

Genetic parameters of methane emissions determined using portable accumulation chambers in lambs and ewes grazing pasture and genetic correlations with emissions determined in respiration chambers¹

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ABSTRACT: Methane (CH₄) emission traits were previously found to be heritable and repeatable in sheep fed alfalfa pellets in respiration chambers (RC). More rapid screening methods are, however, required to increase genetic progress and to provide a cost-effective method to the farming industry for maintaining the generation of breeding values in the future. The objective of the current study was to determine CH₄ and carbon dioxide (CO₂) emissions using several 1-h portable accumulation chamber (PAC) measurements from lambs and again as ewes while grazing ryegrass-based pasture. Many animals with PAC measurements were also measured in RC while fed alfalfa pellets at 2.0 × maintenance metabolizable energy requirements (ME_m). Heritability estimates from mixed models for CH₄ and CO₂ production (g/d) were 0.19 and 0.16, respectively, when measured using PAC with lambs; 0.20 and 0.27, respectively, when measured using PAC with ewes; and 0.23 and 0.34, respectively, when measured using RC with lambs. For measured

gas traits, repeatabilities of measurements collected 14 d apart ranged from 0.33 to 0.55 for PAC (combined lambs and ewes) and were greater at 0.65 to 0.76 for the same traits measured using RC. Genetic correlations (r_g) between PAC in lambs and ewes were 0.99 for CH₄, 0.93 for CH₄ + CO₂, and 0.85 for CH₄/(CH₄ + CO₂), suggesting that CH₄ emissions in lambs and ewes are the same trait. Genetic correlations between PAC and RC measurements were lower, at 0.62 to 0.67 for CH₄ and 0.41 to 0.42 for CH₄ + CO₂, likely reflecting different environmental conditions associated with the protocols used with the 2 measurement methods. The CH₄/(CH₄ + CO₂) ratio was the most similar genetic trait measured using PAC (both lambs and ewes, 63% and 66% selection efficiency, respectively) compared with CH₄ yield (g/kg DMI) measured using RC. These results suggest that PAC measurements have considerable value as a rapid low-cost method to estimate breeding values for CH₄ emissions in sheep.

Key words: animal variation, breeding, greenhouse gas, proxy, spot-sampling, young and mature

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INTRODUCTION

Ruminants are globally a significant source of anthropogenic CH₄ emissions (Schaefer et al., 2016) and one of the main contributors to New Zealand's greenhouse gas inventory (MfE, 2017). Methane emissions per unit of DMI (i.e., CH₄ yield) were found to be heritable and repeatable in sheep fed alfalfa pellets in respiration chambers (RC) (Pinares-Patiño et al., 2013), proving that animal breeding is an option to mitigate CH₄ emissions. However, progress in generating these breeding values for CH₄ emissions is slow and expensive when animals have to be measured in RC. There have also been concerns that measuring CH₄ under controlled conditions may not reflect CH₄ emitted under the grazing conditions that predominate on NZ farms. More rapid spot-sampling methods that can be used on-farm would speed up this selection progress and provide a cost-effective and relevant method to the farming industry for maintenance of breeding values in the future. These methods could also enable extension of similar breeding programs for sheep of different genetic background and in different countries, and provide greater power to estimate correlated animal traits. One such spot-sampling method, that can measure both gas concentrations and flux, is the portable accumulation chamber (PAC) (Goopy et al., 2011). The method involves placing sheep in a simple and transportable sealed container for 40 min to 1 h and measuring the accumulated gas concentrations at regular intervals using a monitoring device attached to a one-way valve. Results of CH₄ output from PAC have been shown to be heritable and repeatable, but are influenced by environmental factors (e.g., trial site, animal age, and diet) and to date have not been compared with strictly controlled conditions, such as RC (Goopy et al., 2016). Significantly, DMI cannot be measured directly in relation to PAC measurements, and therefore, CH₄ yield cannot be determined. The ratio of CH₄ to CO₂ or total gas (CH₄ + CO₂) has been suggested as a proxy for CH₄ yield where DMI is not known (Madsen et al., 2010), but its relationship to CH₄ yield in sheep has not been validated.

The objectives of the current study were to estimate the heritability and repeatability of CH₄- and CO₂-emission parameters determined using repeated PAC measurements as lambs and as ewes grazing ryegrass-based pasture. Furthermore, genetic and phenotypic correlations were determined for different gas emission traits within methods (PAC and RC) and animal category (lamb and ewe), and between PAC measures and the same gas emission parameters determined in RC from lambs fed alfalfa pellets.

MATERIALS AND METHODS

The animal experiments conducted adhered to the guidelines of the 1999 New Zealand Animal Welfare Act and AgResearch Code of Ethical Conduct. The PAC and RC trials of the current study were, respectively, approved by the AgResearch Invermay (Mosgiel, NZ) and AgResearch Grasslands (Palmerston North, NZ) Animal Ethics committees.

Animals

Animals in the dataset were from 7 New Zealand Sheep Improvement Limited (SIL) flocks including 1 AgResearch flock (SIL flock number 2638), 3 Central Progeny Test (CPT) flocks (SIL flock numbers 4640, 4757, 9153), 2 industry flocks (SIL flock numbers 2629, 4474), and the “methane yield selection” flock (SIL flock number 3633). In total, 3601 lambs were measured at least once using PAC or RC of which 2,255 lambs (born between 2012 and 2015; at 7 ± 3 [\pm StDev; range 4 to 13] mo of age) had 4,733 separate 1-h measurement records using PAC and 2,110 lambs (born in 2007 and between 2009 and 2015; at 9 ± 2 [range 6 to 12] mo of age) had 8,655 daily records using RC. Of these, 844 animals had both PAC and RC measurements as lambs. In addition, 1,251 (2,387 records) animals were measured in PAC as yearling/ewes (called ewe in this paper from this point onwards; 42 ± 19 [range 16 to 88] mo of age) of which 874 animals also had RC measurements as lambs and 698 had PAC measurements as lambs. Flock, birth

year, sex, and measurement year and season are detailed in [Supplementary Table S1](#).

