Published online September 14, 2017

More feed efficient sheep produce less methane and carbon dioxide when eating high-quality pellets

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ABSTRACT: The Australian sheep industry aims to increase the efficiency of sheep production by decreasing the amount of feed eaten by sheep. Also, feed intake is related to methane production, and more efficient (low residual feed intake) animals eat less than expected. So we tested the hypothesis that more efficient sheep produce less methane by investigating the genetic correlations between feed intake, residual feed intake, methane, carbon dioxide, and oxygen. Feed intake, methane, oxygen, and carbon dioxide were measured on Merino ewes at postweaning (1,866 at 223 d old), hogget (1,010 sheep at 607 d old), and adult ages (444 sheep at 1,080 d old). Sheep were fed a high-energy grower pellet ad libitum for 35 d. Individual feed intake was measured using automated feeders. Methane was measured using portable accumulation chambers up to 3 times during this feed intake period. Heritabilities and phenotypic and genotypic correlations between traits were estimated using ASReml. Oxygen (range 0.10 to 0.20) and carbon dioxide (range 0.08 to 0.28) were generally more heritable than methane (range 0.11 to 0.14). Selecting to decrease feed intake or residual feed intake will decrease methane (genetic correlation [r_g] range 0.76 to 0.90) and carbon dioxide (r_g range 0.65 to 0.96). Selecting to decrease intake (r_g range 0.64 to 0.78) and methane (r_g range 0.81 to 0.86) in sheep at postweaning age would also decrease intake and methane in hoggets and adults. Furthermore, selecting for lower residual feed intake (r_g = 0.75) and carbon dioxide (r_g = 0.90) in hoggets would also decrease these traits in adults. Similarly, selecting for higher oxygen (r_g = 0.69) in hoggets would also increase this trait in adults. Given these results, the hypothesis that making sheep more feed efficient will decrease their methane production can be accepted. In addition, carbon dioxide is a good indicator trait for feed intake because it has the highest heritability of the gas traits measured; is cheaper, faster, and easier to measure than feed intake and has strong phenotypic and genetic correlations with feed intake. Furthermore, selection for feed intake, feed efficiency, methane, and carbon dioxide can be done early in sheep at postweaning age or hoggets. This early selection reduces the generation interval for breeding, thereby increasing response to selection.

Key words: efficiency, feed intake, genetic parameters, Merino, methane, sheep

 J. Anim. Sci. 2017.95:3839–3850
doi:10.2527/jas2017.1499

INTRODUCTION

Australian breeding programs for sheep should consider the impact of productivity on the environment (van Arendonk, 2011). This means producing more meat and wool more efficiently or from lower feed intake. Increasing efficiency by decreasing feed intake may also decrease wastage through methane and carbon dioxide. Therefore, by breeding for efficient production, sheep breeders would improve the balance between productivity and environmental impact.

Rumen bacteria in sheep produce methane as a byproduct of feed fermentation (Boone et al., 1993). As a result, if sheep eat more, methane production

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Received February 21, 2017.
Accepted July 15, 2017.

increases. Rumen bacteria use energy to produce methane (Johnson and Johnson, 1995), which can increase residual feed intake. Residual feed intake is the difference between how much sheep eat and how much they are expected to eat based on their size and ADG. Inefficient sheep eat more than expected and have a higher residual feed intake. This higher residual feed intake and methane production could be from inefficiently digesting feed, increased protein turnover, thermoregulation, and ADG (Hendriks et al., 2013). Methane production could, therefore, be a good indirect selection criterion for feed intake and be used to increase the efficiency of meat production from sheep.

Decreasing methane production would also be better for the environment. Methane from livestock contributes 10% of Australia's greenhouse gas emissions (Pinares-Patiño et al., 2011), with most livestock methane produced by ruminants (Naqvi, 2011). Given that world demand for livestock products is increasing (Yusuf et al., 2012), emissions will, therefore, increase if breeding or management is not used to decrease methane production.

In this study, we tested the hypothesis that breeding sheep that eat less and have a lower residual feed intake also produce less methane. In other words, more efficient sheep will be better for the environment. We also tested if intake, residual feed intake, and methane are consistent (i.e., the same trait) across ages.

MATERIALS AND METHODS

This project was conducted under approval of the Animal Ethics Committee of the Department of Agriculture and Food Western Australia, in accordance with the Australian code of practice for the care and use of animals for scientific purposes and the Australian Animal Welfare Act 2002 (SLP, 2002).

Experimental Sites, Animal Management, and Feed Intake Measurements

We measured traits in 2,816 animals. We measured live weight, feed intake, and methane (CH_4) from male (n = 867) and female (n = 1,866) Merino sheep at postweaning age (16-40 weeks old; total post-weaning age = 2,733). We also measured live weight, feed intake, and CH_4 and measured O_2 and CO_2 on females at hogget (607 d; n = 1,010) and adult ages (1,080 d; n = 444; more detail in Appendix 1). Not all traits were measured on the same animals. A full summary of the number of animals measured for each trait between ages is in Appendix 2.

The sheep were born between 2009 and 2014 and managed at the University of Western Australia Ridgefield research farm (32°32′ S, 117°05′ E; Pingelly, WA, Australia). At Ridgefield, in between measurements, management for females included natural mating (and lambing) at all ages. The number of matings ranged from 1 to 4 per dam. The pedigree structure is 4 generations with 117 unique sires and 1,939 unique dams. Of the 2,816 animals with measurements, 184 had an unknown dam, 199 had an unknown sire, and 162 had an unknown sire and dam.

Table 1. Mean feed test results for grower pellets (22 samples measured)

Feed test measure	Unit	Amount	SE
DM	%	90.9	0.16
ME	MJ/kg DM	12.0	0.08
CP	% of DM	15.9	0.37
ADF	% of DM	19.9	0.39
Ash	% of DM	6.4	0.24
DM digestibility	% of DM	76.0	0.44
Dry OM digestibility	% of DM	75.1	0.43
Fat	% of DM	3.1	0.16
NDF	% of DM	34.6	0.81

The sheep were transported in groups (n = 28; Appendix 1) of up to 225 from the university farm to the Department of Agriculture and Food Research Station at Medina, Perth (32°13′ S, 115°48′ E; WA, Australia). At Medina, they were equally divided into 2 outdoor pens and fed oaten hay ad libitum and 100 g/sheep per day pellets with 16% CP and 12.0 MJ ME (Table 1). This pellet ration was increased by 100 to 200 g/d for at least 15 d or until intake was ad libitum.

