MYTHBUSTERS: NON-ADDITIVE GENETIC EFFECTS HAD NEGLIGIBLE IMPACT ON WAGYU CARCASS QUALITY

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SUMMARY
Anecdotal evidence suggests that mating specific sire and dam lines will produce superior offspring compared to those of equivalent expected merit but in random combinations. BREEDPLAN allows for genetic selection of sires and dams to advance carcass trait expression in progeny by utilising, mostly, additive genetic relationships. This program does not intentionally account for non-additive genetic effects in the genotype. The influence of non-additive genetic effects in Wagyu, and specifically, their effect on marbling performance has not been widely investigated. Non-additive genetic effects had negligible impact.

INTRODUCTION
Development of a genetic evaluation program in Australia started as the National Beef Recording Scheme (NBRS) in the late 1970's and became BREEDPLAN in 1985 (Graser and Hammond 1985). The purpose of BREEDPLAN is to quantitatively evaluate an individual's genetic merits before they are selected as breeding stock on a breed by breed basis. Genetic variation can be partitioned into two components, additive and non-additive variance (Falconer 1981). BREEDPLAN produces, for each trait analysed, an estimated breeding value (EBV) which is a representation of the additive genetic component of the individual's genotype (Tempelman and Burnside 1989). BREEDPLAN does not intentionally account for non-additive genetic variance, such as dominance or epistatic interactions, although some may be absorbed by a fitted sire x herd interaction effect. This is not reported to breeders, but improves the estimation of the reported EBVs (Graser *et al.* 2005). The program has evolved from the initial two-trait analysis with a sire-maternal grandsire model, to a multi-trait animal model analysis system (Quaas and Pollak 1980), including growth, reproduction and carcass traits. One such carcass trait is marbling performance which is defined as the accumulation of triacylglycerol in muscle tissue occurring primarily within adipocytes located between muscle fibre bundles (Harper and Pethick 2004).

Anecdotal evidence from breeders suggests that matings of specific superior sire and dam lines will produce superior performing offspring compared to other matings of equivalent expected merit but in random combinations. In Wagyu these so called 'superior offspring' would be those that produce the most highly marbled carcasses. This performance above expectation has been attributed to non-additive genetic components in the genotype (Seath and Lush 1940; Tempelman and Burnside 1989) and among breeders is referred to as "Nicking". Few studies have investigated the importance of nicking to marbling performance and even fewer have done so using Wagyu data. The aim of this project is to provide breeders with information as to whether non-additive genetic effects should be included in the genetic evaluation of animals or whether the sole focus should remain on additive genetic effects.

MATERIALS AND METHODS
Data. Data for this study was collected and provided by a single Full-blood Wagyu herd located in the Lower South East agricultural region near Millicent, South Australia. All cattle are born, raised and feedlot finished for 300 days on property. Calves were weaned as a group of

similar age and kept within their respective weaning groups, following the same ration program, until slaughter at 2-2.5 years of age. Data supplied was for animals slaughtered between June 2010 and July 2016 and included pedigree information for all animals slaughtered. The dataset consisted of records for 1357 animals comprising 33 and 994 sires and dams respectively, where all sires included had greater than or equal to 10 progeny each. Pedigree went as deep as 5 generations.

Traits of interest. Raw AUS-MEAT chiller assessment records on hot standard carcass weight (HSCW, kg), marble score (MS, score 0-12), loin eye muscle area (EMA, cm^2) and fat depth at the rump P8 site (P8, mm) were utilised for analysis (n=1357). An indicative carcass value (VALUE, $) was calculated based on approximate current values as HSCWx(4+MS) where a carcass with MS=0 was estimated to receive $4/kg and every increase in MS achieved an additional $1/kg.

The average carcass weight was 412 kg with 16 mm of P8 fat, 95 cm^2 EMA, a marble score of 8 and worth $4945. Marbling and P8 were highly variable with a coefficient of variation (CV) of 23% and 37% respectively followed by VALUE (CV 18%), whereas HSCW and EMA were far less variable (CV 9-10%). All traits were normally distributed with the exception of P8 fat that was transformed by taking the square-root of the record prior to analysis.

Model Development and Statistical Analysis. Data were analysed with a general linear mixed model using ASReml 3.0 (Gilmour *et al.* 2009). Model 1 was developed beginning with a sire model and increasing in complexity to include an animal model with random terms fitted. All models included fixed effects of management group (in this case Kill-date was used to account for calving/weaning group), year and season effects (having a correlation of 0.95 and 0.99 with date of birth and feedlot induction date respectively), age of dam (2-10+ years) and sex (heifers and steers). Models for traits other than HSCW included HSCW as a covariate. All significant (P<0.05) two way interactions among these fixed effects were included. Inbreeding coefficients were calculated based on all available pedigree information (mean 5% and ranging from 0-26%) and were fitted in Model 3. Models varied in the random terms included.