“Methane yield selection” flock animals ([Pinares-Patiño et al., 2013](#)) were progeny of maternal dual-purpose sires generated by the New Zealand industry CPT program ([McLean et al., 2006](#)), comprising Coopworth, Romney, Perendale, Texel, and composite breeds, where the latter breed consisted primarily of combinations of the former breeds with additional infusions of Finn and East Friesian. All rams were mated to composite ewes. Ewe progeny born in 2007 and between 2009 and 2011 (and also ram lambs born in 2009) was measured for CH₄ emissions per unit of feed DMI (i.e., CH₄ yield) ([Pinares-Patiño et al., 2013](#)), with the most extreme low and high 10% retained for further breeding. The lines were closed in 2012 and all sires used from 2012 onwards were born in the high and low CH₄-yield selection flocks, which are currently maintained at 100 ewes per line. Progeny from the CH₄-yield selection flock included in the dataset was born between 2010 and 2015.

Portable Accumulation Chamber Measurements

Sheep were measured in PACs made of polycarbonate sheet with an internal volume of 827 L (1.17-m length × 1.15-m height × 0.615-m width), similar to those described by [Goopy et al. \(2011\)](#). A standard protocol was used where the animals were set stocked for 3 d prior to measurement on ad libitum pasture allowance with average pre- and post-grazing pasture masses of 2500 ± 550 kg DM/ha and 2000 ± 375 kg DM/ha (from ground level), respectively, determined using a rising plate meter (Farmworks Systems Ltd., Feilding, NZ). The day before PAC measurements pasture pluck samples were collected from the paddock grazed, dried at 65 °C, ground through a 1-mm screen, and scanned by near-infrared spectroscopy for nutritional composition analysis as described by [Corson et al. \(1999\)](#). The average pasture DM content was 18 ± 3.1% and contained in % of DM (± StDev): 9 ± 0.8 ash, 4 ± 0.6 lipids, 22 ± 4.2 crude protein, 50 ± 7.8 neutral detergent fiber, 23 ± 2.9 acid detergent fiber, 12 ± 3.4 soluble sugars and starch, and 81 ± 4.5 organic matter digestibility ([Supplementary Table S2](#)).

Before PAC measurements, animals were taken off-pasture at 9:00 a.m., weighed to determine BW, and PAC measurements conducted in lots of 12 animals for 1 h each. The first PAC measurements did not start until the animals were off-pasture for at least 30 min. Animals remained off-pasture until they were recorded, and time after removal from pasture was also recorded. Gas measurements were recorded at the start (0 min), middle (~30 min), and

end (~60 min) of the PAC measurement period along with exact time of measurement. Ambient temperature and atmospheric pressure were also recorded. Concentrations of CH₄, CO₂, and O₂ in the PACs were determined using an ENVCO Eagle 2 hand-held gas meter (The Environmental Collective Ltd., Auckland, NZ) following the manufacturer's instructions, including calibrations and filter checks. The analyzer was calibrated daily, before and after all sheep were measured in PAC, using standard gases containing 100, 1,000, and 5,000 ppm CH₄ (BOC Ltd., Auckland, NZ). Little analyzer drift was detected and the quoted accuracy of the data in the current study is ±5% of the recorded value. The difference between individual measurements at the start and end of the measurement period was transformed using the standard gas (at standard temperature and pressure) equations to calculate g CH₄, g CO₂, and g O₂ ([Brouwer, 1965](#)), with inclusion of a correction for the volume of the animals in the chamber. The volume of the animal was calculated as 1 kg BW = 1.01 liter. The sum of CO₂ and CH₄ production in moles (total gas) and molar CH₄/(CO₂ + CH₄) ratio was calculated, as was the respiration quotient (RQ; i.e., CO₂/O₂). Measurements were discarded where the water seal was broken by animal activity or if other abnormalities were detected. After animal removal from the PAC, a household leaf blower was used to reduce CH₄ and CO₂ concentrations to background levels and the floor was cleaned before the next animals were measured.

Measurements on the same animals using PAC were repeated after approximately 14 d. A subset of 289 lambs had additional repeat PAC measurements in a different season ([Supplementary Table S1](#)). A subset of 32 ewes had repeat PAC measurements in a different season (summer then autumn in 2013), and 19 ewes (born 2009) had PAC measurements in different years (2013 and 2015). The full schedule of measurements using PAC is provided in [Supplementary Table S1](#).

Respiration Chamber Measurements

RC measurements were performed with the standard protocol described by [Pinares-Patiño et al. \(2013\)](#) using a system with 24 open-circuit RC described in detail by [Pinares-Patiño et al. \(2012\)](#). Approximately 96 sheep between 6 and 12 mo of age were fed alfalfa pellets (Dunstan Nutrition Ltd., Hamilton, NZ) at 2.0 × maintenance metabolizable energy requirements (ME_m) according to Australian Feed Standards ([CSIRO, 2007](#)), and measurements were performed for 2 × 48-h periods approximately 14 d apart (round). Animals were weighed before

and after RC measurements to determine their average BW. The management of the 4 groups of 24 animals was staggered consecutively in time. The RC doors were opened twice daily around 08:30 a.m. and 03:30 p.m. for approximately 15 min for excreta removal and feeding. Emissions for these periods were extrapolated by taking the average of the last 12 values before opening the door. There were 2,110 lambs (born 2007 and 2009–2015) with 8655-d measurements in RC between 2008 and 2016.

Animal Allocation to PAC and RC

Animals were allocated to chambers (PAC and RC) using a randomized incomplete block design where allocation to a measurement “lot” of 12 animals in PAC or to a measurement “group” of 24 animals in RC was random within sire but balanced across lots/groups. Subsequent allocation to individual chambers was random across the animals allocated to a lot/group. Analysis revealed no consistent chamber effects, but lot/group effects were significant. This approach reduced confounding between lots/groups and genetic relatedness of individuals.