After adaptation to the pellet diet outside, the sheep were stratified by sire into up to 15 indoor pens (up to 15 sheep per pen). Sheep at postweaning age were also stratified by live weight so that there was less than a 5-kg difference between the heaviest and lightest sheep in each pen. This was to reduce bullying and shy feeding, which was not necessary for older sheep. The sheep were weighed 2 to 3 times each week. The chutes leading to the feeders could be adjusted to the size of the sheep in the pen so that only 1 sheep entered the feeder at a time. To access the feeder, sheep walked past a radio frequency identification aerial that recorded their electronic tag. The duration of feeding and the weight of feed eaten was automatically recorded through electronic scales and weigh bars. The weight of feed eaten was accumulated for each day to calculate daily feed intake. Daily feed intake was measured for 35 to 45 d. The ADFI for the last 35 d of measurements was used to calculate residual feed intake. Some early measurements of feed intake were unreliable and excluded from analyses (animals measured prior to group 12; Appendix 3). Consequently, modifications to the feed intake systems were made, and a weekly calibration procedure using meal-size weights was introduced.

Gas Measurements

During the last 14 to 21 d of the feed intake test, sheep were put into individual portable accumulation chambers (**PAC**) at least twice, with a minimum of 1 wk between each measurement. Methane, O_2, and CO_2 measurements were averaged across measurements and treated as 1 measurement. When we analyzed these traits, we included a weighting for how many times the trait was measured. Feed intake for precisely 24 and 48 h prior to PAC measurements were calculated for each sheep.

Portable accumulation chambers are made of polycarbonate. They are 1.23 m long, 1.24 m high, and 0.53 m wide. They are open at the bottom and have a volume of 0.795 m^3. Methane was measured by putting 16 sheep into 2 races with PAC suspended over them for 40 min. The chambers were lowered over the sheep from the front to the back of each race. The chambers were sealed against 5-mm industrial rubber belting on the floor of the race using elastic straps. The lower edges of the chambers were covered with medium-density foam rubber tape to help completely seal the chambers. The gas measurements were made via a tube attached to the machines and pushed through a 3-mm hole in the chambers. When measurements were not taken, the port was sealed with tape.

Methane concentration (μL/L) was measured at 10-min intervals for 40 min using a flame ionization detector (MX100053; Envco, Wellington, New Zealand). The detector was calibrated against a standard gas bag prior to each 10-min measurement. We analyzed CH_4 recorded at 40 min. Methane concentration was converted to milligrams per minute using the modified formula described by Goopy et al. (2016): CH_4 concentration (mg/min) = (CH_4 concentration (L) at standard temperature (0°C) and pressure × 16.04/22.4 L) × 1,000/60/60, in which 16.04 is the molecular weight of CH_4 concentration and 22.4 is the molar volume of gas at standard temperature and pressure. Atmospheric pressure and temperature data were collected from an on-site electronic weather station at the start and end of every measurement group.

Records were removed if the CH_4 accumulation over the 40 min was not linear (<2%). Simple linear regression with 95% confidence limits was used to test for linearity. This typically occurred if the sheep became unsettled in the PAC and caused it to move off the rubber matting.

Carbon dioxide (μL/L) and O_2 (μL/L) concentrations were measured at 10 and 40 min using an ADC SB1000 gas analyzer (ADC Gas Analysis Ltd., Hertfordshire, UK). Background measurements of CH_4, CO_2, and O_2 were taken at the start of each measurement interval, and measurements were corrected for their respective background levels. We analyzed CO_2 and O_2 recorded at 40 min.

Recoveries were performed on all PAC before and after each group's measurements. For recoveries, pure CH_4 was released at a standard rate of 3 L per minute for 45 s to achieve an approximately 3,000 mg/kg concentration within the PAC. Methane retention was measured every 20 min for 2 h. If gas retention was less than 95% after 2 h, the PAC was examined and repaired for leaks and then another recovery was performed.

Traits

A description of each trait is in Table 2. Live weights were modeled over time separately for each animal using a random coefficient regression including a cubic spline for time (Verbyla et al., 1999). The model fitted was live weight = μ + day + animal + animal.day + spline(day) + animal.spline(day). The term "day" was fitted as a fixed effect, whereas all other terms were fitted as random effects, with a covariance between the animal intercept (animal) and slope (animal.day). The likelihood ratio test was used to assess any spline effects after the previously mentioned terms (day, animal, and animal.day) had been fitted. Average daily gain was the slope from this model, and the live weight was estimated for each animal halfway through the feed intake measurements.

Residual feed intake was estimated using multiple linear regression. Average daily feed intake over 35 d was adjusted by fitting midweight and ADG as covariates. The unexplained variation after fitting this model was the residual feed intake. Residual feed intake was estimated only for groups with significant effects of live weight and ADG from the regression model (groups with reliable intake; Appendix 3).

We included 3 traits for CH_4 adjusted for average daily intake, live weight, and ADG. These traits indicate the amount of CH_4 produced per kilogram intake, live weight, or ADG, with these traits fitted as covariates to CH_4. Fitting these traits as covariates means that issues related to ratios traits, such as nonnormal distributions and skewed means, are avoided (Allison et al., 1995). All significant interactions between these covariates and fixed effects were included. Extreme outliers were removed from traits if they were more than 4 times the SD. Methane, O_2, and CO_2 traits were measured 2 or 3 times per sheep (2 cohorts were measured 3 times as they were part of another CH_4 trial). We analyzed the mean of these traits, but because they were not measured the same number of times, we included a weighting for the number of records.

Fixed Effects

For all traits, we fitted fixed effects for group, birth and rear type, sex, pen, and age of measurement.

For CH_4 adjusted for intake, live weight, and ADG, we fit these covariates as second-order polynomials, because it significantly improved the fit of the model ($P < 0.05$). All significant interactions between fixed effects were also included.

Genetic Analysis

Variance components for each trait were estimated first with a univariate model. The results of these univariate models were used as starting values in the bivariate analysis. To test if the genetic correlations between traits were of magnitude significantly greater than 0, we used likelihood ratio tests to compare the fit of 2 models. The first model was with no restrictions on the estimates for variance and covariance, and the second model restricted the covariance between the 2 traits to 0. The second model therefore reflects our null hypothesis that the genetic correlation is equal to 0. We also tested if genetic correlations were significantly different from 1 or −1 using likelihood ratio tests.

