Selection Differentials of Component Traits in Truncation Selection for a Proportion-Defined Trait

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Abstract In this paper, for one specific type of ratio traits, or a proportion-defined trait (denoted simply as proportion trait), whose numerator trait is contained also in the denominator as its one component, formulae to predict selection differentials for the component traits are derived, assuming upward and downward truncation selection based on phenotypic value of the proportion trait. Two component traits are considered, supposing that these traits follow bivariate normal law and their coefficients of variation are small. The phenotypic changes of component traits are described in terms of a given proportion of population selected, the corresponding truncation point on the proportion trait and phenotypic parameters for the component traits. Using the formulae derived, a deterministic investigation of the selection differentials is conducted for three selected sets of phenotypic parameters for component traits with which the shapes of the distribution of the proportion trait are very nearly symmetric, skewed to the right and skewed to the left. In addition, the signs of the selection differentials are theoretically determined by examining the related inequality including a function of truncation point and the phenotypic parameters. As a consequence, it is revealed that for each of upward and downward selection, there occur three kinds of possible combinations of the signs according to the situations of the phenotypic parameters.

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Characters defined as a proportion such as $x_1/(x_1 + x_2)$, where x_1 and x_2 are quantitative traits, are sometimes considered as a selected trait in livestock improvement. A trait of this type may be called a proportion-defined trait or a proportion trait simply, and is classified as a specific type of ratio traits, as it is obvious from its definition.

Long ago, the statistical and genetic properties of the simplest ratio trait x_1/x_2 as a unit character were investigated by applying a log-scale transformation¹¹⁾ and using, in essence, a Taylor-series expansion¹⁰⁾. These approaches can be applied to a ratio function, but do not utilize all information concerning its dis-

tributonal property. For two correlated normal variates, it is known that their ratio does not follow a normal distribution^{2,6)}. The classical theories of quantitative genetics based on the assumption of linearity and normality¹⁾ may not be applied simply to non-normal traits such as ratio traits^{3,5,7,8)}, since the superiority of selected individuals and realized response in the progeny depend largely on the distributional property of a character of interest.

Gunsett^{3,4)} showed that the response to direct selection for the simplest ratio trait is complicated by the disproportionate fashion by which selection pressure is exerted on the component traits, and taking account

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of this fact, he described the expected values in the phenotypic values of the component traits for truncatedly selected individuals. Moreover, Mather *et al.*⁸⁾ re-examined Gunsett's description to provide the correct signs of selection differentials of component traits for upward and downward selection.

Following these studies, for selection on the proportion trait, Shoji and Iwaisaki⁹⁾ investigated an expression for truncation point under the assumption that phenotypic values of component traits are normally distributed. In this paper, we further examine selection differentials of the component traits expected from truncation selection on the proportion trait.

Materials and Methods

We defined a proportion trait, as follows

$$r = x_1 / (x_1 + x_2), \quad (1)$$

where x_i ($i = 1, 2$) are phenotypic values of the component traits. Herein we assumed that x_i follow a bivariate normal distribution with means μ_i , standard deviations σ_i , covariance σ_{12} , and correlation ρ . Then, we first examined expressions for selection differentials of component traits, assuming upward and downward truncation selection on r .

When supposed upward selection, for instance, the expected values for component traits in the selected population can be written by the standard approach as

$$\begin{aligned} \mu_i^* &= E \{x_i \mid r > z\} \\ &= p^{-1} \int_R x_i f(x_1, x_2) dx_1, dx_2, \end{aligned} \quad (2)$$

with the bivariate normal probability density function

$$f(x_1, x_2) = \{2\pi\sigma_1\sigma_2(1-\rho^2)^{1/2}\}^{-1} \exp[-0.5(1-\rho^2)^{-1} \{ \{\sigma_1^{-1}(x_1-\mu_1)\}^2 - 2\rho(\sigma_1\sigma_2)^{-1}(x_1-\mu_1)$$

$$(x_2-\mu_2) + \{\sigma_2^{-1}(x_2-\mu_2)\}^2 \}] \quad (3)$$

where p is the proportion of population selected truncatedly, z is the truncation point in the distribution of r , and R is the appropriate region of integration. As described by Shoji and Iwaisaki⁹⁾, z is

