

Searching for Phenotypic Causal Links among Meat Quality Traits in Japanese Black Cattle

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ABSTRACT: Meat quality is one of the most important traits determining carcass price in Japanese beef market. Optimized breeding goals and management practices for improvement of meat quality traits require knowledge regarding potential functional relationships among them and with other economically relevant traits. In this context, the objective of this research was to infer phenotypic causal networks involving beef marbling score (BMS), beef color score (BCS), firmness of beef (FIR), texture of beef (TEX), beef fat color score (BFS), and the ratio of saturated fatty acids to mono unsaturated fatty acids (MUS) from 11,855 fattening Japanese Black cattle. An adaptation of the Inductive Causation (IC) algorithm was implemented to search for causal links among these traits, which was applied to their joint distribution conditionally on genetic effects. Such information was obtained from the posterior distribution of the residual (co)variance matrix of a standard Bayesian multiple trait model. The undirected edges among the traits except for BFS were detected by the IC algorithm with 95% highest posterior density (HPD) intervals. Applying smaller HPD intervals resulted in recovering more edges and the undirected edges were changed into directed ones except between FIR and TEX. The analysis uncovered some interesting functional relationships between these traits, for example indicating that BMS would be affected by interventions on MUS and BCS.

Keywords:

Meat quality

Genetic parameter

Inductive causation

Japanese Black

Introduction

Meat quality is one of the most important traits determining carcass price in Japanese beef market. In particular, beef marbling and high ratio of unsaturated fatty acid are of especial interest for Wagyu beef, which are therefore target of breeding goals in Japan. In any breeding or production system based on the multiple traits, it is important to study potential causal relationships among them. Specific statistical and data analysis techniques exist for inferring causal effects from observational data, such as the IC algorithm. Valente et al. (2010) showed that applying the IC algorithm to the posterior distribution of the residual (co)variance matrix of a standard Bayesian multiple trait model recovered the correct network in simulated data. Valente et al. (2011) also applied the IC algorithm to a real data set for five productive and reproductive traits in European quail. In the context of carcass traits in beef cattle, strong correlations have been reported among some meat

quality traits in Wagyu cattle (Shirai et al., 1996; Sato et al., 2013). However, the contribution of functional relationships to such observed correlations remains unclear. The objective of this research was then to search for causal structures among meat quality traits in Japanese Black cattle.

Materials and Methods

Data. Carcass records of 11,855 Japanese Black steers and heifers fattened in Yamagata prefecture, Japan, were used for this research. The pedigree information for 57,523 animals was also used. Meat quality traits included beef marbling score (BMS) which is scored from 1 (poor) to 12 (abundant), beef color score (BCS) scored from 1 (light) to 7 (dark), firmness of beef (FIR) and texture of beef (TEX) scored from 1 (poor) to 5 (excellent), beef fat color score (BFS) scored from 1 (white) to 7 (yellow), and the ratio of saturated fatty acids to mono unsaturated fatty acids (MUS) as an index of desaturation of intramuscular fat. The meat quality traits except for MUS were evaluated between the 6th and 7th rib in accordance with the Japan Meat Grading Association (JMGA, 1988). After the grading, about 2 mm sliced samples including muscle and adipose tissue were shaved off M. trapezius at the same part of the grading. Fatty acid composition was measured by gas liquid chromatography and was calculated as described by Inoue et al. (2011). MUS was calculated as follows:

$$\text{MUS} = (\text{C14:1} + \text{C16:1} + \text{C18:1}) / (\text{C14:0} + \text{C16:0} + \text{C18:0}).$$

Multiple trait analysis. A standard Bayesian multiple trait model was used for estimating genetic and residual (co)variance components. The following multiple trait model was fitted:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where \mathbf{y} is the vector of observation of traits; $\boldsymbol{\beta}$ is the vector of systematic effects, including sex of animals (2 levels), slaughter year (15 levels), slaughter month (12 levels), farm (302 levels), linear and quadratic covariates for age at slaughter (average 31.8 month); \mathbf{u} is the vector of random additive genetic effects; \mathbf{e} is the vector of random residual; and \mathbf{X} and \mathbf{Z} are known incidence matrices. The program GIBBS1F90 (Misztal et al., 2002) was used for obtaining posterior distributions of genetic and residual (co)variances. A Gibbs sampling chain with 200,000 samples was generated, with the initial 100,000 samples discarded as burn-in. Finally, (co)variance components were determined based on the remaining 100,000 samples.