Univariate Analysis. The heritability of traits was estimated using univariate models:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{e} \quad \text{and} \quad [1]$$

$$\mathbf{y} = \mathbf{X_b} + \mathbf{Z_a a} + \mathbf{ZQ_g g} + \mathbf{e}, \quad [2]$$

in which **y** are the observations for the traits, **b** is the vector of fixed effects, **a** is the vector of animal genetic effects, **g** are the genetic group effects, and **e** is the vector of error effects. **X** and **Z** are the incidence matrices and $\mathbf{ZQ_g}$ is the matrix that describes the proportion of genes in each animal that originate from each genetic group. The random effects of **e** are normally distributed with a mean of 0.

Genetic group effects find the variance explained by breed types. Each animal has the contribution from Merino, terminal, or maternal breeds. To test if including genetic groups significantly improved the fit of the traits, we used likelihood ratio tests to compare a model with genetic effects with a model without genetic effects. The effect of genetic group was not significant ($P > 0.05$) for any trait, so it was not included in any model. The same criteria were used to test genetic groups for each trait. Genetic groups were not significant because only 4% of sheep had contributions of more than 25% from genes of maternal and terminal breeds. Therefore, based on the definition of genetic groups that we used, it was difficult to find significant variance in traits due to genetic groups.

After testing for genetic groups, we also tested for maternal genetic effects using the model

Table 2. Description of intake and gas traits measured for sheep with their units

Trait	Unit	Description
Intake	kg DM/d	Average daily intake over 35 d
Intake24	kg DM/d	Total intake for 24 h before CH_4 measurement
Intake48	kg DM/d	Total intake for 48 h before CH_4 measurement
RFI	kg DM/d	Residual feed intake
CH_4	g/d	Methane (standard temperature and pressure)
CO_2	%	Carbon dioxide
O_2	%	Oxygen

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{e}, \quad [3]$$

in which **m** are the maternal genetic due to the dam and $\mathbf{Z_m}$ relate the **m** vectors to the traits (**y**).

Model [3] was tested against model [1] using log-likelihood ratio tests to see if adding maternal genetic effects significantly improved the fit of the model to the data. There were no significant ($P > 0.05$) permanent environmental effects caused by the dam for any traits. Maternal genetic effects were significant ($P < 0.05$) for most traits at postweaning and hogget ages (more detail in Table 3).

Bivariate Analysis. We estimated phenotypic and genetic correlations between all traits using a bivariate model:

$$\begin{bmatrix}\mathbf{y}_{tr1}\\ \mathbf{y}_{tr2}\end{bmatrix} = \begin{bmatrix}\mathbf{X}_{tr1} & 0\\ 0 & \mathbf{X}_{tr2}\end{bmatrix}\begin{bmatrix}\mathbf{b}_{tr1}\\ \mathbf{b}_{tr2}\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{a\,tr1} & 0\\ 0 & \mathbf{Z}_{a\,tr2}\end{bmatrix}\begin{bmatrix}\mathbf{a}_{tr1}\\ \mathbf{a}_{tr2}\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{m\,tr1} & 0\\ 0 & \mathbf{Z}_{m\,tr2}\end{bmatrix}\begin{bmatrix}\mathbf{m}_{tr1}\\ \mathbf{m}_{tr2}\end{bmatrix} + \begin{bmatrix}\mathbf{e}_{tr1}\\ \mathbf{e}_{tr2}\end{bmatrix},$$

in which $\mathbf{y}_{tr1}$ and $\mathbf{y}_{tr2}$ are the observations for the first and second trait in the analysis, $\mathbf{b}_i$ is the vector of fixed effects, $\mathbf{a}_i$ is the vector of additive genetic effects, $\mathbf{m}_i$ is the vector of maternal genetic effects, $\mathbf{e}_i$ is the vector of error effects, and $\mathbf{X}_i$ and $\mathbf{Z}_{a\,i}$, and $\mathbf{Z}_{m\,i}$ are the incidence matrices (i = tr1 and tr2). The random effects $\mathbf{a}_i$, $\mathbf{m}_i$, and $\mathbf{e}_i$ are bivariate and normally distributed with mean 0 and variance

$$\text{var}\begin{bmatrix}\mathbf{e}_{tr1}\\ \mathbf{e}_{tr2}\end{bmatrix} = \mathbf{R} \otimes \mathbf{I}, \text{ in which } \mathbf{R} = \begin{bmatrix}\sigma^2_{e\,tr1} & \sigma_{e\,tr1\,tr2}\\ \sigma_{e\,tr1\,tr2} & \sigma^2_{e\,tr2}\end{bmatrix};$$

$$\text{var}\begin{bmatrix}\mathbf{a}_{tr1}\\ \mathbf{a}_{tr2}\end{bmatrix} = \mathbf{G} \otimes \mathbf{A}, \text{in which } \mathbf{G} = \begin{bmatrix}\sigma^2_{a\,tr1} & \sigma_{a\,tr2\,tr1}\\ \sigma_{a\,tr1\,tr2} & \sigma^2_{a\,tr2}\end{bmatrix}; \text{and}$$

$$\text{var}\begin{bmatrix}\mathbf{m}_{tr1}\\ \mathbf{m}_{tr2}\end{bmatrix} = \mathbf{N} \otimes \mathbf{M}, \text{ in which } \mathbf{N} = \begin{bmatrix}\sigma^2_{m\,tr1} & \sigma_{m\,tr2\,tr1}\\ \sigma_{m\,tr1\,tr2} & \sigma^2_{m\,tr2}\end{bmatrix},$$

in which **I** is the identity matrix, **A** is the additive genetic relationship matrix between animals, and **M** is the maternal genetic relationship matrix between animals.

Variance components and their SE were estimated using ASReml (Gilmour et al., 2006). When maternal genetic effects were significant for both traits, we estimated the covariance between traits. When only one of the traits in the bivariate model had significant maternal genetic effects, we included maternal genetic effects for only that trait.

RESULTS

Trait Means and Heritabilities

Sheep ate more as they aged for all feed intake traits (24 h, 48 h, and 35 d; Table 4). Residual intake was close to zero at all ages (Table 4). Hoggets, on average, produced more CH_4, CO_2, and O_2 than sheep at postweaning age and adults (Table 4).