Statistical Analysis

Initially, a variety of fixed effects and covariate models were tested for traits measured using PAC with lambs, using PAC with ewes and using RC with lambs. For PAC traits, fixed effects fitted included birth/rearing rank (brr; born single, twin or triplet, reared as single, twin, or triplet) and contemporary groups PACcg4 (birth year—birth flock—sex combination) and PACcgp (measurement date—PAClot combination, where PAClot is a group of 12 animals measured together). Covariates fitted were BW at PAC measurement, birth day deviation from birth year within birth flock mean (bdev) and age of dam as both a linear (aod) and a quadratic (aod²) function. For RC traits, fixed effects fitted included brr and contemporary groups cg4 (birth year—birth flock—sex combination) and cg5 (birth year—lot—group—round combination, where lot defines a mob of 96 animals, group is a submob of up to 24 animals within a lot measured contemporaneously, and round indicates the measurement time 14 d apart). Covariates fitted for RC traits were bdev, aod, and aod². PAC and RC trait final models were obtained by backwards elimination (Supplementary Table S3). A choice was made not to fit BW as a covariate, but to estimate the genetic parameters separately, so that both the genetic and phenotypic covariances of the trait with BW could be estimated. This allows greater flexibility for subsequent modeling.

An investigation into whether scaling was required to adjust for the variance within contemporary PAC groups with varying waiting times after removal off-pasture till PAC measurements, and RC groups measured at consecutive times, clearly indicated that it was necessary. This was undertaken by calculating the ratio of the actual value/group mean and multiplying by the overall trait mean. PAC traits, except for BW, were deviated from the contemporary group (PACcgp) mean; RC traits except for BW, CH₄ + CO₂, and CH₄/(CH₄ + CO₂) were deviated from the contemporary group (cg5) mean. For nonscaled traits, PACcgp and cg5 were fitted in the appropriate analysis model for PAC and RC traits, respectively.

Pedigree records were obtained from all 7 birth flocks of animals, born from 1990 to 2015. The data were analyzed in a mixed model using ASREML 3.0 (Gilmour et al., 2009), fitting animal as a random effect with covariances proportional to the numerator relationship matrix (Supplementary Table S3). Maternal random effects were fitted for PAC measures on lambs and for RC traits. Maternal random effect for PAC gas measures in ewes approached zero and was, therefore, excluded from the model. For PAC measures on lambs, permanent environmental effects between rounds 14 d apart, and between seasons, were included in the model. For PAC measures on ewes, an additional permanent environment effect was added to account for measurements in different years. For RC, permanent environment effects were added to account for measurements on separate days within a round and between rounds 14 d apart. Single trait analyses provided heritability (direct and maternal) and repeatability estimates (Table 1 and Supplementary Tables S4–S6), whereas bivariate analyses provided genetic and phenotypic correlations between traits (Tables 2 and 3 and Supplementary Table S7). The heritability (h^2) was classified as low (< 0.2), moderate (0.2 to 0.4), or high (> 0.4); r_g as low (< 0.2), moderate (0.2 to 0.6), and high (> 0.6); and repeatability and r_p as low (< 0.35), moderate (0.35 to 0.75), and high (> 0.75). The efficiency (Q) of indirect selection for CH₄ yield determined in RC using a single measure of emission traits in PAC was calculated as follows: $Q = r_g (h_{PAC}/h_{RC})$, where h is the square root of the heritability (Table 4).

RESULTS

Heritability and Repeatability

All PAC traits for lambs and ewes had moderate heritabilities between 0.16 and 0.35 (Table 1), except RQ, which was not heritable (Supplementary

Table 1. Heritability (h^2) and repeatability estimates (\pm SE) for gas emission parameters of lambs measured using respiration chambers and portable accumulation chambers (PAC) and ewes using PAC

Trait	Mean	StDev	σ_p	h^2 (SE)		Repeatability (SE)		
				Direct	Maternal	14 day	Season	Year
Respiration chamber, lambs								
BW, kg	45.9	8.00	4.80	0.35 (0.05)	0.07 (0.03)	0.89 (0.01)	– ¹	– ¹
CH ₄ , g/d	24.0	2.94	2.81	0.23 (0.04)	0.05 (0.02)	0.65 (0.01)	–	–
CO ₂ , g/d	1066	99.5	94.5	0.34 (0.05)	0.03 (0.02)	0.76 (0.01)	–	–
CH ₄ + CO ₂ , mol/d	25.5	3.71	2.34	0.33 (0.05)	0.03 (0.02)	0.76 (0.01)	–	–
CH ₄ /(CH ₄ + CO ₂), mol/mol	0.059	0.006	0.005	0.17 (0.03)	0.03 (0.02)	0.43 (0.02)	–	–
CH ₄ yield, g/kg DMI	16.0	1.42	1.39	0.13 (0.02)	0.02 (0.02)	0.38 (0.02)	–	–
Portable accumulation chamber, lambs								
BW, kg	39.3	7.79	4.45	0.35 (0.07)	0.08 (0.03)	0.90 (0.005)	0.81 (0.01)	–
CH ₄ , g/d	7.5	2.12	2.13	0.19 (0.04)	0.04 (0.02)	0.33 (0.02)	0.36 (0.03)	–
CO ₂ , g/d	623	117.9	117.9	0.16 (0.04)	0.07 (0.02)	0.41 (0.02)	0.37 (0.03)	–
CH ₄ + CO ₂ , mol/d	14.6	2.73	2.73	0.16 (0.04)	0.07 (0.02)	0.41 (0.02)	0.38 (0.03)	–
CH ₄ /(CH ₄ + CO ₂), mol/mol	0.032	0.008	0.008	0.19 (0.04)	0.02 (0.02)	0.27 (0.02)	0.25 (0.03)	–
Portable accumulation chamber, ewes								
BW, kg	69.9	8.96	7.60	0.33 (0.07)	– ²	0.97 (0.002)	0.88 (0.03)	0.74 (0.08)
CH ₄ , g/d	13.0	3.09	3.08	0.20 (0.05)	–	0.39 (0.03)	0.43 (0.11)	0.14 (0.13)
CO ₂ , g/d	987	232.9	229.7	0.27 (0.05)	–	0.54 (0.02)	0.37 (0.13)	0.15 (0.18)
CH ₄ + CO ₂ , mol/d	23.3	5.39	5.31	0.27 (0.05)	–	0.54 (0.02)	0.40 (0.12)	0.14 (0.18)
CH ₄ /(CH ₄ + CO ₂), mol/mol	0.036	0.009	0.009	0.25 (0.05)	–	0.38 (0.03)	0.21 (0.11)	0.21 (0.11)

