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RELATIONSHIP BETWEEN FEED INTAKE, ENERGY EXPENDITURE AND METHANE EMISSIONS: IMPLICATIONS FOR GENETIC EVALUATION

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SUMMARY

Portable accumulation chambers (PAC) enable enteric gas emissions of sheep to be measured under field conditions. Feed intake is highly correlated with methane emission and should be accounted for in models for parameter estimation of methane emissions, but it cannot be measured in the field. In this study, different linear mixed models were fitted to methane and carbon dioxide emissions and oxygen consumption to investigate the consequences of not adjusting for feed intake, as well as adjusting for effects that indirectly account for feed intake, such as live weight, carbon dioxide or oxygen. The significance of permanent environmental effects was also tested. The results demonstrate that feed intake accounts for a considerable amount of the variance in methane emissions. In this animal house experiment, where sheep were fed at 1.5 x maintenance, much of the variation in feed intake appeared to be related to non-genetic effects of the animal. Consequently, fitting a permanent environmental effect yielded similar heritability estimates to those of models that adjusted for feed intake. Repeated measures of greenhouse gas emission in PAC require more complex models including permanent environmental effects to produce acceptable estimates.

INTRODUCTION

Enteric methane emissions are strongly correlated with feed intake. Criticism has been raised, that, without appropriate measures of production, selection to genetically reduce methane emissions could lead to decreased production because of decreased feed intake (Arthur *et al.* 2009). One approach is therefore to adjust methane emissions for feed intake. Technologies to measure methane and other enteric gas emissions of sheep include respiration chambers (RC) and portable accumulation chambers (PAC). The advantage of PAC is that they can be used in the field; the disadvantage is that under field conditions, it is not possible to measure feed intake.

The aim of this study was quantify the differences in variance components and heritability estimates for enteric gas emissions and oxygen consumption from models with and without adjustment for feed intake, or proxies for feed intake that can easily be measured. In addition, the outcomes of fitting permanent environmental effects were explored.

MATERIALS AND METHODS

Data. Enteric gas emission traits were measured on 512 Information Nucleus Flock (INF) follower ewes at Armidale, New South Wales. The ewes were born between August 2007 and October 2013. Data were collected in an indoor facility using PAC with two measurement protocols that differed in time off feed prior to measurement. Protocol PAC0 measured animals immediately off feed and PAC1 kept animals 1 hr off feed prior to measurement. Methane, CO_2 and O_2 (ml/min), live weights (kg) and feed intake (g) were recorded. Measurements from the two PAC protocols were highly correlated, with genetic correlations ranging from 0.75 to 1.00. Therefore, records for PAC0 and PAC1 were regarded as repeat measures, resulting in two PAC measurements per animal. Ewes were tested from mid-April 2015 to mid-March 2016.

Feed was offered in the mornings at 1.5 x maintenance requirements and feed intake recorded from 8 am on the day prior to PAC measurements to 8 am on the day of measurement (FIDP) and from 8 am on the measurement day until the time the animal entered the PAC (FIOD).

Statistical analysis. Variance components and heritabilities for gas emission traits were estimated using ASReml (Gilmour *et al*. 2009). An extensive back-pedigree with 13 genetic groups was used. Univariate mixed animal repeatability models were run to estimate parameters. Fixed effects included test batch, birth year, measurement date, measurement protocol, testing run (RUN, 7 levels, with 4 for PAC0 and 3 for PAC1), and PAC (from 1 to 12). Ten models were tested for CO_2 and O_2, and twelve models for CH_4. For each gas trait, the first model fitted all significant fixed effects, but not direct or indirect adjustment for feed intake (Model no adj). Other models fitted either feed intake (FIOD and FIDP and their interaction with RUN) as Model FI, live weight (Model LWT), feed intake and live weight (Model FI+LWT), CO_2 (Model CO_2) or O_2 (Model O_2). Only significant fixed effects and interactions were retained in the final models. All models were fitted with and without permanent environmental effect (PE). Random effects included animal ID to estimate the genetic variance and a permanent environmental effect, fitted as an identity matrix of the animal ID.