Maternal genetic effects were not significant or were low for all traits. Hoggets had the highest heritability for all traits (Table 3). Feed intake measured across 35 d was the most heritable (range 0.31 to 0.49; 4). Feed intake across 24 (range 0.15 to 0.19) and 48 h (range 0.18 to 0.20) was less heritable than feed intake measured across 35 d (Table 3). Residual feed intake had low to moderate heritability (range 0.07 to 0.29; Table 3). Oxygen (range 0.10 to 0.20) and CO_2 (range 0.08 to 0.28) had similar heritabilities and were more heritable than CH_4 (range 0.11 to 0.14; Table 3).

Table 3. Phenotypic variance (σ_p^2), heritability (h^2), and maternal heritability (m^2) of intake and gas traits for sheep with SE in parentheses. When maternal genetic effects were not significant we excluded them from the model and from the table (–)

Trait[1]	Age[2]	σ_p^2	h^2	m^2
Intake	PW	0.06 (0.003)	0.31 (0.09)	–
	HG	0.07 (0.004)	0.49 (0.09)	–
	A	0.13 (0.010)	0.42 (0.14)	–
Intake24	PW	0.44 (0.024)	0.15 (0.04)	0.2 (0.03)
	HG	0.24 (0.018)	0.19 (0.07)	–
	A	0.42 (0.043)	0.17 (0.09)	–
Intake48	PW	1.33 (0.084)	0.18 (0.06)	0.03 (0.04)
	HG	1.19 (0.101)	0.20 (0.09)	0.00 (0.00)
	A	2.26 (0.335)	0.20 (0.11)	0.00 (0.00)
RFI	PW	0.03 (0.002)	0.17 (0.07)	–
	HG	0.03 (0.0016)	0.29 (0.08)	–
	A	0.06 (0.004)	0.07 (0.08)	–
CH_4	PW	92 (3.6)	0.11 (0.03)	0.00 (0.00)
	HG	114 (8.0)	0.14 (0.05)	0.02 (0.03)
	A	109 (9.6)	0.10 (0.06)	–
CO_2	PW	0.12 (0.010)	0.18 (0.08)	0.00 (0.00)
	HG	0.23 (0.018)	0.28 (0.09)	0.03 (0.04)
	A	0.34 (0.029)	0.08 (0.06)	–
O_2	PW	0.12 (0.009)	0.20 (0.08)	0.00 (0.00)
	HG	0.27 (0.017)	0.20 (0.06)	–
	A	0.29 (0.031)	0.10 (0.08)	–

[1]Intake = average daily intake over 35 d; Intake24 = total intake 24 h before CH_4 measurement; Intake48 = total intake 48 h before CH_4 measurement; RFI = residual feed intake.

[2]PW = postweaning; HG = hogget; A = adult

Correlations between Traits

Genetic correlations between feed intake measured across 24 h, 48 h, and 35 d were higher than phenotypic correlations except for adults (Table 5). All genetic correlations between feed intake traits were significantly higher than 0 and significantly different from 1 ($P < 0.01$; Table 5). Genetic correlations between intake traits were higher in sheep at postweaning age (range 0.94 to 0.99) than hoggets (range 0.70–0.97) and adults (range 0.46–0.98; Table 5). Genetic correlations (range 0.62 to 0.99) between feed intake traits and residual feed intake were higher than phenotypic correlations (range 0.28 to 0.83; Table 5) for sheep at postweaning age and hoggets. Correlations between feed intake traits and residual feed intake were highest in sheep at postweaning age. All genetic correlations between feed intake traits and residual feed intake in sheep at postweaning age and hoggets, but not adults, were significantly greater than 0 ($P < 0.01$; Table 5).

Table 4. Number of records (no.) and mean value of intake and gas traits for sheep with SD of traits measured at postweaning, hogget, and adult ages

	Postweaning age			Hogget age			Adult age		
Trait[1]	No.	Mean	SD	No.	Mean	SD	No.	Mean	SD
Intake, kg/d	1,476	1.4	0.30	975	2.03	0.32	406	2.18	0.40
Intake24, kg	1,318	1.9	0.95	676	2.2	0.39	361	2.34	0.53
Intake48, kg	1,291	4.2	2.22	602	4.7	0.89	269	5.4	1.31
RFI, kg	1,470	−0.0091	0.21	1,046	−0.0002	0.18	443	0.0006	0.24
CH_4, mg/min	2,665	22.7	5.83	964	25.7	8.36	436	21.9	7.20
CO_2, %	753	2.5	0.37	969	3.3	0.50	439	3.2	0.42
O_2, %	755	18.8	0.38	970	17.9	0.51	439	17.8	0.42

[1]Intake = average daily intake over 35 d; Intake24 = total intake for 24 h before CH_4 measurement; Intake48 = total intake for 48 h before CH_4 measurement; RFI = residual feed intake.

Table 5. Phenotypic (above diagonal) and genetic (below diagonal) correlations between feed intake averaged across 35 d and feed intake measured 24 and 48 h before CH_4 measurements. Bold genetic correlations are significantly different from 0 ($P < 0.05$)

	Intake[1]	Intake24[2]	Intake48[3]	RFI[4]
Postweaning age				
Intake	–	0.67 (0.01)	0.73 (0.01)	0.83 (0.00)
Intake24	0.94 (0.08)	–	0.90 (0.00)	0.49 (0.02)
Intake48	0.99 (0.06)	0.94 (0.04)	–	0.54 (0.02)
RFI	0.87 (0.05)	0.99 (0.16)	0.84 (0.13)	
Hogget				
Intake	–	0.56 (0.02)	0.60 (0.02)	0.64 (0.01)
Intake24	0.70 (0.26)	–	0.81 (0.01)	0.28 (0.03)
Intake48	0.73 (0.18)	0.97 (0.08)	–	0.30 (0.03)
RFI	0.82 (0.06)	0.66 (0.24)	0.62 (0.24)	
Adult				
Intake	–	0.82 (0.01)	0.82 (0.01)	0.65 (0.02)
Intake24	0.46 (0.68)	–	NC[5]	0.47 (0.04)
Intake48	0.98 (0.07)	NC	–	0.45 (0.04)
RFI	0.33 (0.89)	0.42 (0.81)	0.74 (0.49)	

[1]Intake = average daily intake over 35 d.

[2]Intake24 = total intake 24 h before CH_4 measurement.

[3]Intake48 = total intake 48 h before CH_4 measurement.

[4]RFI = residual feed intake.

[5]NC = the model did not converge because of singularity problems.