¹Not determined.²Maternal random effect for PAC gas measures in ewes approached zero and is, therefore, excluded from the model.**Table 2.** Genetic correlation (\pm SE; below diagonal) and phenotypic correlation (\pm SE; above diagonal) for gas emission parameters within lambs in respiration chambers or portable accumulation chambers or within ewes in portable accumulation chambers

Trait	BW	CH ₄	CO ₂	CH ₄ + CO ₂	CH ₄ /(CH ₄ + CO ₂)	CH ₄
	Kg	g/d	g/d	mol/d	mol/mol	g/kg DMI
Respiration chamber, lambs						
BW, kg	–	0.61 (0.01)	0.78 (0.01)	0.78 (0.01)	0.04 (0.02)	0.003 (0.02)
CH ₄ , g/d	0.83 (0.04)	–	0.74 (0.01)	0.77 (0.01)	0.65 (0.01)	0.67 (0.01)
CO ₂ , g/d	0.96 (0.01)	0.84 (0.04)	–	~1	–0.05 (0.02)	0.11 (0.02)
CH ₄ + CO ₂ , mol/d	0.93 (0.02)	0.85 (0.04)	~1	–	0.01 (0.02)	0.15 (0.02)
CH ₄ /(CH ₄ + CO ₂), mol/mol	0.09 (0.12)	0.50 (0.09)	–0.01 (0.13)	0.01 (0.11)	–	0.84 (0.01)
CH ₄ , g/kg DMI	0.02 (0.13)	0.50 (0.10)	0.06 (0.13)	0.07 (0.13)	0.93 (0.02)	–
Portable accumulation chamber, lambs						
BW, kg	–	0.43 (0.02)	0.36 (0.02)	0.38 (0.02)	0.22 (0.02)	–
CH ₄ , g/d	0.52 (0.11)	–	0.41 (0.01)	0.44 (0.01)	0.79 (0.01)	–
CO ₂ , g/d	0.55 (0.11)	0.37 (0.14)	–	~1	–0.19 (0.02)	–
CH ₄ + CO ₂ , mol/d	0.56 (0.11)	0.41 (0.13)	~1	–	–0.16 (0.02)	–
CH ₄ /(CH ₄ + CO ₂), mol/mol	0.21 (0.14)	0.82 (0.05)	–0.21 (0.15)	–0.17 (0.16)	–	–
Portable accumulation chamber, ewes						
BW, kg	–	0.31 (0.02)	0.40 (0.02)	0.41 (0.02)	–0.07 (0.03)	–
CH ₄ , g/d	0.59 (0.13)	–	0.26 (0.03)	0.35 (0.02)	0.67 (0.02)	–
CO ₂ , g/d	0.65 (0.10)	0.32 (0.02)	–	~1	–0.47 (0.02)	–
CH ₄ + CO ₂ , mol/d	0.65 (0.10)	0.33 (0.15)	~1	–	–0.45 (0.02)	–
CH ₄ /(CH ₄ + CO ₂), mol/mol	–0.13 (0.15)	0.60 (0.02)	–0.60 (0.11)	–0.58 (0.11)	–	–

Tables S4 and S5). Maternal heritability was significant for total gas and CO₂ production. These heritabilities were in a similar range to the heritability determined in RC (Table 1). Repeatabilities of gas measurement with PAC (for lambs and

ewes) within season (14 d apart in PAC chambers) and between seasons were moderate, ranging from 0.21 to 0.54, which were, in general, lower than the comparable repeatabilities 14 d apart across rounds in RC. Repeatability of PAC gas

Table 3. Genetic and phenotypic correlations (\pm SE) for gas emission parameters determined using respiration chambers for lambs or portable accumulation chambers (PAC) for lambs and ewes