$$\begin{aligned} &[\mu_1(\mu_1+\mu_2) - t^2(\sigma_1^2+\sigma_{12}) + \alpha\beta \{(\mu_1\mu_2 - t^2\sigma_{12})^2 - \\ &(\mu_1^2 - t^2\sigma_1^2)(\mu_2^2 - t^2\sigma_2^2)\}^{1/2}] / \{(\mu_1+\mu_2)^2 - t^2(\sigma_1^2+\sigma_2^2 + 2\sigma_{12})\}, \end{aligned} \quad (4)$$

where t is the value of truncation point in the standard normal distribution, given the specified value of p , α takes $+1$ and -1 for upward and downward selection, respectively, and $\beta = +1$ if $p < 0.5$ and $\beta = -1$ if $p > 0.5$. When $p = 0.5$, z is $\mu_1/(\mu_1+\mu_2)$, since $t = 0$.

Equation (2) was evaluated by employing two transformations in turn. First, x_i were transformed to the standardized normal variates u_i , where the Jacobian of the transformation was $\sigma_1\sigma_2$. The second transformation was then $v_1 = u_1$ and $v_2 = (1-\rho^2)^{-1/2}(u_2 - \rho v_1)$, having $(1-\rho^2)^{1/2}$ as the Jacobian of the transformation. Consequently, for μ_i^* , we had

$$\begin{aligned} \mu_i^* &= (2\pi p)^{-1} \mu_i \int_R \int \exp\{-0.5(v_1^2 + v_2^2)\} dv_1 dv_2 \\ &+ (2\pi p)^{-1} \sigma_i \int_R \int v_i \exp\{-0.5(v_1^2 + v_2^2)\} \\ &dv_1 dv_2, \end{aligned} \quad (5)$$

where the region of integration R was given as

$$(\mu_1 + \sigma_1 v_1) / [\mu_2 + \sigma_2 \{\rho v_1 + (1-\rho^2)^{1/2} v_2\}] > z / (1-z). \quad (6)$$

The corresponding expression for μ_i^* was obtained similarly, performing the transformation $v_1 = (1-\rho^2)^{-1/2}(u_1 - \rho v_2)$ and $v_2 = u_2$, where the region R was yielded as

$$[\mu_1 + \sigma_1 \{(1-\rho^2)^{1/2} v_1 + \rho v_2\}] / (\mu_2 + \sigma_2 v_2) > z / (1-z). \quad (7)$$

Table 1. Parameter sets considered

Parameter for component trait	Set		
	I	II	III
Trait x_1			
Population mean (μ_1)	1.0	1.0	2.5
Phenotypic standard deviation (σ_1)	0.05	0.05	0.5
Trait x_2			
Population mean (μ_2)	1.0	2.5	1.0
Phenotypic standard deviation (σ_2)	0.05	0.5	0.05
Phenotypic correlation (ρ)	0.5	0.5	0.5

Thus, further carrying out the required integration by the standard procedure and finally calculating $\mu_i^* - \mu_i$, selection differentials of component traits were derived in terms of phenotypic parameters for component traits.

Next, using the resulting expressions, patterns of selection differentials of component traits were evaluated deterministically for three selected populations with different combinations of the parameter values for component traits. The parameter sets considered (denoted as sets I, II and III), taken from Shoji and Iwaisaki⁹⁾, are listed in Table 1. With sets I, II and III, the shape of distribution of the proportion trait was very nearly symmetric, skewed to the right, and skewed to the left, respectively. Both the cases of upward and downward selection were examined, and a total of five levels for the proportion of population selected were considered.

