0.05$). The base model for feed intake in the *ad libitum* group described 53% of the variance for intake.

Residual efficiency models

Residual liveweight change for ewes on the restricted diet ranged between –36 g/day and 56 g/day; so, at the same level of intake, there was a 92 g/day difference between the least efficient and the most efficient sheep on a daily basis. Similarly, for the ewes on the *ad libitum* diet, RLWC ranged between –51 g/day and 43 g/day, so there was a difference of 94 g/day between the least efficient and most efficient ewes. Ultrasound measurements for fat and muscle did not contribute significantly to the amount of variance explained by the liveweight-change base models, and sire ASBVs were also not significant.

Residual feed intake for ewes on the *ad libitum* diet ranged between –1 MJ/day and 1.1 MJ/day, so that the least efficient ewes were consuming 2.1 MJ of ME more per day than were the most efficient ewes, to gain a similar liveweight. There was a negative association with subcutaneous fat ($P < 0.05$)

so that ewes with more subcutaneous fat had lower feed requirements at a constant liveweight and level of liveweight change. ME intake was reduced by 0.31 MJ/day for each extra 1 mm of fat. The inclusion of subcutaneous fat in the model explained a further 11% of RFI. Mean CS was also assessed as a covariate, and there was a trend for it to be negatively associated with RFI. While not significant ($P = 0.09$), the inclusion of CS in the model explained 7% of the variance in RFI.

Residual feed intake and RLWC were significantly and negatively correlated ($r = -0.44$, $P < 0.05$; Table 2). RFI was positively correlated with ME intake ($r = 0.75$, $P < 0.001$), and with ME intake as a percentage of liveweight ($r = 0.89$, $P < 0.001$). RLWC was positively correlated with gross feed efficiency ($r = 0.82$, $P < 0.001$).

Concentration of leptin in plasma

Plasma leptin ($P < 0.05$) concentration increased across the three bleed time points (Days –1, 35 and 71), and this was four times greater for ewes on the *ad libitum* diet than for ewes on the restricted diet ($P < 0.01$, Table 3). There was an effect of ewe source on leptin concentration, with the extremes being Turretfield and Katanning (1.28 ± 0.7 ng/mL and 0.96 ± 0.07 ng/mL, $P < 0.001$). The concentration of leptin was not significantly associated with liveweight, or with the sire ASBVs for fat, eye muscle depth or growth.

Residual efficiency indicators and their association with the
concentration of leptin in plasma

Leptin was negatively associated with RFI ($P < 0.05$, Fig. 2). Ewes with higher concentrations of leptin had more negative values for RFI. Hence, ewes with leptin concentrations of 1.6 ng/mL required 0.8 MJ of ME per day less than those with concentrations of 0.8 ng/mL. Leptin explained 27% of the variation in RFI.

Leptin was also positively correlated with RLWC ($P < 0.01$, Fig. 2). Regardless of the diet group, ewes with leptin concentrations of 1.6 μg/mL were more liveweight efficient (gaining more weight, or

losing less weight) by 28 g/day than were ewes with leptin concentrations of 0.8 μg/mL. Leptin explained 17% of the variation in RLWC.

Discussion

Adult Merino ewes with higher proportions of fat were more feed efficient and lost less weight than did leaner ewes when consuming a poor-quality diet. This was in agreement with our hypothesis that was based on evidence that ewes from sires with higher ASBVs for fat lost less weight in some areas of Australia, particularly in Mediterranean regions and especially where annual liveweight loss was greater than 10 kg (Blumer *et al.* 2016). In contrast to our results, Richardson *et al.* (2004) found a positive relationship between RFI and whole body fat in growing cattle and fatness explained 5% of the variance in RFI. Our results showed that fatness measured by ultrasound explained 11% of the variance in RFI and the relationship was negative. This relationship was confirmed through the measurement of plasma leptin concentration, which explained 27% of the variation in RFI and was significantly higher in sheep that were more efficient and required less feed than their cohort. Much of the published work concerning efficiency examines young, growing animals rather than adults. It is well established that accumulating fat is energy expensive (Roux 2013); so, in young animals gaining liveweight and fat, leaner animals are more efficient. However, adult metabolism is adapted towards maintenance of body tissues rather than growth (Graham 1980), and the maintenance of fat tissue is energetically inexpensive in comparison with the energy required to maintain protein synthesis (Graham 1980; Ball and Thompson 1995). Feed efficiency during growth and feed efficiency during adulthood must be considered as separate traits, and given that adult Merino ewes make up a large proportion of the Australian flock (~55%; Curtis 2009), adult efficiency traits should be given greater consideration in future work.