Trait	Genotypic correlation				Phenotypic correlation					
	BW	CH ₄	CO ₂	CH ₄ + CO ₂	CH ₄ /(CH ₄ + CO ₂)	BW	CH ₄	CO ₂	CH ₄ + CO ₂	CH ₄ /(CH ₄ + CO ₂)
PAC, lambs vs respiration chamber, lambs										
BW, kg	0.90 (0.03)	0.71 (0.10)	0.49 (0.13)	0.51 (0.12)	0.42 (0.14)	0.80 (0.01)	0.34 (0.02)	0.30 (0.02)	0.31 (0.02)	0.12 (0.03)
CH ₄ , g/d	0.63 (0.09)	0.67 (0.11)	0.04 (0.17)	0.08 (0.17)	0.73 (0.13)	0.54 (0.02)	0.27 (0.02)	0.19 (0.02)	0.20 (0.02)	0.14 (0.02)
CO ₂ , g/d	0.79 (0.06)	0.65 (0.11)	0.41 (0.13)	0.43 (0.13)	0.37 (0.15)	0.66 (0.01)	0.29 (0.02)	0.25 (0.02)	0.26 (0.02)	0.11 (0.03)
CH ₄ + CO ₂ , mol/d	0.82 (0.05)	0.68 (0.11)	0.40 (0.13)	0.42 (0.13)	0.44 (0.15)	0.69 (0.01)	0.32 (0.02)	0.26 (0.02)	0.27 (0.02)	0.12 (0.03)
CH ₄ /(CH ₄ + CO ₂), mol/mol	0.08 (0.15)	0.38 (0.15)	-0.36 (0.18)	-0.33 (0.18)	0.57 (0.13)	0.05 (0.03)	0.08 (0.02)	0.01 (0.02)	0.01 (0.02)	0.08 (0.02)
CH ₄ , g/kg DMI	0.05 (0.16)	0.34 (0.15)	-0.38 (0.18)	-0.35 (0.18)	0.54 (0.14)	0.03 (0.03)	0.08 (0.02)	0.01 (0.02)	0.01 (0.02)	0.08 (0.02)
PAC, ewes vs. respiration chamber, lambs										
BW, kg	0.81 (0.08)	0.56 (0.14)	0.34 (0.13)	0.35 (0.13)	0.03 (0.13)	0.55 (0.02)	0.20 (0.03)	0.22 (0.03)	0.22 (0.03)	-0.02 (0.03)
CH ₄ , g/d	0.57 (0.11)	0.62 (0.14)	0.15 (0.14)	0.16 (0.14)	0.32 (0.15)	0.36 (0.03)	0.16 (0.03)	0.13 (0.03)	0.13 (0.03)	0.03 (0.03)
CO ₂ , g/d	0.76 (0.09)	0.58 (0.14)	0.43 (0.12)	0.44 (0.12)	-0.03 (0.14)	0.46 (0.02)	0.18 (0.03)	0.21 (0.03)	0.21 (0.03)	-0.03 (0.03)
CH ₄ + CO ₂ , mol/d	0.75 (0.09)	0.59 (0.13)	0.41 (0.12)	0.41 (0.12)	0.01 (0.14)	0.48 (0.02)	0.19 (0.03)	0.22 (0.03)	0.23 (0.03)	-0.02 (0.03)
CH ₄ /(CH ₄ + CO ₂), mol/mol	0.14 (0.14)	0.33 (0.15)	-0.18 (0.14)	-0.17 (0.14)	0.50 (0.14)	0.06 (0.03)	0.05 (0.02)	-0.01 (0.03)	-0.01 (0.03)	0.06 (0.02)
CH ₄ , g/kg DMI	0.15 (0.14)	0.29 (0.15)	-0.22 (0.15)	-0.23 (0.15)	0.47 (0.14)	0.05 (0.03)	0.06 (0.02)	0.01 (0.02)	0.01 (0.02)	0.05 (0.02)
PAC, lambs vs PAC, ewes										
BW, kg	0.89 (0.07)	0.65 (0.11)	0.58 (0.13)	0.60 (0.13)	0.36 (0.15)	0.67 (0.02)	0.30 (0.03)	0.31 (0.03)	0.32 (0.03)	0.10 (0.03)
CH ₄ , g/d	0.71 (0.12)	0.99 (0.10)	0.34 (0.16)	0.38 (0.16)	0.85 (0.12)	0.25 (0.03)	0.21 (0.02)	0.10 (0.03)	0.11 (0.03)	0.14 (0.02)
CO ₂ , g/d	0.61 (0.12)	0.44 (0.13)	0.93 (0.08)	0.93 (0.08)	-0.25 (0.15)	0.24 (0.03)	0.12 (0.03)	0.31 (0.02)	0.31 (0.02)	-0.07 (0.03)
CH ₄ + CO ₂ , mol/d	0.62 (0.12)	0.46 (0.13)	0.93 (0.08)	0.93 (0.08)	-0.23 (0.15)	0.24 (0.03)	0.13 (0.03)	0.31 (0.02)	0.31 (0.02)	-0.07 (0.03)
CH ₄ /(CH ₄ + CO ₂), mol/mol	0.10 (0.14)	0.38 (0.14)	-0.65 (0.12)	-0.62 (0.12)	0.85 (0.09)	0.02 (0.03)	0.08 (0.03)	-0.17 (0.03)	-0.17 (0.03)	0.18 (0.02)

Table 4. Heritability (h^2) (\pm SE) of emission parameters (determined using respiration chambers [RC] for lambs or portable accumulation chambers for lambs and ewes) without or with covariates, genetic correlations (r_g) (\pm SE), and efficiency (Q)¹ for a single emission parameter measure to select indirectly for RC CH₄ yield (g/kg DMI)

Trait	Covariate	h^2	r_g with RC CH ₄ yield	Q value (%)
Respiration chamber, lambs				
CH ₄ , g/d	–	0.27 (0.04)	0.50 (0.10)	73
	BW, kg	0.27 (0.04)	0.50 (0.10)	73
	CO ₂ , g/d	0.20 (0.03)	0.76 (0.06)	95
	CH ₄ + CO ₂ , mol/d	0.20 (0.03)	0.78 (0.06)	97
CH ₄ /(CH ₄ + CO ₂), mol/mol	–	0.18 (0.03)	0.93 (0.02)	105
Portable accumulation chamber, lambs				
CH ₄ , g/d	–	0.18 (0.04)	0.34 (0.15)	40
	BW, kg	0.15 (0.03)	0.40 (0.15)	43
	CO ₂ , g/d	0.18 (0.04)	0.51 (0.14)	60
	CH ₄ + CO ₂ , mol/d	0.18 (0.04)	0.53 (0.14)	61
CH ₄ /(CH ₄ + CO ₂), mol/mol	–	0.16 (0.03)	0.54 (0.14)	61
Portable accumulation chamber, lambs				
CH ₄ , g/d	–	0.19 (0.05)	0.29 (0.15)	35
	BW, kg	0.14 (0.04)	0.29 (0.17)	30
	CO ₂ , g/d	0.19 (0.05)	0.42 (0.15)	49
	CH ₄ + CO ₂ , mol/d	0.19 (0.05)	0.43 (0.15)	51
CH ₄ /(CH ₄ + CO ₂), mol/mol	–	0.24 (0.05)	0.48 (0.15)	65

¹Q = $r_g (h_{PAC_emission\ trait} / h_{RC_CH4\ yield})$, where h is the square root of the heritability.

measurements of ewes between years was lower than within and between seasons of the same year. Repeatability was in general lower for the ratio traits [CH₄/(CH₄ + CO₂) and CH₄ yield] than for gas production traits (CH₄, CO₂, and CH₄ + CO₂) for all 3 gas measurement datasets.

Genetic and Phenotypic Correlations

Genetic and phenotypic correlations within and between measurement datasets are given in Tables 2 and 3 and Supplementary Table S7. Within all 3 measurement datasets, r_g were moderate to high (0.52 to 0.96) for BW with gross emissions (CH₄, CO₂, and CH₄ + CO₂) and for CH₄ (g/d) with CH₄/(CH₄ + CO₂) (0.50 to 0.82) (Table 2). Corresponding r_p were also moderate to high (0.31 to 0.78) for BW with gross emissions (CH₄, CO₂, and CH₄ + CO₂) and for CH₄ with CH₄/(CH₄ + CO₂) (0.65 to 0.79). Genetic correlations of CH₄ production with CO₂ or CH₄ + CO₂ were moderate (0.32 to 0.41) when measured using PAC (both lambs and ewes), whereas these correlations were strong in RC (0.84 and 0.85). Phenotypic correlations of CH₄ production with CO₂ or CH₄ + CO₂ also were moderate (0.26 to 0.44) when measured using PAC (both lambs and ewes), whereas these correlations were moderate to strong in RC (0.74 to 0.77). Within RC data, CH₄ yield (g/kg DMI) had a strong r_g and r_p with CH₄/(CH₄ + CO₂) ratio (0.93 and 0.84, respectively) and

moderate r_g and r_p with CH₄ production (0.50 and 0.67, respectively). Methane yield did not correlate significantly with other parameters. Genetic correlations for all gas emission parameters (e.g., CH₄ and CO₂) of PAC measurements as lambs and ewes were very strong (r_g = 0.85 to 0.99) and much higher than the corresponding r_p (0.18 to 0.31) (Table 3).