Results and Discussion

Selection differentials for component trait i ($i=1, 2$), or $\mu_i^* - \mu_i$, was obtained as

$$\Delta s_i = \alpha \varepsilon_i \sigma_i p^{-1} \{2\pi (\gamma_i^2 + 1)\}^{-1/2} \exp \{-0.5 (\gamma_i^2 + 1) \delta_i^2\}, \quad (8)$$

where

$$\gamma_1 = \{z\sigma_2(1-\rho^2)^{1/2}\} / \{(1-z)\sigma_1 - z\sigma_2\rho\}, \quad (9)$$

$$\delta_1 = \{z\mu_2 - (1-z)\mu_1\} / \{(1-z)\sigma_1 - z\sigma_2\rho\}, \quad (10)$$

and ε_i is equal to 1 if $(1-z)\sigma_1 > z\sigma_2\rho$ and to -1 if

not, and

$$\gamma_2 = \{(1-z)\sigma_1(1-\rho^2)^{1/2}\} / \{z\sigma_2 - (1-z)\sigma_1\rho\}, \quad (11)$$

$$\delta_2 = \{(1-z)\mu_1 - z\mu_2\} / \{z\sigma_2 - (1-z)\sigma_1\rho\}, \quad (12)$$

and ε_2 equals -1 if $z\sigma_2 > (1-z)\sigma_1\rho$ and equals 1 if not.

Selection differentials for component traits, which were predicted using the derived formulae, are presented in Table 2 for the three selected sets of the parameters for component traits. These values are expressed in terms of the corresponding phenotypic standard deviation for each component trait, which will be denoted as Δs_i^* and clearly show how selection pressure is placed on each of component traits.

For set I, in the case of upward selection, the standardized selection differentials Δs_i^* were positive for the component trait 1, or the numerator trait, and negative for the trait 2 which was included only in the denominator. With downward selection, a reverse pattern of the signs was found. Specifically, for this parameter set, absolute values of Δs_1^* and Δs_2^* for upward selection were equal to those of Δs_2^* and Δs_1^* for downward selection, respectively, and with $p=0.5$, absolute values of the selection differentials expected were found to be the same for all the cases, regardless of type of selection. When $p < 0.5$ and $p > 0.5$, however, Δs_1^* was lower and higher in absolute value than Δs_2^* for upward selection, respectively, and *vice versa*

Table 2. Standardized selection differentials of component traits¹⁾ for three parameter sets

Selection	Proportion selected (%)	Set I		Set II		Set III	
		Δs_1^*	Δs_2^*	Δs_1^*	Δs_2^*	Δs_1^*	Δs_2^*
Upward	1	1.0933	-1.5583	-1.0207	-2.6425	2.4994	0.4484
	5	0.9015	-1.1560	-0.7269	-2.0352	1.9569	0.4137
	10	0.7918	-0.9605	-0.5896	-1.7263	1.6744	0.3820
	50	0.3989	-0.3989	-0.2213	-0.7745	0.7745	0.2213
	90	0.1067	-0.0880	-0.0424	-0.1860	0.1918	0.0655
Downward	1	-1.5583	1.0933	0.4484	2.4994	-2.6425	-1.0207
	5	-1.1560	0.9015	0.4137	1.9569	-2.0352	-0.7269
	10	-0.9605	0.7918	0.3820	1.6744	-1.7263	-0.5896
	50	-0.3989	0.3989	0.2213	0.7745	-0.7745	-0.2213
	90	-0.0880	0.1067	0.0655	0.1918	-0.1860	-0.0424

¹⁾ Δs_i^* = standardized selection differential of component trait i .

Table 3. Signs of selection differentials of component traits¹⁾

Condition	Upward selection ($\alpha = +1$)	Downward selection ($\alpha = -1$)
$\rho < (1-z)\sigma_1/z\sigma_2$ ($\varepsilon_1 = +1$)	$\Delta s_1 > 0$	$\Delta s_1 < 0$
$\rho > (1-z)\sigma_1/z\sigma_2$ ($\varepsilon_1 = -1$)	$\Delta s_1 < 0$	$\Delta s_1 > 0$
$\rho > z\sigma_2/(1-z)\sigma_1$ ($\varepsilon_2 = +1$)	$\Delta s_2 > 0$	$\Delta s_2 < 0$
$\rho < z\sigma_2/(1-z)\sigma_1$ ($\varepsilon_2 = -1$)	$\Delta s_2 < 0$	$\Delta s_2 > 0$

¹⁾ Δs_i = selection differential of component trait i .