Table 6. Phenotypic (above diagonal) and genetic (below diagonal) correlations between CH_4, CO_2, and O_2. Bold genetic correlations are significantly different from 0 ($P < 0.05$)

	CH_4	CO_2	O_2
Postweaning age			
CH_4	–	0.78 (0.01)	−0.66 (0.02)
CO_2	0.76 (0.12)*	–	−0.71 (0.01)
O_2	−0.48 (0.19)	−0.93 (0.07)	–
Hogget			
CH_4	–	0.74 (0.01)	−0.59 (0.02)
CO_2	0.86 (0.07)*	–	NC[1]
O_2	−0.71 (0.16)	NC	–
Adult			
CH_4	–	0.71 (0.02)	−0.62 (0.03)
CO_2	0.34 (0.60)	–	−0.90 (0.00)
O_2	−0.13 (0.67)	−0.98 (0.07)	–

[1]NC = the model did not converge because of singularity problems.

*Genetic correlations are not significantly different from 1 ($P < 0.05$).

At all ages, CH_4 and CO_2 had strong phenotypic (range 0.71 to 0.74) and genetic correlations (range 0.34 to 0.86; Table 6). Genetic correlations between CH_4 and CO_2 were not significantly different from 1 ($P < 0.05$; Table 6). At all ages, O_2 had strong negative phenotypic (range −0.62 to −0.90) and genetic (range −0.13 to −0.98; Table 6) correlations with CO_2 and CH_4. The genetic correlations between CO_2 and O_2 were significantly different from 0 in sheep at postweaning age and adults ($P < 0.05$; Table 6). The bivariate analysis between CO_2 and O_2 in hoggets did not converge. It probably did not converge because the traits were too similar.

Intake traits had positive phenotypic correlations with CH_4, CH_4 yield traits, and CO_2 (range 0.24 to 0.74; Table 7). Some of these correlations in adults were close to 0. Most of the negative phenotypic correlations between intake traits and O_2 were medium to high (range −0.48 to −0.70; Table 7), with adults having mostly low positive correlations. Residual feed intake had phenotypic correlations with CH_4, CH_4 yield traits, O_2, and CO_2 in the same direction as intake but not as strong (Table 7). Correlations between residual feed intake, CH_4, CH_4 yield, and CO_2 ranged from 0.08 to 0.30 (Table 7) and with O_2 ranged between −0.25 and −0.27 (Table 7). Intake traits and residual feed intake in adults had inconsistent phenotypic correlations in the opposite direction than in sheep at postweaning age and hoggets except for O_2, CH_4 produced per kilogram eaten, and CH_4 produced per kilogram ADG (Table 7).

Intake and residual feed intake had genetic correlations with gas traits mostly in the same direction as the phenotypic correlations (Table 8). All intake and residual feed intake traits in hoggets had significant positive genetic correlations with CH_4 ($P < 0.01$; range 0.76 to 0.90; Table 8). All intake and residual feed intake traits in sheep at postweaning age and hoggets had significant positive genetic correlations with CO_2 ($P < 0.01$; range 0.65 to 0.96; Table 8). All intake and residual feed intake traits in sheep at postweaning age and hoggets had significant negative genetic correlations with O_2 ($r < 0.01$; range −0.95 to −0.62; Table 8), apart from residual feed intake in sheep at postweaning age. All intake and residual feed intake traits in hoggets had significant genetic correlations with CH_4 produced per kilogram ADG ($P < 0.05$; range 0.66 to 0.89; Table 8). The only other significant correlation was between intake and CH_4 produced per kilogram intake in hoggets ($P < 0.01$; 0.90; Table 8).

Correlations between Ages

All correlations for each trait between ages were positive (Table 9). All genetic correlations between ages were significantly lower than 1 ($P < 0.05$; Table 9). Genetic correlations were higher than phenotypic correlations (Table 9). Most of the genetic correlations between hoggets and adults (range 0.62 to 0.90) were higher than those between sheep at postweaning age and hoggets (range 0.36 to 0.81) and those between sheep at postweaning age and adults (range 0.00 to 0.64). Residual feed intake generally was not phenotypically or

Table 7. Phenotypic correlations between intake and gas traits

Intake trait[1]	Gas trait[2]					
	CH_4	CO_2	O_2	CH_4/LW	CH_4/Intake	CH_4/ADG
Postweaning age						
Intake	0.46 (0.02)	0.74 (0.01)	−0.70 (0.02)	0.48 (0.02)	0.20 (0.02)	0.32 (0.02)
Intake24	0.49 (0.02)	0.57 (0.02)	−0.55 (0.02)	0.48 (0.02)	0.33 (0.02)	0.37 (0.02)
Intake48	0.52 (0.02)	0.57 (0.02)	−0.56 (0.02)	0.51 (0.02)	0.32 (0.02)	0.38 (0.02)
RFI	0.16 (0.02)	0.30 (0.04)	−0.25 (0.04)	0.11 (0.03)	0.08 (0.03)	0.14 (0.02)
Hogget						
Intake	0.54 (0.02)	0.71 (0.01)	−0.67 (0.01)	0.24 (0.04)	0.45 (0.02)	0.44 (0.03)
Intake24	0.49 (0.02)	0.57 (0.02)	−0.48 (0.03)	0.29 (0.03)	0.37 (0.03)	0.39 (0.03)
Intake48	0.43 (0.03)	0.52 (0.03)	−0.48 (0.03)	0.20 (0.04)	0.30 (0.03)	0.31 (0.03)
RFI	0.18 (0.03)	0.29 (0.03)	−0.27 (0.03)	−0.34 (0.03)	0.21 (0.03)	0.18 (0.03)
Adult						
Intake	0.57 (0.03)	0.01 (0.07)	−0.00 (0.07)	0.00 (0.07)	0.52 (0.03)	0.47 (0.04)
Intake24	0.61 (0.03)	0.51 (0.04)	0.25 (0.04)	0.37 (0.05)	0.55 (0.03)	0.50 (0.04)
Intake48	0.01 (0.07)	0.68 (0.03)	0.00 (0.05)	−0.00 (0.07)	0.39 (0.05)	0.24 (0.06)
RFI	−0.70 (0.02)	−0.00 (0.07)	−0.32 (0.04)	−0.30 (0.05)	0.28 (0.04)	0.28 (0.04)

[1]Intake = average daily intake over 35 d; Intake24 = total intake 24 h before CH_4 measurement; Intake48 = total intake 48 h before CH_4 measurement; RFI = residual feed intake.