Genetic correlations of PAC measurements as lambs and ewes with the same parameters measured in RC were moderate (r_g = 0.41 to 0.67), but higher than corresponding r_p (0.06 to 0.27).

The efficiency (Q) of indirect selection for RC CH₄ yield using PAC traits (both as lambs and ewes) was greater using CH₄/(CH₄ + CO₂) ratio and CH₄ production with CH₄ + CO₂ as a covariate than for CH₄ production without a covariate or with BW as a covariate (Table 4).

DISCUSSION

Genetic Parameters of Methane Production

The heritability estimates for CH₄ production (g/d) and CH₄ yield (g/kg DMI) (0.23 and 0.13, respectively) with RC in the current study, which included an additional 3,400 records in addition to the record reported in Pinares-Patiño et al. (2013), remained similar to those previously reported (0.29 and 0.13, respectively)

(Pinares-Patiño et al., 2013). Similar heritability estimates for CH₄ production and yield (0.27 and 0.22, respectively) were found for Angus beef cattle when measured in RC (Hayes et al., 2016). The heritability estimates for CH₄ production in PAC as lambs and ewes were similar (0.19 and 0.20, respectively) to those in RC in the current study and similar heritability estimates were reported for sheep at different sites in Australia measured 2 or 3 times in PAC for 1 h (0.19 and 0.23, respectively) (Robinson et al., 2014). There was a strong r_g for CH₄ production measured in PAC as lambs and ewes with CH₄ production in RC (0.67 and 0.62, respectively) in the current study, suggesting that they are similar genetic traits. Repeatability of CH₄ production approximately 14 d apart in PAC (both as lambs and ewes) was, however, only about half the repeatability in RC (0.33 to 0.39 vs. 0.65), which is consistent with previous findings in sheep (0.24 vs. 0.49, respectively), reported by Bickell et al. (2011). During the course of PAC measurements, the quality of the pasture varied over time, DMI varied due to ad libitum feed being offered, and the time of removal from pasture until the time of PAC measurement differed for the same individual sheep on which for PAC measurements were made 14 d apart. In contrast, the batch of alfalfa pellets, the feeding level, and measurement time were the same for RC measurements made on the same individual sheep 14 d apart. These likely explain the lower repeatability with PAC compared with the controlled experimental conditions during RC measurements. Interestingly, repeatability of CH₄ production in PAC 14 d apart and in different seasons (within 1 yr) was similar, suggesting that the accuracy of the measurement remained consistent over a long time period. Donoghue et al. (2016) also found a similar repeatability of CH₄ production and CH₄ yield in beef cattle when comparing a RC measurement and repeat measurements after between 61 and 120 d and after between 121 and 450 d.

Genetic Parameters of Methane Yield

Methane yield (g/kg DMI) could not be determined with grazing sheep measured using PAC since DMI is not known. There was, however, a moderately positive r_g for CH₄ production measured in PAC both as lambs and ewes (0.34 and 0.29) with CH₄ yield measured in RC, and an r_g of 0.50 for CH₄ production measured in RC with CH₄ yield measured in RC. These suggest that genetic selection for reduced CH₄ production in PAC will also reduce

CH₄ yield, with a moderate efficiency (Q-value) of 40% and 35% for lambs and ewes, respectively.

The main driver of CH₄ production is DMI, explaining 76% and 90% of the variation in sheep and cattle fed cut pasture (Swainson et al., 2018; Jonker et al., 2017a). Selection for reduced CH₄ production might therefore result in selection of animal with lower DMI. This is not a problem if these animals have similar performance (e.g., low residual feed intake trait and same number of lambs born), whereas animal numbers on the farm remain the same. However, if growth performance is proportionally reduced, or lambs born per ewe are decreased, then total gross emissions of the farm system might remain similar or increase. However, selection for reduced CH₄ production can also result in selection of animals with reduced CH₄ yield either due to increased DMI effects (Swainson et al., 2018) or due to sheep genetics (Pinares-Patiño et al., 2013). Therefore, if selecting animals with similar performance traits (McLean et al., 2006; Byrne et al., 2012; Paganoni et al., 2017), selection for PAC CH₄ production should result in animals with either lower DMI (but similar performance) or lower CH₄ yield (or both) and therefore reduce gross farm system emissions. This selection might, however, result in a wide range of phenotypes with low CH₄ emissions, and this might result in animals with different CH₄ genotypes when individuals with different underlying phenotypes are used for breeding.

Relationship of CO₂ and CH₄ Emissions

Voluntary DMI with ad libitum feed offered is in general related to the BW of the animal (CSIRO, 2007) and to gaseous carbon emissions (Aubry and Yan, 2015; Jonker et al., 2016). The use of animal BW or CH₄ + CO₂ emissions as a covariate for CH₄ production (Herd et al., 2016) or using the ratio of CH₄ to CH₄ + CO₂ emissions (Madsen et al., 2010; Lassen et al., 2012) has therefore been suggested as indicators of CH₄ yield when DMI is unknown. The genetic correlation with CH₄ yield in RC was greatest for the CH₄/(CH₄ + CO₂) ratio measured with PAC (both as lambs and ewes) (r_g = 0.54 and 0.47), slightly lower for CH₄ production with CH₄ + CO₂ emissions as a covariate (r_g = 0.53 and 0.43), and much lower for CH₄ production with BW as a covariate (r_g = 0.40 and 0.29). Within RC, r_g with CH₄ yield was stronger for the CH₄/(CH₄ + CO₂) ratio (r_g = 0.93) than for CH₄ production with either CH₄ + CO₂ emissions (r_g = 0.78) or BW (r_g = 0.53) as a covariate. Therefore, CH₄/(CH₄ + CO₂) ratio appears to most genetically similar to CH₄ yield, followed

by CH₄ production with CH₄ + CO₂ emissions as a covariate, whereas CH₄ production with or without BW as a covariate appeared genetically less similar to CH₄ yield in the current study. In growing beef cattle, however, there was a strong r_g and r_p between CH₄ per unit of BW and CH₄ yield (Donoghue et al., 2013; Herd et al., 2014). This metric has been suggested as a possible measure of CH₄ intensity (per unit of animal product) in growing sheep and beef cattle (Donoghue et al., 2013; Herd et al., 2014; Robinson et al., 2014), which is probably suitable for growing animals of similar age but might result in the selection of heavier animals when determined in mature ewes.