Ultrasonic subcutaneous-fat measures, hormone levels and condition scoring were used in the current study to quantify the fat-tissue component of ewes. The measurement of leptin in blood plasma had a stronger association with the residual efficiencies than subcutaneous fat and CS. Leptin has been

highly and positively correlated with whole-body fatness (Blache *et al.* 2000; Chilliard *et al.* 2000; Delavaud *et al.* 2000) and is implicated in the regulation of energy balance (Ahima *et al.* 2000; Delavaud *et al.* 2000) and feed intake (Ahima *et al.* 2000). Leptin inhibits feeding, andAhima *et al.* (2000) found that rats that were fasted but given an exogenous supply of leptin had a reduced intake on re-feeding, in comparison with rats that were fasted and not given leptin. Ahima *et al.* (2000) demonstrated that low concentrations of leptin stimulated food-seeking behaviour and this was further associated with an increase in the secretion of stress hormones. The effects of stress have been demonstrated to affect metabolic efficiency (Stratakis and Chrousos 1995). Grazing behaviour is also energy expensive and sheep in poor condition will also have to account for the added energy expense of the longer rumination time required for poor-quality feeds above that required for maintenance (Osuji 1974). Extrapolation of the findings of our pen experiment to a paddock situation suggested that extended periods of poor nutrition could favour lowered energy expenditure, and animals with more body fat would have a lower drive to eat, would conserve energy through reduced activity and would have more fat reserves available for mobilisation.

The ultrasound measurement of subcutaneous fat was also a predictor of efficiency; however, the relationship was not as strong as that between leptin and efficiency. Subcutaneous fat is a labile fat depot (Little and Sandland 1975) and is rapidly depleted during nutritional restriction, while other fat depots are mobilised more slowly (Bocquier *et al.* 2000). Further, unlike the other fat measures examined (CS, ultrasound fat and leptin), sire ASBVs for fat were not associated with efficiency in the current study. This is possibly due to insufficient animal numbers in the present study to test the range of breeding values for fat; however, it could also indicate that a breeding value based on a single measurement of subcutaneous fat in a young animal is a relatively poor indicator of whole-body fatness in adult ewes. This is supported by the results of Greeff *et al.* (2003) who concluded that ultrasonically measured fat and muscle measured on rams at 16 months were not good indicators of those tissues when measured again at slaughter, and also by the results ofThompson (2006) who demonstrated very large differences in whole-body fat measured by dual-energy X-ray absorptiometry in adult wethers that were not significantly different for subcutaneous-fat measurements. Hopkins *et*

al. (2007) showed that estimated breeding values for fat based on ultrasound measurement of subcutaneous fat are a good indicator of whole-body fatness at slaughter; however, this has not been tested in adult sheep. If fatness in adult ewes is to be investigated as a useful tool for commercial practice, then additional tools for accurately assessing fat tissue may need to be explored.