[2]CH_4/LW = CH_4 per kilogram live weight; CH_4/Intake = CH_4 per kilogram intake; CH_4/ADG = CH_4 per kilogram ADG.

genetically correlated between ages. Intake (range 0.64 to 0.78) and CH_4 (range 0.62 to 0.86) had consistent high correlations between ages (Table 9). Oxygen and CO_2 had high genetic correlations between sheep at postweaning age and hoggets (range 0.72 to 0.76) and between hoggets and adults (range 0.69 to 0.90; Table 9). Oxygen and CO_2 had low genetic correlations between sheep at postweaning age and adults (range 0.03 to 0.16; Table 9).

All traits had genetic correlations significantly higher than 0 between sheep at postweaning age and hoggets ($P < 0.01$; Table 9), apart from residual feed intake. Only intake and CH_4 had significant genetic correlations ($P < 0.01$; Table 9) between sheep at postweaning age and adults. All traits had genetic correlations significantly higher than 0 between hoggets and adults ($P < 0.01$; Table 9) except for CH_4 and residual feed intake.

DISCUSSION

Merino sheep that eat less and are more feed efficient produce less CH_4. We therefore accepted our hypothesis that breeding sheep that eat less and have a lower residual feed intake produce less CH_4. More efficient sheep are, therefore, also better for the environment. In addition, selecting for intake and gas traits in sheep at postweaning age and hoggets will also select the best-performing adults for these traits.

The phenotypic and genetic correlations between intake and residual feed intake with CH_4 ratio traits were positive but weaker than just CH_4. Most genetic correlations were not significant, although hoggets that eat more and are inefficient produce more CH_4 per kilogram of ADG. Also, hoggets that eat more also produce more CH_4 per kilogram of feed they eat. Sheep that have a lower residual feed intake eat less, but this relationship appears to weaken as the sheep age. This may be because sheep at postweaning age, hoggets, and adults have different requirements for ADG and maintenance, and perhaps this is influenced by reproduction.

Our results are consistent with other research that found that more efficient animals produce less CH_4 (Hegarty et al., 2007; Alcock and Hegarty, 2011). Efficient animals produce less CH_4 perhaps because a proportion of GE from feed is lost as CH_4 (Eckard et al., 2010). The percentage of dietary GE lost as CH_4 decreases as intake increases, but these fractional losses are low on high-quality grain diets (2–3% in cattle; Johnson and Johnson, 1995). This increased efficiency of animals may be better explained using CH_4 production corrected for live weight. There is genetic and phenotypic variation in this trait, and there are some animals that eat the same but produce different amounts of CH_4. The proportion of GE intake lost as CH_4 may be a better way to select for CH_4–efficient animals than residual feed intake.

Feed intake and residual feed intake are favored traits for increasing the efficiency of production. Feed intake, however, is expensive and impractical to measure in large numbers and unlikely to be commercially used by Australian sheep breeders. We found that feed intake measured over 24 and 48 h was similar to that measured over 35 d. This is important because measuring over a short period would reduce costs, time, and labor and make feed intake easier to measure. These 24- and 48-h measurements were after at least 14 d in the feed intake shed (on ad libitum feed of high quality).

Table 8. Genetic correlations between intake and gas traits. Bold correlations are significantly different from 0 ($P < 0.05$)

Intake trait[1]	Gas trait[2]					
	CH_4	CO_2	O_2	CH_4/LW	CH_4/Intake	CH_4/ADG
Postweaning age						
Intake	0.42 (0.18)	0.86 (0.07)	−0.82 (0.09)	0.44 (0.18)	0.16 (0.21)	0.20 (0.22)
Intake24	0.53 (0.21)	0.71 (0.16)	−0.76 (0.13)	0.51 (0.21)	0.23 (0.24)	0.35 (0.25)
Intake48	0.51 (0.19)	0.79 (0.12)	−0.74 (0.13)	0.47 (0.20)	0.14 (0.23)	0.32 (0.23)
RFI	0.17 (0.25)	0.68 (0.22)	−0.40 (0.25)	0.14 (0.25)	0.07 (0.24)	0.06 (0.26)
Hogget						
Intake	0.77 (0.13)	0.96 (0.03)	−0.95 (0.03)	0.44 (010)	0.90 (0.10)	0.71 (0.17)
Intake24	0.88 (0.13)*	0.86 (0.10)	−0.62 (0.20)	0.21 (0.55)	0.65 (0.25)	0.66 (0.25)
Intake48	0.90 (0.14)	0.62 (0.19)	−0.63 (0.20)	0.22 (0.71)	0.60 (0.28)	0.78 (0.26)
RFI	0.76 (0.18)	0.65 (0.14)	−0.62 (0.15)	−0.87 (3.60)	0.46 (0.24)	0.89 (0.27)
Adult						
Intake	0.69 (0.21)*	0.35 (0.32)	−0.23 (5.52)	−0.28 (0.42)	0.47 (0.27)	0.65 (0.26)
Intake24	0.64 (0.28)*	0.20 (4.27)	−0.88 (0.18)	0.27 (0.51)	0.37 (0.37)	0.64 (0.34)
Intake48	0.51 (0.34)	0.49 (1.64)	−0.12 (4.50)	−0.31 (0.49)	0.12 (0.40)	0.28 (0.47)
RFI	0.21 (0.73)	0.06 (2.40)	−0.09 (1.00)	−0.04 (0.71)	0.36 (0.55)	0.81 (0.88)

[1]Intake = average daily intake over 35 d; Intake24 = total intake 24 h before CH_4 measurement; Intake48 = total intake 48 h before CH_4 measurement; RFI = residual feed intake.

[2]CH_4/LW = CH_4 per kilogram live weight; CH_4/Intake = CH_4 per kilogram intake; CH_4/ADG = CH_4 per kilogram ADG.

*Genetic correlations are not significantly different from 1 ($P < 0.05$).

Therefore, we need to find out how many days are needed to get accurate measurements of feed intake. These strong genetic correlations are encouraging, however, for measuring feed intake on high-quality diets.

Feed intake had strong genetic correlations with CH_4, CO_2, and O_2. Therefore, these traits are good alternatives for measuring feed intake. These gas traits were measured with PAC over 40 min. They are, therefore, a lot cheaper and faster to measure than feed intake. Therefore, genetic improvement of gas production is one way to get permanent and continuous reductions in CH_4 and simultaneously potentially improve efficiency.

Robinson and Oddy (2016) found that including CH_4 into a breeding index will improve profit because of its high genetic relationship with feed intake, particularly when feed intake is not measured. Therefore, the high economic value of intake and the strong genetic correlation between intake and CH_4, CO_2, and O_2 could make these traits very important. The relationship between feed intake and gas production should be tested across several feed types to understand the full potential of using gases to select for feed intake.