RESULTS AND DISCUSSION

Basic features of the dataset and the distribution of their raw phenotypes are shown in Table 1. Table 2 shows the variance components and resulting heritability estimates for CH_4, CO_2 and O_2 from the different models, with and without adjustment for feed intake or a substitute (LWT, CO_2 or O_2) without and with permanent environmental effect (+PE). For all traits, the phenotypic variances decreased after fitting FI, LWT, FI and LWT or CO_2 or O_2, as might be expected. For CH_4, feed intake accounted for the most variation, whereas O_2 accounted for most of the variation in CO_2 and vice versa. As a consequence of the reduction in phenotypic variances, genetic and environmental variances were also reduced, with environmental variance being less affected than genetic variance.

Table 1. Mean (±sd: standard deviation), minimum (Min) and maximum (Max) of methane (CH_4), carbon dioxide (CO_2) and oxygen (O_2) (in ml/min)

	Mean (+ sd))	Min	Max
CH_4	36.27 ± 9.35	4.97	75.31
CO_2	422.30 ± 82.56	207.40	734.90
O_2	-451.60 ±77.43	-732.50	-257.80

The change in heritability estimates also reflects the substantial amount of variance related to the covariates fitted. Previously reported heritabilities for CH_4 from field measurements of sheep in PAC ranged from 0.05 – 0.19 (Robinson *et al.* 2014a; Goopy *et al.* 2016). As might be expected, the results from this controlled animal house study were higher than published estimates from field measurements. Results from the different models in this study support the conclusion of Robinson *et al.* (2014b), that a substantial proportion of the variation in CH_4 emissions is related to variation in feed intake. In fact, economic modelling of breeding objectives suggests that methane measurements can be used as a proxy for feed intake, and that the resulting improvements in feed efficiency will often be more valuable than the reductions in greenhouse gas emissions (Robinson and Oddy 2016).

Robinson *et al.* (2014b) highlighted the importance of PE effects in regards to CH_4 emission traits. They noted significant effects of twins being reared as singles and hypothesised about other causes, such as diet, rumen volume and their impacts on short or long-term variation in rumen microbial composition. In our study, the effect of fitting a permanent environmental effect was tested for all models (+PE). As assessed by likelihood ratio tests, the significance of PE was not associated with a particular trait, but appeared to depend on the covariates that were fitted. The more variance

could be captured by the covariate, i.e. FI and also CO_2 for O_2 emissions, the less variance was due to the PE effect. Interestingly, fitting a permanent environmental effect in model no adj yielded similar heritability estimates for CH_4, CO_2 and O_2 to those from model FI. The repeated measures in this dataset allowed both permanent environmental effects and measurement errors to be estimated. Another approach would be to explore the measurements from PAC0 and PAC1 in a bivariate analysis as correlated traits.

Table 2. Genetic (V_G), residual (V_E), phenotypic (V_P) and permanent environmental (V_{Pe}) variance component (including significance), log likelihood (Logl) for each model with and without permanent environmental effect and heritability estimates (h^2) for CH_4, CO_2 emission and O_2 consumption

