PROBLEMS ASSOCIATED WITH SELECTION FOR TRAITS DEFINED AS A RATIO OF TWO COMPONENT TRAITS

FIELDS C. GUNSETT, USA

Summary

Selection for a trait defined as a ratio of two component traits has generally failed to consider how selection is working on each of the components directly. Direct selection for a ratio is equivalent to an index that is forced through the origin of a bivariate distribution and whose slope is determined by the intensity of selection. The selection pressure that is ultimately placed on each trait changes in a non-linear fashion as the intensity of selection that is placed directly on the ratio changes. This complex relationship between the parameters, both genotypic and phenotypic, of the bivariate distribution and the intensity of selection placed on a ratio is thought to influence the ability of selection to mediate change in the ratio.

Introduction

Selection for a trait defined as a ratio involves selection for two traits simultaneously. Generally when selection is practiced on more than a single trait a linear index, that weights each trait in a way to promote the greatest rate of genetic change, is utilized. Selection for a ratio does not weight the traits in any obvious fashion and assumes that the ratio behaves with the properties of a single trait.

An example of a trait that is a ratio of two component traits is the feed conversion of an individual. In this case the components of the ratio are feed intake and growth rate. The feed conversion ratio is a useful measurement to determine the rate at which feed is converted to body growth. This trait is extremely important since feed intake generally represents the greatest input cost and growth represents a measure of output for a production system. It is assumed that if this ratio is small then feed is being converted efficiently to growth. Due to the perceived importance of the feed conversion ratio it has generally been included as a trait in most selection programs, assuming that feed intake can be measured.

The heritability of the feed conversion ratio for swine has generally been estimated in the moderate range. McPhee et al. (1979) estimated the heritability for feed conversion as .27 for pigs fed ad libitum and presented an average value from five other studies that practiced limit feeding of .45. The heritability is commonly estimated by using the correlation among relatives, generally full sibs or half sibs, this estimate is then used to predict genetic change. Jacquard (1983) pointed out that the heritability predicted from the correlation among relatives may not be the same heritability that predicts

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1 Department of Animal Science, North Carolina A&T State Univ. Greensboro, NC 27411
performance in future generations.

Bernard and Fahmy (1970) analyzed data from a 10 generation experiment where selection was based on feed conversion. The heritability estimate from the correlation among relatives was 0.16 while the realized heritability was estimated to be 0.11. Jungst et al. (1981) selected for feed conversion for five generations and reported a heritability from the correlation among relatives of .12 while the realized heritability was estimated to be .09. Finally, Webb and King (1983) selected for six generations on the basis of feed conversion and reported a realized heritability of .007.

The realized heritabilities from selection experiments consistently have been less than estimates obtained from the correlation among relatives. This suggest that the understanding of how selection works on a ratio is not fully understood. The purpose of this report is to consider how selection directly on a ratio affects the component traits of the ratio. From this understanding of how selection works directly on the ratio alternative selection criteria can be utilized to enhance the rate of change for ratio traits.

Hypothetical Population

In order to demonstrate how selection is practiced on a trait defined as a ratio a data set is required that closely represents a population of the traits of interest. A data set was obtained from Farmers Hybrid Companies, a swine seedstock supplier in the United States, that consists of 1054 pens of pair fed individuals that were evaluated for average daily gain (ADG) and feed intake (ADF) under ad libitum feeding. The pens were comprised of like sexed littermate pairs that were evaluated on a weight to weight basis. The average weight of a pen on test was 30.3kg and the average pen weight off test was 105kg. After correction for differences due to breeds, sex, and the season tested the data were pooled and considered a single homogeneous population.

The phenotypic parameters estimated from the population are presented in table 1. The genetic parameters utilized were obtained from McPhee et al. (1979) who estimated the heritabilities for average daily gain and feed intake along with the genetic correlation between them (table 1). The combination of phenotypic and genotypic parameters provide adequate information to describe this hypothetical population.