Oxygen and CO_2 were more heritable than CH_4 and so are better candidate traits for feed intake. Also, phenotypically and genetically, feed intake is most closely explained by CO_2 and O_2. Methane also has medium to strong phenotypic and genetic correlations with intake but not as strong as CO_2 and O_2. Because of these close relationships between intake and gas traits, sheep that are more efficient with lower residual feed intake also produce less CH_4 and CO_2.

Robertson (1959) suggested that genotype × environment interactions are important if the genetic correlation is below 0.8. Therefore, selecting for low CH_4 in sheep at postweaning age will also select the hoggets and adults with the lowest CH_4. Also, selecting for low CO_2 in hoggets will also select the adults with lower CO_2. Alternatively, Mulder et al. (2006) suggested that optimal breeding strategies are affected when genetic correlations between environments are below 0.61. Therefore, breeders can select for intake in sheep at postweaning age and residual feed intake, O_2, and CO_2 in hoggets without having to select again in adults. This is important for breeding programs because it decreases the generation interval and increases the response to selection. In other words, the best animals can be identified earlier and used earlier for breeding. Therefore, their genes are passed on earlier, making the breeding program more effective.

If CH_4 were to be included into a selection index, then it may be best to include CH_4 concentration instead of CH_4 yield. Hegarty and McEwan (2010) suggested that CH_4 produced per kilogram of product should be used instead of including CH_4 alone. Methane yields, however, involve traits that often have high phenotypic or genetic correlations with CH_4, which makes it difficult to control the direction of change for both traits in the yield. For example, Blaxter and Clapperton (1965) found that the lowest CH_4 was yielded (CH_4 produced per kg eaten) at the highest feed intakes on forages. The positive genetic correlations between lower CH_4 corrected for intake and intake suggest that increasing CH_4 yield will also increase intake. A decrease in feed intake

Table 9. Phenotypic and genetic correlations between ages for feed intake, residual feed intake, CH_4, CO_2, and O_2. Bold genetic correlations are significantly different from 0 ($P < 0.05$)

Trait[1]	Postweaning/hogget ages	Postweaning/adult ages	Hogget/adult ages
Phenotypic			
Intake	0.48 (0.03)	0.25 (0.05)	0.58 (0.03)
RFI	0.15 (0.03)	0.04 (0.05)	0.33 (0.04)
CH_4	0.40 (0.03)	0.38 (0.04)	0.32 (0.04)
CO_2	0.43 (0.03)	0.32 (0.05)	0.46 (0.03)
O_2	0.38 (0.04)	0.25 (0.06)	0.45 (0.03)
Genetic			
Intake	0.74 (0.09)	0.64 (0.17)	0.78 (0.12)
RFI	0.36 (0.22)	0.00 (0.53)	0.75 (0.74)
CH_4	0.81 (0.14)	0.86 (0.15)	0.62 (0.26)
CO_2	0.76 (0.16)	0.03 (0.56)	0.90 (0.22)
O_2	0.72 (0.17)	0.16 (0.50)	0.69 (0.40)

[1]Intake = average daily intake over 35 d; RFI = residual feed intake.

will increase CH_4 yield. Therefore, for a simultaneous decrease in intake and CH_4 yield, the reduction in CH_4 will have to be higher than the reduction in intake. Therefore, it is difficult to include CH_4 yield in breeding programs. Therefore, including yield in breeding programs for sheep would not be more effective than simultaneously selecting for lower CH_4 and intake. In addition, the differences in heritability and additive genetic variance between intake and CH_4 suggest that responses to selection would be easier for feed intake compared with CH_4. Therefore, more selection pressure would be needed for CH_4 than intake to decrease it compared with feed intake. In conclusion, to have a more transparent selection strategy, CH_4 should be in an index with other production traits and feed intake.

We used a high-quality pellet in our experiments, but most Merino sheep in Australia are managed outdoors in warm to hot summer Mediterranean climatic zones (Squires, 2006). These areas have high variation in pasture quality and quantity during the year (Rossiter, 1966). Therefore, we need to understand if these relationships between intake, residual feed intake, CH_4, and other gas traits are consistent on different types of feed; for example, in cattle, the relationship between CH_4 and feed intake depends on the diet. Nkrumah et al. (2006) found that steers selected for low residual feed intake produced less CH_4 on concentrates than on a silage and hay diet. Jones et al. (2011) found that cows selected for low residual feed intake had lower CH_4 emissions per kilogram of live weight on high-quality pasture but not on low-quality pasture. Feed efficiency and CH_4 production can also be affected by feeding method.

Robinson et al. (2013) found that automatic feeder pens where animals may need to wait for the feeder can decrease residual feed intake. Therefore, there could be difficulties applying these results to grazing conditions. Furthermore, a high-energy diet would cause significant changes in the rumen environment, particularly when adjusting from a grass diet. Also, CH_4 production depends on feeding pattern, including how often and for how long animals eat (Johnson et al., 1998). Also, CH_4 production depends on how fast feed flows through the rumen (Czerkawski and Breckenridge, 1969). If feed is digested more slowly on lower-quality feed, then this could change the amount of CH_4 produced. Therefore, our results need to be tested using different quality feeds before they can be applied to commercial conditions.

Our estimate of heritability for CH_4 production (0.09) was similar to the estimate by Goopy et al. (2016; 0.13) measured in portable respiration chambers but lower than that by Pinares-Patiño et al. (2013; 0.29) measured in respiration chambers. Our estimate of CH_4 yield (CH_4 corrected for intake; 0.19) was higher than that of Pinares-Patiño et al. (2013; 0.13). Our estimate of heritability for feed intake and residual feed intake (intake = 0.47 and residual feed intake = 0.26) was similar to the estimate of Snowder and van Vleck (2003; intake = 0.39 and residual feed intake = 0.26). Therefore, our feed intake estimates are similar to those of other research, suggesting that our feed intake experiments were successful. In addition, removing groups of feed intake that did not regress with live weight and ADG was justified.

Some of the adult correlations were inconsistent with those between postweaning and hogget ages for intake and gas traits; however, this could simply be a result of the number of adult records available ($n = 444$) and not enough animals linked between postweaning and hogget ages with adults. It may also be that multiple years of reproduction may also be influencing the traits measured. The lack of precision for the adult results suggests that more adult records are required to validate these results.