			CH_4			
	V_G	V_E	V_P	V_{Pe}	Logl	h^2
no adj	45.25	27.10	72.35	--	-2697.32	0.63 (0.03)
no adj + PE	25.77	26.88	70.62	17.98	-2696.89	0.36 (0.14)
LWT	36.64	27.32	63.97	--	-2666.19	0.57 (0.03)
LWT + PE	9.54	26.88	61.70	25.28**	-2660.79	0.15 (0.13)
CO_2	20.62	17.64	38.26	--	-2416.55	0.54 (0.03)
CO_2 + PE	15.06	17.52	37.85	5.27	-2415.14	0.40 (0.13)
O_2	17.54	18.34	35.88	--	-2404.53	0.49 (0.03)
O_2 + PE	12.70	18.20	35.56	4.66	-2403.16	0.36 (0.13)
FI	5.09	14.32	19.41	--	-2974.91	0.26 (0.04)
FI + PE	3.78	14.22	19.35	1.35***	-2173.48	0.20 (0.11)
LWT+FI	4.35	14.17	18.53	--	-2158.48	0.23 (0.04)
LWT+FI+PE	2.98	14.06	18.48	1.44	-2157.50	0.16 (0.10)
			CO_2			
	V_G	V_E	V_P	V_{Pe}	Logl	h^2
no adj	2805.21	1750.00	4555.20	--	-4866.12	0.62 (0.03)
no adj + PE	1554.93	1734.66	4455.60	1156.03*	-4863.86	0.35 (0.14)
LWT	1775.60	1772.57	3548.20	--	-4793.18	0.50 (0.03)
LWT + PE	63.73	1734.82	3424.70	1626.17***	-4783.88	0.02 (0.12)
O_2	48.67	584.76	633.44	--	-3990.31	0.08 (0.04)
O_2 + PE	15.66	577.65	633.13	39.83	-3988.94	0.02 (0.08)
FI	765.72	1309.08	2074.80	--	-4578.01	0.37 (0.04)
FI + PE	232.22	1288.01	2044.80	524.61*	-4574.84	0.11 (0.12)
LWT+FI	670.32	1262.78	1933.10	--	-4547.54	0.35 (0.04)
LWT+FI+PE	224.89	1243.27	1911.00	442.86*	-4544.99	0.12 (0.12)
			O_2			
	V_G	V_E	V_P	V_{Pe}	Logl	h^2
no adj	1985.11	1099.85	3085.00	--	-4666.59	0.64 (0.03)
no adj + PE	1366.19	1093.60	3028.40	568.65	-4665.34	0.44 (0.15)
LWT	1200.57	1113.36	2313.90	--	-4583.37	0.52 (0.03)
LWT + PE	50.39	1092.20	2227.00	1084.39***	-4574.16	0.02 (0.12)
CO_2	182.16	543.77	725.93	--	-4058.93	0.19 (0.04)
CO_2 + PE	93.33	535.94	722.72	93.33	-4057.45	0.13 (0.10)
FI	621.80	887.77	1509.60	--	-4420.35	0.41 (0.04)
FI + PE	212.64	876.54	1482.50	393.31**	-4417.26	0.14 (0.13)
LWT+FI	543.05	851.49	1394.50	--	-4686.23	0.39 (0.04)
LWT+FI+PE	116.01	837.05	1369.90	416.81***	-4382.35	0.08 (0.12)

Significance of log likelihood ratio test: $P < 0.05$ *;$P < 0.01$ **, $P < 0.001$***

Despite relatively small numbers of animals (total of 512), the PE was more often significant

than not. Live weight, is of course highly heritable, and when it was accounted for in Model LWT, the estimate of genetic variation was small for CO_2, but there was still variation due to PE effects. One possible explanation is that in some animals both CO_2 production and O_2 consumption have a different relationship with live weight, and, to a lesser extent, feed intake. What this might be is yet to be determined, but could include learned behaviour such as stress responses that might contribute to additional PE variation in O_2 consumption and CO_2 emissions.

Robinson *et al*. (2016) noted that the repeatability of methane measurements diminishes over time, falling from an average of 0.48 for measurements in the same week to 0.20 for the average of 6 repeated measurements on the same animals from 2009-2014. This suggests that some of the variation attributed to PE effects could in fact be temporary and (perhaps to a greater extent than genetic effects) relate to factors affecting the animal during the particular month each batch of sheep spent in the animal house.

CONCLUSION

Ideally feed intake is accounted for in models for genetic parameter estimation of CH_4 emission, however feed intake measures are difficult to obtain in the field. Repeated measures of enteric gas emission in sheep provide an opportunity to estimate both measurement errors and non-genetic animal environmental effects. The latter were usually significant and accounted for some variation in feed intake and other factors that, in models ignoring the PE effect, would be included in estimates of the genetic variance and result in inflated estimates of heritability.

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