σ_i = phenotypic standard deviation for component trait i .

ρ = phenotypic correlation between component traits.

z = truncation point on proportion trait.

for downward selection. The shape of the distribution of r with set I is almost symmetrical, but strictly speaking, those in the upper and lower tails are slightly different from each other⁹⁾, following that selection pressure put on r acts on component traits by a disproportionate fashion.

In the case of set II with which the distribution of r is skewed to the right, though with $p=0.5$, the absolute values of selection differentials in one component trait for two directions of selection were also equal to each other, it was found that direct selection on r , regardless of direction of selection, places the majority of selection pressure on the trait 2, or the component trait with higher standard deviation. Both of Δs_1^* and Δs_2^* resulting from upward selection were expected to be negative, but the absolute value for the trait 1 was relatively smaller, given a proportion selected. Therefore, for the shape of the distribution of this type, it is seen that a positive selection differential for r is accomplished by differentially decreasing the means of component traits. In contrast, downward selection under set II led to increased means for the two component traits. However, the increment of the mean for the trait 2 was expected to be larger than that for the trait 1, or the numerator trait, which gives a negative phenotypic response in the proportion trait.

For each of the directions of selection, the third combination of signs for Δs_1^* and Δs_2^* was found with set III. For upward selection, being different from the two upward cases with set I and II, the signs of Δs_1^* and Δs_2^* were both positive for all considered proportions selected, and Δs_1^* was always higher than Δ

s_2^* , given a proportion selected. With downward selection, selection differentials for component traits were both in the negative sign, showing relatively large phenotypic response for the trait 1 with higher standard deviation.

The numerical results given in Table 2 have demonstrated that with the three selected sets of the phenotypic parameters for component traits, there are three possible patterns of the combination of signs for Δs_i for each of upward and downward selection on r . Using the terms α and ε_i , these findings may be confirmed theoretically. For instance, $\Delta s_1 > 0$ is given, when α and ε_1 are 1 or when both of these terms are -1 . The conditions corresponding to the former case are given as $(1-z)\sigma_1 > z\sigma_2\rho$, equivalently $\rho < (1-z)\sigma_1/(z\sigma_2)$, and upward selection. For all combinations of α and ε_i , signs of the selection differentials are summarized in Table 3. However, note that the patterns of $\Delta s_1 < 0$ and $\Delta s_2 > 0$ for upward selection and of $\Delta s_1 > 0$ and $\Delta s_2 < 0$ for downward selection do never occur, since $-1 \leq \rho \leq 1$. Moreover, with $\rho \leq 0$, it is found that $\Delta s_1 > 0$ and $\Delta s_2 < 0$, and $\Delta s_1 < 0$ and $\Delta s_2 > 0$ occur in the upward and downward selection, respectively. On the other hand, if $\rho > 0$, then it is also possible that phenotypic changes for component traits are both positive or wholly negative. That is, for upward selection, both of Δs_1 and Δs_2 are expected to be in the positive sign, if $1/q < \rho < q$, and be in the negative sign, if $q < \rho < 1/q$, where $q = (1-z)\sigma_1/(z\sigma_2)$. In contrast, for downward selection, we have $\Delta s_1 > 0$ and $\Delta s_2 > 0$ with $q < \rho < 1/q$ and $\Delta s_1 < 0$ and $\Delta s_2 < 0$ with $1/q < \rho < q$. Hence, it is seen that the sign and the relative magnitude of phenotypic

correlation between component traits play an important role in determining signs of selection differentials for component traits considered in the proportion trait, and that correspondingly, for the case of $\rho > 0$, the signs of the selection differentials are dependent on the type of distribution of r .

In this study, for the proportion-based truncation selection, it was revealed that the directions of the phenotypic changes of component traits are automatically determined by the situation of phenotypic parameters for these traits. It was found that selection pressure put on each component trait is obviously disproportionate. Moreover, it was noticed that according to the situation of phenotypic parameters for component traits, for each of upward and downward selection, there occur three combinations of the signs of selection differentials of these traits. The aspect of the genetic changes, which has more interest for us, will be considered in another paper.

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