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The problem of using ratio traits when improving feed and methane efficiency

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Introduction

Animal breeding programs aim to improve productivity while reducing input costs and resource use. As sustainability has become a central concern, feed intake and enteric methane emissions now feature more prominently in breeding objectives, supported by an increasing availability of individual-animal measurements. With expanding phenotypic datasets for methane output in sheep and cattle, an important question is how to incorporate these traits most effectively in selection indices aimed at improving both resource efficiency and environmental outcomes. A seemingly appealing strategy is to use ratio traits, such as production per unit of feed intake or methane emitted per unit of product, as direct indicators of efficiency. However, ratio traits pose several conceptual and statistical problems. Selection on ratio traits is less efficient than selecting on the component trats directly (Gunsett, 1984) When ratio traits are used as selection criteria, the response to selection is driven largely by the genetic coefficient of variation (σ_a/μ) of each component trait (Sutherland, 1965). The purpose of this paper is to provide clarity about the differences between selection indices that have ratios and those that have linear functions of the component traits

Materials & Methods

Parameters of ratio traits. Assume a ratio of two phenotypes of component traits, x and y, with means μ_x and μ_y, variance σ_x^2 and σ_y^2, covariance σ_{xy} and heritability h_x^2 and h_y^2. Using a Taylor series approximation as in Lynch and Walsh (1998) the phenotypic variance of the ratio can be shown to be $\sigma^2\left(\frac{x}{y}\right) = \left(\frac{\mu_x}{\mu_y}\right)^2 (vp_x^2 - 2r_p vp_x v_y + vp_y^2)$ where r_p is the phenotypic correlation between the component traits and $vp_i = \frac{\sigma_i}{\mu_i}$ is the coefficient of phenotypic variation of trait i. Similarly, we can derive the genetic variance of the ratio by using genetic variances ($\sigma_{a.i}^2$) and the genetic correlation (r_g) between the component traits: $\sigma_a^2\left(\frac{x}{y}\right) = \left(\frac{\mu_x}{\mu_y}\right)^2 (va_x^2 - 2r_g va_x va_y + va_y^2)$, where $va_i = \frac{\sigma a_i}{\mu_i} = \frac{h_i \sigma_i}{\mu_i} = h_i v_i$ is the coefficient of genetic variation of trait i. The heritability of the ratio trait is $h_r^2 = \sigma_a^2\left(\frac{x}{y}\right)/\sigma^2\left(\frac{x}{y}\right) = \frac{(\lambda_a^2 - 2r_g\lambda_a + 1)}{(\lambda_p^2 - 2r_p\lambda_p + 1)} h_y^2$ where λ_p is the ratio of coefficients of phenotypic variation of traits x and y, ($\lambda_p = vp_x/vp_y$) and $\lambda_a = va_x/va_y$ is the ratio of coefficients of genetic variation.

The correlation between the ratio trait and the component traits can be derived using the approximation by Pearson (1898) (as cited by Gunsett, 1984), and results in phenotypic correlations $r_{\frac{x}{y},x} \cong \frac{(\lambda_p - r_p)}{(\lambda_p^2 + 1 - 2r_p\lambda_p)^{1/2}}$ and $r_{\frac{x}{y},y} \cong \frac{(\lambda_p r_p - 1)}{(\lambda_p^2 + 1 - 2r_p\lambda_p)^{1/2}}$ and the genetic correlation between the ratio trait and each of the component traits are

$$rg_{\frac{x}{y},x} = \frac{(\lambda_a - r_g)}{(\lambda_a^2 + 1 - 2r_g\lambda_a)^{1/2}} \quad \text{and} \quad rg_{\frac{x}{y},y} = \frac{(\lambda_a r_g - 1)}{(\lambda_a^2 + 1 - 2r_g\lambda_a)^{1/2}}$$

These genetic correlations are important as they determine the response in the component traits when selecting on a ratio trait (see next section).