Model 1. The base "animal" model, which served as a baseline, included the random term of animal to account for the additive genetic effects inherited by the calf.
Model 2. Model 1 plus the maternal additive genetic effect to account for the genes inherited by the dam that affect performance of offspring (e.g. milk production).
Model 3. Model 2 plus non-additive effects modelled as inbreeding and sire by maternal grandsire (SxMGS) interaction were fitted together where;

- Inbreeding was fitted as a random covariate to test the importance of dominance genetic effects contributing to Nicking;
- SxMGS accounts for epistatic genetic effects, inherited from two sire lines, associated with Nicking.

To formally test the importance of the non-additive genetic effects, the likelihood ratio test was used to determine which random terms were significant (P<0.05).

RESULTS AND DISCUSSION

Carcass weight, EMA, MS and VALUE were all moderately heritable (0.24, 0.33, 0.39 and 0.36 respectively, Table 1) while P8 was lowly heritable (0.19). The non-additive genetic effect of nicking as estimated from the sire by maternal grand-sire effect was minimal, accounting for up to 0.6% of the phenotypic variance for the muscling traits (HSCW and EMA) and zero variance for the fat traits (P8 and MS). Additionally there was no evidence to suggest that inbreeding accounted for any of the phenotypic variation across traits (Table 1).

Table 1. Chi Squared (χ^2 probability) test of significance (Model 2 vs 3) and proportion (%) of phenotypic variance accounted for by random terms (Model 3) as well as the direct heritability (h_a^2) and accompanying standard error (SE) for each trait of interest (Model 2)

Trait	Additive[1]	Inbreeding[1]	SxMGS[1]	Dam additive[1]	χ^2 Prob	h_a^2	SE of h^2
HSCW (kg)	24.0	0.0	0.5	6.9	0.95	0.24	0.11
P8 (mm)*	19.5	0.0	0.0	3.9	1.00	0.19	0.09
MS (0-12)*	37.5	0.0	0.0	2.1	1.00	0.39	0.12
EMA (cm^2)*	32.5	0.0	0.6	0.0	0.99	0.33	0.09
VALUE ($)	30.9	0.0	0.0	6.0	1.00	0.36	0.11

* indicates trait adjusted for HSCW

[1] random terms fitted in Model 3: Additive; Additive genetic effects, Inbreeding; Inbreeding coefficient partitioning dominance, SxMGS; Sire by maternal grandsire interaction effect partitioning epistatic interactions, Dam additive; partitioning additive genetic effects inherited by the dam.

As inbreeding depression is resultant of increasing homozygosity and hence the loss of dominance effects (reduction in genetic variation), the SxMGS term then would be partitioning any epistatic effects while inbreeding partitioned dominance. Model 3 was not significantly different from Model 2 indicating that the additional random terms, accounting for non-additive genetic components, did not offer a significant statistical improvement on the additive model. However, despite Model 3 not statistically improving the model, it was able to estimate a variance component attributed to nicking for the muscling traits which suggests that these values should not be completely discounted.

Few studies in beef cattle exist to compare these results with and even fewer that include Wagyu data. However, many authors have commented on the influence of non-additive genetic effects on dairy production. Johnson *et al.* (1940) investigated the effect of nicking in Jersey cows and concluded that while their study had not shown nicking to influence pounds of milk butterfat yielded, there was not enough evidence to suggest that nicking does not exist amongst Jersey matings. Seath and Lush (1940) reported similar inconclusive results regarding milk production and butterfat percentage while Tempelman and Burnside (1989) reported that dominance effects, which nicking has been partly ascribed to, were important for milk fat yield. It is clear the previous dairy studies have attributed nicking to dominance effects while the present study has partitioned nicking as epistatic effects. It is possible that the pedigree herein is not sufficiently deep enough to account for all the dominance variation through fitting inbreeding coefficient as a random effect and hence some dominance variation has been absorbed into the SxMGS term.

In a genome wide association scan fitting additive and dominance effects of single SNPs, Bolormaa *et al.* (2015) found that significant (P<0.001) dominance effects occur for IMF% accounting for 10% of the phenotypic variance in the trait. This suggests that dominance effects would have an impact on marble score however that was not the result in the present study. The results of Bolormaa *et al.* (2015) were similar with the study herein, in that dominance effects accounted for 0% of the phenotypic variance for P8 fat depth however the author stated that the inclusion of dominance effects did not improve the accuracy of predicting genetic value of individuals.

It could be argued that nicking effects may be present when multi-trait selection is considered, as is currently practiced in industry since multiple traits affect profitability. To investigate this, a multi trait index (VALUE) was created encompassing the estimated dollar value of HSCW and

MS which are the most important economic traits to Wagyu producers. There was no-evidence to suggest that nicking had any effect on VALUE (Table 1).

The results herein demonstrated that non-additive genetic effects (dominance and epistasis) have a negligible impact on carcass traits. This is consistent with a study by Hill *et al.* (2008) that found additive genetic effects have the greatest influence by far, accounting for often 50 to 100% of the total genetic variance for complex traits. Hence the inclusion of non-additive genetic variances in the estimation of individual genetic merit is not likely to result in any potential reward, except for perhaps slight increases in estimation accuracy, and therefore additive genetic variance should continue to have sole focus in Wagyu breeding programs.

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