Table 1. Phenotypic and genotypic values for average daily gain and feed intake for a hypothetical population of swine.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Phenotypic Mean</th>
<th>Phenotypic Variance</th>
<th>Phenotypic Correlation</th>
<th>Genotypic Heritability</th>
<th>Genotypic Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADG</td>
<td>.80</td>
<td>.0117</td>
<td>.56</td>
<td>.36</td>
<td>.57</td>
</tr>
<tr>
<td>ADF</td>
<td>2.35</td>
<td>.1175</td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

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Selection For A Ratio

Figure 1 presents a graphic display of the 90% confidence region for the hypothetical population. The line that begins at the point 0,0 and passes through the ellipse represents the truncation line based on the ratio value. The line passes through the mean of both traits, every point on the line has a ratio value 2.95, representing a selection intensity of .5. If the selection criteria for this population was the retention of individuals with feed conversion ratio values less than or equal to 2.95 then the portion of the population above the line would be retained. If more intensive selection were required the line in figure 1 would be pivoted upwards, through the origin, until the desired portion of the population to be retained is obtained.

Figure 1. 90% Confidence region for the hypothetical population, with a vector representing individuals with a value of X/Y.

This clearly shows that a ratio can be selected with linear index of the two component traits. If the line in figure 1 can be described by a set of linear weights \( I = W_1 \text{ADG} - W_2 \text{ADF} \) individuals with values superior for I would be retained and inferior I values culled. Obviously, the index is always forced through the origin of the population. Therefore, the linear index that describes selection on the ratio when intensive selection is practiced will give ADF values more weight than when weak selection is practiced.

Figure 2 shows the weights that would be used to develop a linear index to retain any portion of the population. These weights were determined by using the Index-In-Retrospect (IIR) procedure described by Dickerson et al. (1954). The IIR weights use the selection differentials for each trait along with the phenotypic parameters to determine the weight placed on each trait.
Figure 2 shows that the weights placed on the numerator and denominator of the ratio change at a non-linear rate. The weights change in a near linear fashion when between 20%-95% of the population is retained, outside of this region the weights change at a disproportionate rate with respect to one another.

It would be naive to think that this index, based only on the phenotypic distribution of the component traits and the selection intensity, would be optimal in the sense of promoting the maximum rate of genetic change. An index that maximizes the correlation between a phenotype, defined as a linear index of ADG and ADF, with a genotype, defined as the ratio ADF:ADG, was presented by Gunsett (1984). For the hypothetical population described in table 1 the optimal linear index is, I = 2.1ADG - ADF. This index takes into account both the phenotypic and genotypic distributions of the component traits. The linear index also maintains equal pressure on the traits, while direct selection on the ratio will vary the pressure placed on each component. The concept that as the selection intensity increases for feed conversion the selection pressure placed on ADG and ADF change in a disproportionate fashion is shown in table 2. Notice that when selection becomes intense the selection differential of ADF for the selected population continues to change while the selection differential of ADG appears to remain constant. This is due to the greater variability of ADF in the population, increasing the probability of selecting favorable feed conversion values by an individual having a low ADF value rather than high ADG values.

Table 2. Selection differentials for ADG and ADF, when selection is practiced directly on the feed conversion ratio, for various intensities of selection.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Proportion (%) of Population Selected</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100</td>
</tr>
<tr>
<td>ADG</td>
<td>0.0</td>
</tr>
<tr>
<td>ADF</td>
<td>0.0</td>
</tr>
</tbody>
</table>
The variable selection intensity that is placed on each trait may aid or detract from overall genetic change dependent on the heritabilities of the traits and the genetic correlation between the numerator (ADF) and denominator (ADG) of the ratio. For the hypothetical population if intensive selections were practiced directly on the feed conversion ratio, the selection pressure would increase at a non-linear rate against feed intake. For the example, ADF is highly heritable (.62) and it would be expected that feed intake would be reduced at a more rapid pace than ADG.

Conclusions

Consideration of how response to selection is mediated when a trait is defined as a ratio of two component traits has generally ignored the role of each of the component traits individually. A graphic representation, figure 1, of the population selected when the trait is defined as a ratio is helpful in understanding how selection is practiced on each trait.

When the selections criteria is a trait defined as a ratio of two components, the following factors should be considered when the response to selection fails to meet the anticipated level,

1. Selection directly on a ratio is a form of index selection that always intercepts the origin of the bivariate distribution,

2. The selection index that results from selection on the ratio is determined solely by the phenotypic parameters and the intensity of selection,

3. As selection becomes more intense the selection differential becomes disproportionately larger for the more variable trait (regardless of the genetic distribution), and

4. Since the intensity of selection will change the relative weight placed on the two traits, it is possible that males that are intensely selected will not represent the same genetic sample as the females which are selected less intensely.

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References


