Inferring phenotypic causal structures among feed efficiency traits in a commercial turkey population (*Meleagris gallopavo*)

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Summary

Feed costs are significant in animal production, consequently improving feed efficiency in animals has long been a selection goal. Variance component estimates for feed efficiency traits have been reported in the literature, however, in order to optimize breeding programs and management, potential functional relationships between traits should be examined. The objective of this study was to infer the phenotypic causal networks among feed intake (FI), body weight gain (WG), metabolic mid-weight (MMW), residual feed intake (RFI) and residual feed intake & body weight gain (RIG). Data from 5,619 toms with feed efficiency data was used for the analysis. As the causal links between these traits were not known a priori, the inductive causation (IC) algorithm was applied to search for them based on the joint distribution of genetic effects obtained from a standard Bayesian multi-trait model (MTM). Different highest posterior density (HPD) intervals were applied for the IC algorithm. Although the HPD interval 95% detected undirected links among the traits, lower HPD intervals (90%, 85%, 80% and 75%) uncovered identical fully directed graphs. Estimates of genetic variances and covariances for downstream traits were not similar between the two modeling approaches and the heritability estimates for those traits were higher under the structural equation model. The functional relationships (i.e., direct genetic effects) showed that hard interventions on WG would affect FI, but the reverse would not hold true. Similarly, hard intervention on FI would affect RIG, but not conversely. These causal effects suggest favorable conditions for the joint improvement and selection of MMW and RFI. Higher MMW and RFI would lead to higher WG. It is well known that WG is strongly associated with FI and there is a negative relationship between FI and RIG. The results indicate that the functional relationships between these traits should be carefully considered in designing optimized breeding programs that target improving feed efficiency in turkeys. In addition, adding behavior traits to the model may increase knowledge about causal effects for feed efficiency traits.

Keywords: feed efficiency, causal inference, residual feed intake

Introduction

Feed represents approximately 70% of the overall cost of production in turkeys. Variance components, as well as genetic correlations between feed efficiency traits, have been reported in the literature (e.g., Willems et al., 2013). However, it is important in a breeding program to study the potential causal relationships among the traits (Rosa et al., 2011). Such relationships cannot be inferred by traditional multi-trait models (MTM). Specifically, MTM are only capable of studying the probabilistic relationships between phenotypic traits in the absence of external interventions. The causality relationship between traits can be explored using the
inductive causation (IC) algorithm (Valente et al., 2013). Afterwards, structural equation models (SEM) can be then be applied to increase the prediction accuracy of external intervention effects. Such applications of SEM may potentially help in optimizing the management practice strategies and in decision-making at the farm level. In addition, SEM have properties to infer the direct genetic effects among traits and also their magnitudes. The use of SEM may accelerate genetic gain compared to MTM. Therefore, the objective of this study was to infer the causal structures among feed efficiency traits in a commercial turkey population, as well as to fit a structural equation model using the selected links based on the results of the IC algorithm to quantify the relationships between these traits.

Materials and methods

Feed efficiency data from 5,619 toms was used in the study. The birds were reared under a standard feeding system with group housing and shared feeders and drinkers until 15 weeks of age. From this age on, feed intake was measured using a previously described system (Tu et al., 2011). Body weight gain (WG) for each animal was obtained as the difference between the weight at the start and the end of the trial. Feed intake (FI) was the amount of feed consumed throughout the trial. The metabolic mid-weight (MMW), residual feed intake (RFI) and residual intake & body weight gain (RIG) were calculated following Willems et al. (2013). A linear mixed animal model was used to analyze the feed efficiency traits considered in this study. The model was implemented using a Bayesian approach with vague conjugate priors. The joint posterior distribution was approximated using a Markov chain Monte Carlo (MCMC) method based on Gibbs sampling. A single MCMC chain with 600,000 iterations was run and the first 100,000 samples were discarded as burn-in for convergence. The remaining samples were thinned with intervals of 20 samples and used to calculate posterior features of interest such as posterior means and standard deviations. The residual variance-covariance parameters obtained from the MTM were then used for the subsequent analysis of the IC algorithm. As the IC works based on partial correlations between any given two traits, declarations of null hypotheses for any partial correlations were based on highest posterior density (HPD) intervals. As such, the correlation was declared null if the interval contained the value 0. Accordingly, the probability content applied for each decision may show different outputs and may change the structure of the causal relationships. HPD intervals of 95%, 90%, 85%, 80% and 75% were applied. While the 95% HPD showed links among the traits without directions (results not shown), the other HPD intervals revealed fully connected directed acyclic graphs (DAG) as shown in Figure 1 which was chosen for fitting the SEM. The following SEM was fitted:

\[ y = (\Lambda \otimes I_n)y + X\beta^* + Zu^* + e^* , \]

while \( \Lambda \) is a \((t \times t)\) matrix with zeroes in the diagonal and structural coefficients in the off-diagonal, \( t \) is the number of traits. The vectors \( y, \beta^*, u^*, e^*, X, Z, A \) and \( I \) hold similar meanings to those for the traditional MTM. Specifically, they serve as systematic and random effects directly affecting each trait. The structural coefficients represent the linear effects between pairs of traits, and the joint distribution and assumptions of vectors \( u^* \) and \( e^* \) can be described as:

\[
\begin{bmatrix}
u^* \\
e^*
\end{bmatrix} \sim N 
\begin{bmatrix}
0 \\
0
\end{bmatrix}, 
\begin{bmatrix}
G_0^* \otimes A & 0 \\
0 & \Psi_0 \otimes I_n
\end{bmatrix},
\]

while \( A \) is a \((t \times t)\) matrix with zeroes in the diagonal and structural coefficients in the off-diagonal, \( t \) is the number of traits. The vectors \( y, \beta^*, u^*, e^*, X, Z, A \) and \( I \) hold similar meanings to those for the traditional MTM. Specifically, they serve as systematic and random effects directly affecting each trait. The structural coefficients represent the linear effects between pairs of traits, and the joint distribution and assumptions of vectors \( u^* \) and \( e^* \) can be described as:
$G_0^*$ is the structural equation additive genetic variance-covariance matrix, which describes variances and covariances of direct genetic effects, and $\Psi_0$ is a diagonal matrix representing the structural equation model residual variances. In SEM, the simultaneous effect between any given two or more traits can be accounted for by the model (covariate variable effects). Consequently, the residual covariances between the traits were set to 0, and with this restriction in parametrization, it allows the structural coefficients to be identifiable.

**Results and discussion**

Table 1 shows the posterior means of heritability estimates and their corresponding posterior standard deviations (PSD) and highest posterior density (HPD) intervals from the SEM. Notable differences between heritability estimates obtained based on the traditional MTM compared to those based on SEM were found. Upstream traits (i.e. MMW and RFI) showed dissimilar variation between the two modeling approaches, and their estimated parameters remained with no changes. Genetic effects can be direct or indirect and, in contrast to MTM, the SEM has the ability to identify these two types of effects. This leads to different variance component estimates for traits conditioned on other traits in directed acyclic graphs in Figure 1.

<table>
<thead>
<tr>
<th>Trait</th>
<th>MTM Mean</th>
<th>MTM PSD</th>
<th>MTM HPD interval (95%)</th>
<th>SEM Mean</th>
<th>SEM PSD</th>
<th>SEM HPD interval (95%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>WG</td>
<td>0.252</td>
<td>0.033</td>
<td>0.229, 0.275</td>
<td>0.294</td>
<td>0.034</td>
<td>0.252, 0.328</td>
</tr>
<tr>
<td>FI</td>
<td>0.150</td>
<td>0.021</td>
<td>0.133, 0.167</td>
<td>0.211</td>
<td>0.033</td>
<td>0.188, 0.232</td>
</tr>
<tr>
<td>MMW</td>
<td>0.373</td>
<td>0.031</td>
<td>0.340, 0.400</td>
<td>0.374</td>
<td>0.030</td>
<td>0.329, 0.411</td>
</tr>
<tr>
<td>RFI</td>
<td>0.301</td>
<td>0.032</td>
<td>0.268, 0.369</td>
<td>0.323</td>
<td>0.034</td>
<td>0.281, 0.359</td>
</tr>
<tr>
<td>RIG</td>
<td>0.214</td>
<td>0.034</td>
<td>0.183, 0.237</td>
<td>0.261</td>
<td>0.031</td>
<td>0.234, 0.286</td>
</tr>
</tbody>
</table>

1Body weight gain (WG), feed intake (FI), metabolic mid-weight (MMW), residual feed intake (RFI) and residual intake & body weight gain (RIG).

While the MTM represents the overall genetic effects that include all direct and indirect (i.e. mediated by other phenotypic traits) effects on each trait, the SEM represents only direct effects (i.e. not mediated by other traits in the causal network). These parameters could be overestimated under hard interventions affecting the traits upstream. On the other hand, the genetic variance and heritability estimates for downstream traits increased slightly when the SEM was applied. The variation in the estimated genetic variance between the MTM and the SEM suggest that external interventions on upstream traits may cause a delay in achieving breeding goals if decisions were made based on an MTM. The structural coefficient for the path from RFI to WG showed that a unit improvement in RFI results in an increase of WG by 0.12 in the causal structures. Similarly, a unit improvement in MMW results in an increase of WG by 0.10 in the causal structures. Interestingly, hard interventions on MMW and WG would affect FI, but not conversely. Similarly, FI and in presence of external intervention may affect RIG, but the reverse would not hold true. These findings of the effects of functional relationships cannot be achieved through the MTM. The causal effects inferred in this study favor a joint improvement and selection of MMW and RFI which would lead to higher WG. Studies (e.g., Willems et al., 2013) have shown that WG is strongly associated with FI and that
there is a negative relationship between FI and RIG. This may point to including feeding behavior traits to uncover more connections among feed traits, as well as the effect of those behaviors on the ability of birds in converting feed into body weight. The correlation between direct genetic effects should be ultimately considered through a reduced SEM or a MTM. SEM provides insights and hypotheses about how causal relationships among traits contribute to the outcome.

![Figure 1](image)

**Figure 1.** Links and posterior means of structural coefficients between traits with directed link between feed efficiency traits. Links represent causal relationships toward arrowheads.

**Conclusions**

The findings of this study indicated that external interventions on WG would affect FI, but not conversely. The same scenario can be applied to the link between FI and RIG. Under SEM, heritability estimates for traits that are conditioned on other traits in the directed acyclic graphs were higher compared to MTM. For these reasons, optimizing animal breeding programs requires critical consideration of the causal relationship between these traits. Moreover, including some behavior traits to the model may reveal more information about the connections between these traits.

**List of References**


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