The heritability estimates for the CH₄/(CH₄ + CO₂) ratio (0.17 to 0.25) and CH₄ production with either CH₄ + CO₂ emissions (0.19 to 0.20) or BW (0.15 to 0.27) as a covariate determined using RC or PAC with lambs and ewes were also, in general, slightly greater than for CH₄ yield in RC (0.13). A similar heritability estimate (0.16) for CH₄/CO₂ ratio was found in dairy cows when measured in multiple spot-samples during visits to milk robots (Lassen and Løvendahl, 2016). Heritability of CH₄ production with BW as a covariate (0.19) was previously found to be similar to CH₄ yield (0.21) in beef cattle measured in RC (Donoghue et al., 2013). Altogether these results suggest that CH₄/(CH₄ + CO₂) ratio and CH₄ production with CH₄ + CO₂ emissions as a covariate in PAC are the most similar genetic traits to CH₄ yield in RC.

Methane yield in sheep decreases with increasing DMI, even with small increases in DMI (Swainson et al., 2018; Jonker et al., 2018), whereas the CH₄/CO₂ ratio increases with increasing DMI (Lassen et al., 2012; Jonker et al., 2016). Also, the CH₄/CO₂ ratio is not constant during the day, with the ratio being higher during the day than during the night in lactating dairy cows (Lassen et al., 2012; Brask et al., 2015). It decreases in sheep with increasing time off-pasture (Robinson et al., 2014). Robinson et al. (2014) found that there was quite a steep decline in CH₄ emissions in sheep with increasing time from pasture, whereas CO₂ emissions declined only slightly during the same time. Scaling of contemporary groups (12 animals measured at once in separate PAC units) was performed in the current study relative to overall mean value, which should eliminate this effect of time off-pasture. Within RC measurements from 684 sheep, it was found that there is a strong positive r_g for CH₄ production (0.89) and yield (0.76) separated in 24 × 1-h intervals with daily average of the same parameters (McEwan et al., 2012), suggesting that sampling time would have a minor effect on the genetic selection. This correlation was, however, not reported for the CH₄/(CH₄ + CO₂) ratio.

Hellwing et al. (2013) found that CH₄ production predicted with CH₄/CO₂ ratio explained 55% of the variation in actual CH₄ production in lactating dairy cows, with the majority of the rest of the variation explained by differences in CH₄, CO₂, milk production, and BW. There was a negligible to low r_g and r_p for BW with CH₄/(CH₄ + CO₂) within any of 3 datasets (PAC with lambs and ewes and lambs in RC) in the current study, suggesting that selection for CH₄/(CH₄ + CO₂) would not lead to selection for animals with a greater BW. There was a positive r_g and r_p for CH₄ production with CH₄/(CH₄ + CO₂) in all 3 datasets in the current study, which was also observed, in terms of r_p , in sheep (Robinson et al., 2016) and in 3 datasets generated from beef cattle fed 3 different diets (Herd et al., 2016). A similar trend was found within RC, with CH₄ production having a positive r_g and r_p with CH₄ yield in the current study, as also found in growing beef cattle (Donoghue et al., 2013; Herd et al., 2014). These positive relationships are favorable traits indicating that selection for reduced CH₄/(CH₄ + CO₂) or CH₄ yield will also reduce gross CH₄ emissions. In ewes (but not in lambs with either RC or PAC), however, the daily CO₂ and CH₄ + CO₂ production had moderate negative r_g and r_p with CH₄/(CH₄ + CO₂). The selection for reduced CH₄/(CH₄ + CO₂) using PAC in ewes might, therefore, concurrently result in selection for increased CO₂ and CH₄ + CO₂ production, which had positive correlations with gross CH₄ emissions. To avoid unintended selection for increased CO₂ and CH₄ + CO₂ production (strong positive relationship with DMI), which might happen as one selects for reduced CH₄/(CH₄ + CO₂), at least with PAC in ewes, it has been suggested that CH₄ production with CH₄ + CO₂ as a covariate or regressed against CH₄ + CO₂ production with a residual CH₄ production trait (Herd et al., 2016) could be a suitable metric. However, in practice, the best approach is to use the heritability and r_g of the individual objective traits weighted by their economic value, either positive for production traits or negative for inputs such as DMI (related to CO₂ or CH₄ + CO₂ production) and CH₄ production. This approach does, however, require accurate estimates of the r_g PAC and RC emissions and with DMI, which is currently in progress.

Emissions From Lambs and Ewes

Genetic selection for reduced CH₄ emissions in NZ has been performed in growing lambs to make the fastest genetic progress possible (Pinares-Patiño et al., 2013). Approximately 20 million ewe population that produces approximately 25 million lambs (tailed or marketed) in NZ (StatsNZ, 2015),