Additionally, adults ate more than hoggets and so are expected to produce more CH_4. Hoggets, however, produced more CH_4 and more variation in CH_4 production. The phenotypic correlation between hoggets and adults for feed intake was higher (0.58) than for CH_4 (0.33). The genetic correlation between hoggets and adults for feed intake (0.78) was also slightly higher and more accurate than that for CH_4 (0.62). Therefore, feed intake is both phenotypically and genetically more consistent across ages than CH_4 production. Also, the residual correlation between hoggets and adults was lower for CH_4 than for feed intake. Therefore, hoggets produce more CH_4 per kilogram of intake due to unexplained variance that is not heritable.

Appendix 1. Summary of records per trait for each age as females and males

Trait[1]	Age[2]	Females	Males
Intake	PW	1,251	216
Intake	HG	934	31
Intake	A	441	0
Intake24	PW	1,170	163
Intake24	HG	649	23
Intake24	A	363	0
Intake48	PW	1,143	160
Intake48	HG	579	19
Intake48	A	270	0
RFI	PW	1,250	216
RFI	HG	934	31
RFI	A	441	0
CH_4	PW	1,910	767
CH_4	HG	928	31
CH_4	A	438	0
CO_2	PW	706	54
CO_2	HG	933	31
CO_2	A	441	0
O_2	PW	708	54
O_2	HG	934	31
O_2	A	441	0

[1]Intake = average daily intake over 35 d; Intake24 = total intake 24 h before CH_4 measurement; Intake48 = total intake 48 h before CH_4 measurement; RFI = residual feed intake.

[2]PW = postweaning; HG = hogget; A = adult.

Appendix 2. Summary of records per trait measured in the same animals across ages

	Age[2]		
Trait[1]	Age 1	Age 2	Number
Intake	PW	HG	788
Intake	PW	A	373
Intake	HG	A	392
Intake24	PW	HG	461
Intake24	PW	A	288
Intake24	HG	A	250
Intake48	PW	HG	408
Intake48	PW	A	181
Intake48	HG	A	196
RFI	PW	HG	788
RFI	PW	A	373
RFI	HG	A	392
CH_4	PW	HG	943
CH_4	PW	A	447
CH_4	HG	A	386
CO_2	PW	HG	474
CO_2	PW	A	228
CO_2	HG	A	390
O_2	PW	HG	476
O_2	PW	A	230
O_2	HG	A	390

[1]Intake = average daily intake over 35 d; Intake24 = total intake 24 h before CH_4 measurement; Intake48 = total intake 48 h before CH_4 measurement; RFI = residual feed intake.

[2]PW = postweaning; HG = hogget; A = adult.

Conclusions

Selecting for lower feed intake and residual feed intake will reduce methane and carbon dioxide production in Merino sheep eating high-quality pellets. Additionally, carbon dioxide could be used as an indicator trait to select for feed intake. Carbon dioxide is a good indicator trait because it has high genetic and phenotypic correlations with feed intake and a higher accuracy than methane and oxygen. Therefore, it can be cheaply and quickly measured in portable accumulation chambers, providing a good alternative to expensive feed intake measurements. Finally, sheep can be selected for feed intake, residual feed intake, or gas traits at either postweaning or hogget ages.

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Appendix 3. The coefficients, SE, *t*-probability (t pr.), and variation explained (%ve) from linear regression of weight and ADG of 28 groups of male and female Merino sheep measured for feed intake at postweaning (PW), hogget (HG), or adult (A) ages between 2010 and 2016. Intake was considered reliable for groups that had significant coefficients for live weight and growth.

Group	Age	Sex	No.	Weight	SE	t pr.	ADG	SE	t pr.	%ve
1	PW	Male	163	0.04	0.019	0.049	1.38	0.547	0.013	7
2	PW	Female	120	0.04	0.024	0.069	2.53	0.709	<0.001	17
3	PW	Female	99	0.06	0.031	0.06	3.07	1.510	0.046	11
4	PW	Male	76	0.01	0.020	0.543	2.06	0.865	0.020	11
5	PW	Female	190	0.08	0.015	<0.001	1.02	0.353	0.004	21
6	PW	Male	196	0.09	0.019	<0.001	0.46	0.594	0.443	11
7	PW	Male	48	0.05	0.045	0.244	−1.00	1.760	0.574	0
8	PW	Female	41	0.00	0.036	0.99	1.34	1.440	0.357	0
9	PW	Male	208	0.03	0.016	0.026	1.30	0.539	0.016	6
10	PW	Female	224	0.09	0.016	<0.001	1.24	0.681	0.069	16
11	PW	Female	222	0.04	0.017	0.014	1.18	0.830	0.157	6
12	PW	Male	176	0.05	0.014	<0.001	2.20	0.549	<0.001	17
13	PW	Female	193	0.04	0.011	<0.001	−3.41	0.413	<0.001	30
14	HG	Male	41	0.16	0.017	<0.001	1.47	0.304	<0.001	75
15	HG	Female	188	0.12	0.007	<0.001	1.19	0.230	<0.001	67
16	HG	Female	97	0.08	0.014	<0.001	3.14	0.372	<0.001	69
17	PW	Female	133	0.09	0.010	<0.001	0.62	0.295	0.039	47
18	PW	Female	202	0.08	0.005	<0.001	1.64	0.166	<0.001	76
19	HG	Female	220	0.10	0.009	<0.001	0.63	0.170	<0.001	45
20	PW	Female	105	0.08	0.009	<0.001	1.32	0.352	<0.001	68
21	PW	Female	119	0.11	0.011	<0.001	0.61	0.218	0.006	55
22	HG	Female	225	0.06	0.008	<0.001	1.71	0.224	<0.001	48
23	PW	Female	218	0.06	0.005	<0.001	1.67	0.177	<0.001	62
24	A	Female	102	0.09	0.016	<0.001	2.59	0.391	<0.001	58
25	HG	Female	66	0.08	0.013	<0.001	1.61	0.384	<0.001	49
26	A	Female	224	0.04	0.008	<0.001	3.34	0.257	<0.001	49
27	HG	Female	214	0.05	0.008	<0.001	2.85	0.176	<0.001	62
28	A	Female	118	0.05	0.010	<0.001	2.67	0.266	<0.001	62
Total animals			2,816							
Total PW animals			2,733							
Total PW males			874	(371 reliable intake)						
Total PW females			1,866	(1,405 reliable intake)						
Total HG males			41	(41 reliable intake)						
Total HG females			1,010	(1,010 reliable intake)						
Total A females			444	(444 reliable intake)						

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