Inductive causation algorithm. After fitting the multiple trait model, the Inductive Causation (IC) algorithm was applied to the residual (co)variances obtained from the multiple trait analysis. The residual (co)variances were considered as information from the joint distributions of the traits conditionally on genetic effects, which corrects the search for confounding due to such effects when they are correlated (Valente et al., 2010). The IC algorithm performs a series of statistical decisions based on partial correlations between traits and consists of the following three steps (Pearl, 2009):

Step1. If all partial correlations of two traits conditional on each possible set of the other traits are different from 0, the two traits are connected with an undirected edge (e.g. $y_1 - y_2$).

Step2. In the undirected graph obtained by step 1, if partial correlations of two non-adjacent traits (e.g. y_1 and y_3) with a common adjacent trait (e.g. y_2 in $y_1 - y_2 - y_3$) are dependent conditional on any possible set including the adjacent trait (y_2), arrowheads pointing to the common adjacent trait (y_2) are added ($y_1 \rightarrow y_2 \leftarrow y_3$).

Step3. In the partially oriented graph obtained from the step 2, as many undirected edges as possible are oriented without creating a new unshielded collider or a cycle.

Statistical decisions regarding declaring partial correlations as null or not null were based on highest posterior density (HPD) intervals. If the interval contained the value 0, the correlation is declared as null. Outputs may differ accordingly to the probability content used for the decisions. We applied different HPD content magnitudes (80, 85, 90, and 95%) to evaluate the structure sensitivity to such content.

Results and Discussion

Multiple trait analysis. The results of the multiple trait analysis, in terms of posterior means of heritability, genetic and residual correlations of meat quality traits are shown in Table 1 and the respective posterior SD are presented in Table 2. Heritability estimates of meat quality traits were moderate (0.38 for BCS) to high (0.74 for BMS) except for BFS (0.10). These estimates were similar to the results reported by Yokota et al. (2011) with the same Japanese Black breed. Genetic correlations of BMS with FIR and TEX and between FIR and TEX were almost 1.00, with also high residual correlations between them (0.52 to 0.71). This result was similar to reports in Wagyu breeds: Japanese Brown cattle (Shirai et al., 1996) and Japanese Shorthorn cattle (Sato et al., 2013). Genetic and residual correlations of BCS with BMS, FIR, and TEX were negative and second highest (around -0.70 and -0.15 for genetic and residual correlations, respectively). Shirai et al. (1996) reported similar negative correlations in Japanese Brown cattle. By contrast, both correlations between BFS and the other traits were almost 0.00 with the 95% HPD region including 0. Similarly, genetic correlations of MUS with the other traits were low (-0.13 to 0.08) except with BFS (0.51). Yokota et al. (2011) reported high genetic correlation between BFS and mono unsaturated fatty acid which is highly associated with MUS. On the other hand, residual correlations of MUS with

BMS, FIR, and TEX were rather high (0.13 to 0.20). This result was also similar to the report by Yokota et al. (2011). However, only the genetic correlation between MUS and BMS was different from the previous reports (Yokota et al., 2011; Inoue et al., 2011).