however, contributes to the majority of all CH₄ emissions (approximately 75% to 80%) from sheep in NZ (Muetzel and Clark, 2015; Swainson et al., 2018). It is therefore very important to prove that the low CH₄ trait selected in lambs is also expressed in ewes. Previous results from sheep fed alfalfa pellets measured in RC indicated that CH₄ production and CH₄ yield traits were similarly repeatable for measurements 14 d apart and across different years (Pinares-Patiño et al., 2013), and suggest that these traits were also expressed at adult age. There were strong r_g (0.85 to 0.99) for all traits measured using PAC in lambs compared with those measured using PAC in ewes in the current study. The r_g for emission traits measured in RC (lambs) were similar to emission traits measured using PAC with either lambs (0.41 to 0.67) or ewes (0.41 to 0.62) in the current study. The heritability and repeatability of all emission parameters determined in PAC were also similar for lambs and ewes. These suggest that emission traits determined as lambs were genetically similar to those measured as ewes. Robinson et al. (2016) also found a strong r_p between CH₄ and CO₂ production (0.64 and 0.75, respectively) measured using PAC as lambs and as ewes; Paganoni et al. (2017) found a strong r_g for PAC measured CH₄ production (>0.60) at post-weaning, yearlings, and as adult sheep; and Oddy et al. (2018) found no interaction between progeny sire and measurement age (12, 21, and 28 mo of age). Opposite, Dominik and Oddy (2015) suggested, based on repeatability estimates, that CH₄ traits measured using PAC in Merino ewes (15 mo) on pasture were not a reliable indicator of the adult (27 mo) CH₄ trait. However, the range in repeatabilities they reported (0.17 to 0.40) for CH₄ with BW as a covariate was in a similar range to those in the current study for the same trait (0.10 to 0.40). Recent meta-analysis of RC data from sheep fed cut pasture suggested that also the regression for CH₄ emissions and DMI was similar for lambs (<1 yr) and older sheep (>1 yr) (Muetzel and Clark, 2015; Swainson et al., 2018). Altogether, these suggest that the CH₄ emission trait selected in lambs is a genetic trait that is also expressed when the animal is an ewe as also suggested by Oddy et al. (2018). However, they recommended to measure CH₄ traits in dry ewes, not when pregnant or lactating, although without clear explanation other than that CH₄ yield was lower in pregnant and lactating sheep than in dry ewes and lambs.

Repeatability of Emissions on Different Diets

The initial studies screening sheep for low CH₄ emission traits in NZ were performed while sheep were fed alfalfa pellets at a fixed feeding level

(Pinares-Patiño et al., 2013), which is very different from the typical grazing conditions on NZ farms. The average CH₄ yield on alfalfa pellets is very low, at approximately 16 g/kg DMI (Pinares-Patiño et al., 2013) compared with the CH₄ yield of approximately 21 to 23 g/kg DMI more typically found in sheep fed cut pasture in RC (Muetzel and Clark, 2015; Swainson et al., 2018). Genotype × environment interactions were found for CH₄ emissions in some studies, including effects of diet changes, although these effects mainly affected the magnitude of differences between CH₄ selection lines (Pinares-Patiño et al., 2003; Pinares-Patiño et al., 2011b; Robinson et al., 2015; Goopy et al., 2016). There is therefore some uncertainty if the CH₄ emission trait selected on a particular diet is also expressed when animals are fed a different diet. The similar heritability and repeatability and moderate r_g for CH₄/(CH₄ + CO₂) in PAC off-pasture with CH₄/(CH₄ + CO₂) in RC on alfalfa pellets in the current study suggest that both are a similar genetic trait. Differences in CH₄ yield between the low and high CH₄ yield line sheep ($n = 96$) were 10% when fed alfalfa pellets and on average 9% when fed cut pasture in 3 periods measured using RC (Jonker et al., 2017b). Selection of low CH₄ yield sheep on relatively fibrous low energy mixed alfalfa:oaten chaff in Australia resulted in selection of animals with a smaller rumen and increased rumen digesta passage kinetics (Goopy et al., 2014), which is similar to phenotypic findings for sheep with low CH₄ yield selected on alfalfa pellets in NZ (Pinares-Patiño et al., 2011a; Bain et al., 2014; Elmes et al., 2014). These suggest that a CH₄ emission trait selected in sheep on a particular diet is also expressed when the same animals are fed another diet.

Phenotypic Parameters of Methane Emissions

In general, r_p were lower (0.004 to 0.27) than r_g (0.41 to 0.67) for PAC emission parameters (as lambs and ewes) with RC emission parameters. Environmental conditions imposed before and during PAC vs. RC measurements were different, which likely explains the low r_p in the current study. During RC, alfalfa pellets were fed at a fixed feeding level and the same batch of pellets was fed during the repeat measurement after 14 d, whereas before PAC, animals had ad libitum access to pasture, likely resulting in more variable DMI among animals. Pasture quality also varied during repeat measurements. In addition, age and BW differed during PAC and RC measurements. Robinson et al. (2015) also found negligible r_p (0.04 to 0.19) for sheep measured using PAC at 5 occasions using different measurement

protocols with measurements of the same sheep in RC. The r_p of CH₄ production measured using PAC and RC were, however, much greater (0.56 to 0.71) when animals entered PAC direct after removal from RC (Bickell et al., 2011; Goopy et al., 2011). The regression for PAC with RC measurements presented by Goopy et al. (2011) revealed some bias, with an underestimation of CH₄ emissions at low CH₄ concentrations in PAC. This might explain the low CH₄ production estimated using PAC in the current study relative to CH₄ production from sheep fed cut pasture in RC (Muetzel and Clark, 2015; Swainson et al., 2018). The CH₄ production estimates using PAC in ewes in the current study were, however, in a similar range as previously found using PAC (Robinson et al., 2014; Robinson et al., 2015; Goopy et al., 2016). Accuracy of PAC measurements was similar when performed for 1 and 2 h (Goopy et al., 2011) and also when performed for 40 min and 1 h (Robinson et al., 2014). Therefore, more frequent spot-sampling will likely be required to estimate absolute values more precisely. Even so, the current protocol with 2 PAC samples off-pasture is suitable to estimate relative differences in CH₄ emissions for genetic selection.

CONCLUSIONS

The ranking of CH₄ emission traits in sheep for the purpose of selection for low emissions using PAC was highly correlated (r_g) with selection using RC. Furthermore, methane emissions measured in lambs were highly genetically correlated (>0.9) with measures as ewes. There were some differences, mainly attributed to the ability of the animal to vary DMI, variable pasture quality on offer, and shorter sampling time during PAC measurements. PAC have several major advantages over RC as they enable measurement of methane emissions on farm at pasture, at lower cost, and more animals can be measured in a shorter time. Before wide-scale industry use, accurate estimates of the genetic correlations of PAC and RC gas measurements with DMI are required.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Animal Science* online.

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