Ratio traits as a selection criterion. Based on selection index theory and using the approximate parameters for a ratio trait, we can predict the response to selection for the component traits when using a ratio trait in the index. Single trait selection on a ratio trait would yield a correlated response in the component traits, calculated as the regression of the ratio on the breeding values of each of trait x and y. The response for trait x for a selection differential of one standard deviation of the selection criterion will be $R_x = rg_{\frac{x}{y}x}.r_r.\sigma_{ax}$ and for trait y it is $R_y = rg_{\frac{x}{y}y}.r_r.\sigma_{ay}$, where r_r is the accuracy of the estimated breeding value for the ratio trait. It appears that the relative responses for the component traits, in units of genetic standard deviation, are equal to the ratio of the genetic correlation of the ratio trait with the component traits. Note that for $\lambda_a = 1$, the response ratio R_x / R_y will be *(1-r_g)/(r_g-1)* which is always -1. In other words, with equal genetic coefficient of variation, the absolute value of the response in units of σ_a will be equal for the two component traits. If $\lambda_a < 1$, trait y dominates and the absolute value of the response (in σ_a units) in trait y will always be larger than that in trait x. The response in trait x will be in the same direction as in trait y if $\lambda_a < r_g$, which is more likely for relative high values of r_g. Conversely, if $\lambda_a > 1$, trait x dominates and the absolute value of the response (in σ_a units) in trait x will always be larger than that in trait y. The response in trait x will be equal to zero if $\lambda_a = r_g$ and the response for trait y will be zero if $\lambda_a = 1/r_g$.

Ratio traits in the breeding objective. A single trait breeding objective defined as a ratio x/y is equivalent to a linear objective with economic weights μ_y and $-\mu_x$ for traits x and y, respectively. This was shown by Lin (1980) but a different and perhaps easier way to show this is, is to take the derivatives of each of the component trait if the objective function is equal to μ_x / μ_y, as $\frac{\partial(\frac{\mu x}{\mu y})}{\partial x} = -\mu_y^{-1}$ and $\frac{\partial(\frac{\mu x}{\mu y})}{\partial y} = -\mu_x\mu_y^{-2}$. Multiplying both weights by μ_y^2 gives weights μ_y and $-\mu_x$ for traits x and y, respectively.

An example model. A small example of feed conversion (feed intake/average daily gain) in beef cattle will be used to illustrate the theory, using parameters from Torres-Vázquez et al (2018). Trait means for FI (feed intake, kg/day) and ADG (average daily gain, kg/day) are 14.9 and 1.59, coefficients of variation are 0.13 and 0.22; heritabilities are 0.55 and 0.33 and phenotypic and genetic corelations are 0.45 and 0.72. The resulting lambda value is 0.76 so the ratio is ‘”y-dominant”. The response to selection is predicted based on selection index theory. Genetic correlations of the ratio FI/ADG with FI and ADG are 0.06 and -0.65, respectively. The assumed economic values are \$-60 and \$750. The information assumed known for each trait was equal to 10 progeny records.

Results

Response to selection is shown in Table 1 for various selection strategies. Selecting on a linear index gives the highest profit and increases ADG while FI also increases. The latter is undesirable but economically offset by gain in ADG.

When selecting on a ratio of FI/ADG, the genetic change in profit is 7.4% lower (\$59.98 vs \$64.75) and leads mostly to less response in ADG whereas the response in FI is now negative. The response is units of genetic standard deviation are -0.04 for FI and 0.38 for ADG. This is consistent with a ratio that is “y-dominant” with λ_a <1. Single trait selection on a ratio trait gives always the same response in the component traits, independent on whether the breeding

objective is a linear combination or a ratio of the component traits. While selecting on a ratio trait give less genetic change in profit, the response in the ratio is higher compared with selecting on a linear index.

Table 1. Response to selection for the ratio and component traits for feed conversion and overall profit of genetic improvement of one index SD.

Breeding objective[1]	Selection Criterion[2,3]	Response FI (kg/day)	Response ADG (kg/day)	Response FI/ADG	Response Profit ($)
v_1.FI + v_2.ADG	EBV_{FI} , EBV_{ADG}	0.377	0.116	-0.450	$ 64.75
-FI/ADG	$EBV_{FI/ADG}$	-0.052	0.076	-0.479	$ 59.98
-FI/ADG	EBV_{FI} , EBV_{ADG}	-0.018	0.079	-0.480	$ 60.67
v_1.FI + v_2.ADG	$EBV_{FI/ADG}$	-0.052	0.076	-0.479	$ 59.98
v_1.FI + v_2.ADG	$EBV_{FI/ADG}$, EBV_{ADG}	0.377	0.116	-0.450	$ 64.75
v_1.FI + v_2.ADG	$EBV_{FI/ADG}$, EBV_{FI}	0.377	0.116	-0.450	$ 64.75

[1] v_1 and v_2 are economic values for FI and ADG, respectively

When selecting on a linear combination of the component traits while the breeding objective is a ratio trait, the response in profit is 6.3% lower ($60.67 vs $64.75) compared to a linear profit objective that uses the correct economic weights. The response is in fact identical to a linear objective that uses economic weights equal to 1.59 and -14.9, i.e. μ_y and $-\mu_x$ (result not shown in Table 1).