The efficiency measures for both intake and liveweight change for sheep on a poor-quality diet varied significantly among individual sheep. The least efficient sheep were eating ~2 MJ more than the most efficient sheep on a daily basis, to achieve the same change in liveweight. Similarly, the difference between the most efficient and least efficient sheep for liveweight change was more than 90 g per day at the same level of intake, and this was consistent regardless of the diet treatment. These are the extreme values; however, the sheep in the top 25% for feed efficiency were still consuming 0.6 MJ of ME/day less than the sheep in the bottom 25%, so as to maintain weight, and there was a difference of 30 g per day between the top- and bottom-quartile groups for liveweight efficiency. The quartile differences would equate to a 3 kg reduction in liveweight loss over a 100-day period. Utilising the model of an integrated dryland agricultural system (MIDAS), Young *et al*. (2011) valued liveweight loss at AU$2.30/kg per ewe (derived from costs incurred through increased requirement for supplementary feeding, and deleterious effects on reproduction) in a whole-farm economic analysis, provided the differences in liveweight loss were due to differences in feed efficiency rather than appetite (Young *et al*. 2011). In the current study, as differences in efficiency were the key driver of liveweight loss, this suggests that ewes in the top 25% for liveweight efficiency could be AU$6.90 per head more profitable than ewes in the bottom 25%. Ewes that are more efficient and lose less weight when there is a shortage of paddock feed are potentially more profitable than ewes that lose more weight because they may require less supplementary feeding or could be grazed at higher stocking rates during autumn–winter, provided that these more efficient sheep can be easily identified.

The models used to estimate RFI in the present paper accounted for 53% of the phenotypic variance in intake, which aligns with similar models described by Knott *et al*. (2008), where the models accounted for 56% of the intake for rams at 13 months of age. Knott *et al*. (2008) also utilised the model originally described by Koch *et al*. (1963) that uses liveweight change as the dependent

variable. In our experiment, the models for RLWC in ewes on an *ad libitum* diet accounted for 42% of the variance in liveweight change, again being similar to Knott *et al.* (2008) where the variance described was 48%. The variance described for ewes on the restricted diet was lower (34%) and this will be due to the constraints of restricting intake according to liveweight. The base models for intake and for liveweight change contained the same three variables and, logically, the regression of feed intake adjusted for liveweight and gain should be highly correlated with the regression of gain adjusted for liveweight and intake. However, this was not the case ($r^2 = 0.6$), and the discrepancy shown in our results has been previously described by Koch *et al.* (1963) who demonstrated that the correlation between the modelled results will be high only when the range of efficiency is small (and the measurement error is minimised). In our experiment, the opposite was true, with a wide range of intake required for liveweight maintenance. Knott *et al.* (2008) showed that the variance explained was generally higher for lambs at 6 months than those at 13 months and also suggested that animals may re-rank for efficiency as they age. The proportion of the variance explained in our work is generally slightly lower again. While residual efficiency measures will always include error generated during measurement, the alignment with previous research gives confidence that the current analysis and conclusions are robust.

Conclusions

The results of the present paper require testing under commercial conditions, across varied feed types and production systems, as well as further economic modelling, before recommendations can be made to sheep producers. Weight loss due to poor nutrition in adult ewes over summer–autumn in Mediterranean environments is economically expensive due to immediate costs such as feed and labour, but also due to ongoing costs to reproductive success and ewe health. Maximising the accretion of fat tissue during spring via genetics or nutritional management may be a useful strategy to reduce feed requirements during summer–autumn because the ewes will be more efficient and have larger fat reserves to lose before achieving a lower critical limit.

Acknowledgements

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Table 1. Parameters for liveweight, condition score and range of sire-estimated breeding values for Merino ewes from four different sources and allocated to one of two dietary groups

LW, liveweight; CS, condition score; YFAT, Australian (estimated) sheep breeding value for yearling fat; YEMD, Australian (estimated) sheep breeding value for yearling eye muscle depth

Ewe source	Diet	n	LW (kg)	CS (1–5)	Sire YFAT range	Sire YEMD range
Armidale	*ad libitum*	8	53.1	2.8	−0.65–0.45	−0.89–1.30
	Restricted	8	51.0	2.9	−0.69–1.01	−1.31–1.91
Turretfield	*ad libitum*	8	62.3	3.0	−0.94–0.42	−1.41–1.16
	Restricted	8	64.4	3.1	−1.28–0.79	−1.40–0.80
Katanning	*ad libitum*	8	59.1	2.8	−0.77–0.90	−1.25–2.30
	Restricted	8	61.0	3.0	−0.50–0.72	−0.68–2.56
Pingelly	*ad libitum*	8	61.1	3.3	−0.16–0.80	0.14–1.54
	Restricted	8	61.4	3.4	0.14–0.68	0.57–1.80