IC algorithm. Applying the IC algorithm based on the different HPD interval content, resulted in the two alternative graphs depicted in Figure 1. Using 95% HPD intervals, edges among the meat quality traits except for BFS were detected, although their direction was not resolved (Fig. 1 (a)). Applying 90% and 85% HPD intervals detected one more edge between BCS and FIR (not shown in Figure). Using 80% HPD intervals recovered an edge of BCS with BMS and the undirected edges were changed into directed ones except for between FIR and TEX (Fig. 1 (b)). Due to applying smaller HPD intervals, more edges were recovered and this shows that the posterior distributions of the traits might not be too sharp. In addition to recovering more edges, reducing the HPD intervals detected unshielded colliders in step 2 of the IC algorithm. There could be reasonable biological explanations for some of those detected directed edges in the graph. In the directed acyclic graph (DAG) of the set of $MUS \rightarrow BMS \leftarrow BCS$, the directed edge from MUS to BMS might be affected by management factors during and before the fattening period, which could not be removed fitting multiple traits model. Also, the directed edge from BCS to BMS might be considered as a result of the contrast on the surface at the graded area. It is well known that BMS is strongly related to fat content and there are negative relationships between the ratio of fat content and moisture in meat. Less moisture in meat improves firmness and texture of meat. This fact might explain the directed edges from BMS to FIR and TEX in the DAGs of $BMS \rightarrow FIR$ and $BMS \rightarrow TEX$. However, potential reasons to explain the observed directed edges from BCS to FIR and TEX are still unclear.

If interventions existed in a scenario where traits present causal effects among themselves, the breeding strategy based on only multiple traits analysis could lead to wrong breeding goals. In particular, the most concerning issue is about the effect of interventions that would affect selection for BMS, which is the most influential trait determining the price of a carcass in Japanese market, in this system. For example, if interventions were on MUS and BCS, only the direct genetic effects contribute to BMS as interventions would block the indirect genetic effects through MUS or BCS (Valente et al., 2013). Such direct genetic effects could be inferred by fitting a mixed effects structural equation model with a causal structure following Fig. 1(b), which is being currently performed by our group.

Conclusion

Potential functional relationships were detected among the meat quality traits except for BFS. Applying smaller HPD intervals detected more edges and the undirected edges were changed into directed ones except for that between FIR and TEX. The final DAG generated suggests that BMS would be affected by interventions on

MUS and BCS. If interventions on MUS or BCS existed in this scenario, the efficiency of selection for BMS on multiple traits analysis would be decreased. On the other hand, from the management point of view, this graph indicates that an improvement on BMS, FIR, and TEX might increase the average of MUS through management factors without affecting for BCS.

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Table 1. Posterior means of heritability (diagonal), genetic (above) and residual (below) correlations

	BMS	BCS	FIR	TEX	BFS	MUS
BMS	0.74	-0.70	0.99	0.99	-0.04	-0.13
BCS	-0.15	0.38	-0.72	-0.72	0.04	0.08
FIR	0.57	-0.16	0.66	0.99	-0.05	-0.13
TEX	0.52	-0.16	0.71	0.62	-0.06	-0.13
BFS	-0.04	0.03	-0.05	-0.04	0.10	0.51
MUS	0.20	0.05	0.15	0.13	0.03	0.63

Table 2. Posterior SD of heritability (diagonal), genetic (above) and residual (below) correlations

	BMS	BCS	FIR	TEX	BFS	MUS
BMS	0.049	0.053	0.000	0.002	0.132	0.065
BCS	0.072	0.048	0.051	0.053	0.136	0.081
FIR	0.062	0.060	0.046	0.002	0.130	0.065
TEX	0.061	0.058	0.032	0.046	0.135	0.067
BFS	0.053	0.026	0.043	0.041	0.022	0.102
MUS	0.109	0.058	0.089	0.083	0.037	0.045

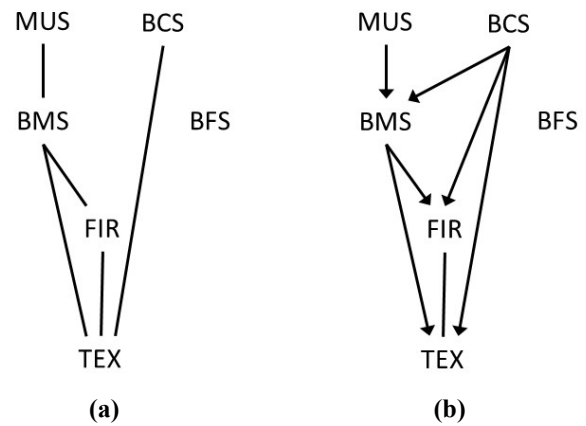


Figure 1. Links between traits detected by the IC algorithm with 95% (a) and 80% (b) of HPD intervals