The last two rows on Table 1 show that when including a ratio trait alongside one of the component traits in the index, the response is again the same as when selecting on the two component traits. This is the case, independent of which component trait is included alongside the ratio trait. When both component traits are included, the index weight on the ratio trait becomes zero, and the response is the same as the linear index on component traits.

Discussion

Single trait selection on a ratio of component traits leads to a selection response that is determined by the ratio of coefficient of genetic variation between the component traits ($\lambda_a = va_x/va_y$). If the denominator trait has a higher va_i most of the response will be focused on reducing the denominator trait. And while this gives a higher response for the ratio, it is not the most profitable response. A ratio can be altered by changing either the nominator or the dominator trait, i.e. in the example by either reducing FI or by increasing ADG. Because ADG has a higher coefficient of genetic variation, selecting on a ratio will mostly change ADG. However, the economic optimum is to mainly decrease FI. The example shows that maximizing response in a ratio is not always economically most optimal. However, as also demonstrated in this paper, as soon as the component trait is used in the index alongside the ratio trait, the index becomes equivalent to a linear index with the two component traits. It appears that the dependency of the ratio trait on the parameters of the component traits leads to an equivalence between these indexes, i.e. either an index with both component traits, or an index with the ratio trait and one of the component traits. Including both component traits would make the information on the ratio trait redundant and the index weight will be zero. So, in fact, there is no problem with using a ratio trait as a selection criterion, as long as one component traits is also used. This is equivalent to simply including the component traits as a selection criterion.

Using a ratio trait as a single objective trait will not give an economically optimal response, as it implies that the weights for the component traits in the objective are proportional to μ_y and $-\mu_x$, which are in most cases not the same as the actual economic weights. Using a breeding

objective that includes both a ratio trait and one of the component traits was not tested in this study and could possibly give an equivalent result to a linear objective with both component trats. However, deriving economic values for a component trait as well as a ratio trait is not straightforward because of the mathematical dependency between the two variables. It seems easier to simply include component traits.

The results of this study will have implications for examples to selection for productivity, feed efficiency and methane intensity, the latter two both ratio traits. The study shows that ratio traits could be included in indexes as long as one of the component traits is also included. However, care must be taken when deriving economic weights for ratio traits due to the mathematical dependency on the component traits.

In this study selection index theory was used, using phenotypic and genetic parameters that can be derived from the parameters of the component traits. These are approximations and there maybe some bias. For example, Gunsett showed that response also is affected by the selection intensity. This maybe another reason to simply include component traits in the index.

Residual traits such as residual feed intake (RFI) or residual methane are sometimes proposed as alternatives to ratio traits. Using residual traits in breeding objectives or indices is statistically equivalent to including the component traits directly, with appropriate adjustments to genetic parameters and economic weights (Kennedy et al, 1993). Defining residual traits at the phenotypic level is less desirable because it requires that both component phenotypes be measured on the same animals. Instead, EBVs for residual traits can be generated from EBVs of the underlying component traits using their estimated variances and covariances. A more robust strategy is to include methane production directly in a selection index and optimise index weights according to an explicit breeding objective that balances profitability with reduced methane output at the industry level. While an industry goal maybe to reduce methane intensity, the genetic parameters in an index will help decide whether that is best achieved by improved productivity or by reducing methane production per head. Genetic correlations among methane, feed intake and production traits are critical and will determine the achievable improvement in methane intensity. Given current carbon prices, a desired-gains index may be required, as economic signals alone are currently too low to sufficiently incentivise breeding for reduced methane emissions per head.

Conclusions

Single trait selection on a ratio of component traits is not economically optimal as selection response is determined by the ratio of coefficient of genetic variation of the component traits rather than by their economic value. Similarly, using a ratio trait as a single trait objective uses implicitly weights relative to the means of the component traits, which is not economically optimal. An index including a ratio trait as well as one of the component traits is equivalent to a linear index of the two component traits. A breeding objective with both a ratio trait and a component trait requires correct tuning of economic values of component traits. Therefore, to optimize selection for traits like feed efficiency and methane intensity, the simplest approach is to just include the component traits such as feed intake and methane production in both the breeding objective and the index.

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