Table 2. Phenotypic correlations for residual feed intake (RFI), residual liveweight change (RLWC), metabolisable energy intake as a percentage of liveweight (ME%), gross feed efficiency (GFE) and metabolic energy intake (ME)

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Trait	RFI	ME%	GFE	ME
RLW	−0.44	−0.05	0.82	0.08
	*	n.s.	***	n.s.
RFI		0.89	0.11	0.75
		***	n.s.	***
ME%			0.50	0.74
			**	***
GFE				0.44
				*

Table 3. Predicted means (±s.e.) for leptin (ng/mL) on Days –1, 35 and 71 in adult Merino ewes sourced from four farms (Armidale, New South Wales, Turretfield, South Australa, and Katanning and Pingelly, Western Australia) and fed a poor-quality diet either at a restricted or *ad libitum* level

Means in the same row with the same letters are not significantly different ($P > 0.05$)

Parameter	Day –1	Day 35	Day 71
	Diet		
ad libitum	0.97 (0.06)	1.22 (0.06)	1.42 (0.06)
Restricted	1.05a (0.05)	1.16b (0.05)	1.11ab (0.05)
	Ewe source		
Armidale	0.90 (0.08)	1.17 (0.08)	1.32 (0.08)
Turretfield	1.13a (0.08)	1.32b (0.08)	1.39b (0.08)
Katanning	0.83a (0.08)	1.00b (0.08)	1.06b (0.08)
Pingelly	1.17a (0.07)	1.27ab (0.07)	1.29b (0.07)

Fig. 1. Liveweight (kg) change over the experimental period (days) in 4-year-old Merino ewes under two dietary treatments, with the aim of achieving maintenance (pale grey line) and liveweight loss (steel grey line). Bars represent s.e.m., and dietary treatments commenced on Day 21.
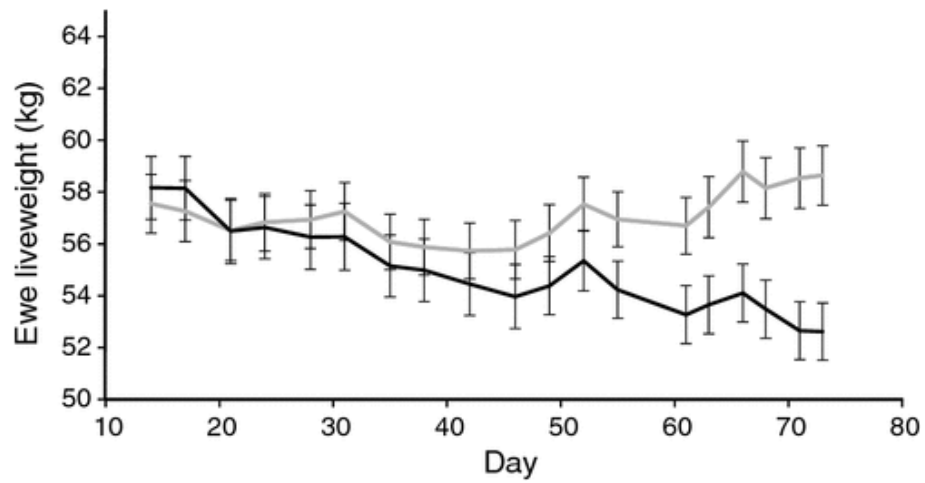
Fig. 2. Residuals for (*a*) feed intake and (*b*) liveweight change derived from the base models, and their relationships with the raw average value for leptin in blood plasma collected at three points over 71 days. The diamonds represent adult ewes on an *ad libitum* diet ($n = 29$). The open circles represent ewes on a restricted diet ($n = 30$). The solid lines represent predicted values from models, with residual values as the dependent variable. Dashed lines represent ± standard error.