Relative efficiency of selection methods to improve a ratio of two traits in *Tribolium*

J. L. Campo and M. Rodríguez

Department of Animal Production, National Institute of Agrarian Investigations, P.O. Box 8.111, E-28080 Madrid, Spain

Summary. Three generations of upward selection for the egg mass/adult weight ratio were carried out in *Tribolium castaneum*. The experiment involved five lines: E – selected for increased egg mass; W – selected for decreased adult weight; R – selected for egg mass/adult weight directly; L – linear index selected with economic weights of m_2: $-m_1$ egg mass to adult weight (m_1 and m_2 are the means for adult weight and egg mass, respectively); NL – nonlinear index selected. Adult weight (7 days after adult emergence) and egg mass (between 7 and 11 days) were measured. The NL, E, and L lines had the greatest observed responses for the ratio; the R and W lines were not effective in improving the egg mass/adult weight ratio. It was expected that the NL line would be superior to the E, L, and R lines, and that the W line would respond the least. Observed response was significant for egg mass in the NL line, and for adult weight in the E, W, and R lines. Strong selection to increase egg mass seems to represent the optimal criterion for the ratio to be improved. The usefulness of nonlinear indices as selection criteria to improve a nonlinear trait, previously found to be optimal for a trait defined as the product of two component traits, appears to hold also for the selective improvement of the ratio of two traits. Serious limitations expected for direct selection of the ratio have been confirmed in this experiment.

Key words: Traits defined as ratios – Nonlinear indices – Linear indices – Ratio-based selection – *Tribolium*

Introduction

Ratios of two traits are often used as selection goals in animal breeding. Feed efficiency, defined as the ratio of output (gain in a trait such as body weight) to feed intake, is one of the most important characters to be improved; its reciprocal, i.e., feed conversion, is also used at times, as are proportions. Furthermore, ratios of dimensions of body parts are often used as systematic criteria. It is of interest, therefore, to compare different selection criteria for improving the ratio of two traits. These criteria include the linear index developed for the logarithm of the ratio (Turner 1959; Smith 1967), the linear index obtained by approximating the ratio by a linear (Harris 1970; Lin 1980; Gunsett 1984; Ponzoni 1985) or quadratic function (Itoh and Yamada 1988), the nonlinear index which is a maximum likelihood estimate of the ratio (Henderson 1963), the nonlinear index obtained by substituting index values for each trait into the ratio (Harris 1970), direct selection for the ratio, and indirect selection for the numerator or the denominator trait. Gunsett (1984, 1986, 1987) and Mather et al. (1988) have emphasized the serious limitations to the usefulness of ratios as selection criteria. Relative efficiency of indirect selection depends on the correlation between the ratio and its numerator or denominator (Sutherland 1965; Yüksel 1979).

Some researchers have used the ratio or a component trait as the criterion for selection, while others have taken the linear index approach, in studies involving broilers (Wilson 1969; Pym and Nicholls 1979; Pym and James 1979; Leenstra and Pit 1987; Leclercq et al. 1980), mice (Sutherland et al. 1970; Yüksel et al. 1981; Gunsett et al. 1981; Sharp et al. 1984; Eisen and Prasetyo 1988), rats (Notter et al. 1976; Wang and Dickerson 1984), beef cattle (Davis 1987), turkeys (Nestor and Bacon 1986), and laying hens (Harris 1969; Manson 1973).

As far as we know, nonlinear selection indices have not been used experimentally as a criterion to improve traits defined as ratios. Fairfull et al. (1977) and Campo

and Sánchez (1988) compared the efficiency of nonlinear and linear indices with direct selection for the pupal weight × family size product, or with indirect selection on only one component, in *Tribolium castaneum*. The objective of our study was to compare five selection criteria for improving the egg mass/adult weight ratio in *Tribolium*. The selection methods comprised indirect selection for increased egg mass, indirect selection for decreased adult weight, direct selection on the ratio of egg mass to adult weight, linear index of egg mass and adult weight, and nonlinear index of egg mass and adult weight.

Materials and methods

The base population of *Tribolium castaneum* used for this study was the Consejo; it has been maintained in this laboratory since 1964. All lines were kept at 33 °C and 70% relative humidity on 95% whole wheat flour and 5% dried brewer's yeast medium. The traits selected were egg mass and adult weight; both traits were scored to the closest 0.01 mg, egg mass 7 through 11 days and adult weight 7 days after emergence.

Selection was intended to improve the ratio $H = (m_1 + G_1)/(m_2 + G_2)$, where m_1 and m_2 are the population means for egg mass and adult weight, respectively, and G_1 and G_2 are the breeding values. Five selection criteria were used: selection for increased egg mass (line E), selection for decreased adult weight (line W), direct selection for increased egg mass/adult weight (line R), linear selection index (line L), and nonlinear selection index (line NL). There were three replicates and three generations of selection per line. To start each replicate, 20 males and 20 females were sampled as pupae from the population cage and paired randomly.

Five male and five female offspring were assessed as selection candidates from each pair mating (200 individuals in each generation, line, and replicate). The 20 males and 20 females with the highest ranks based on the selection criterion from a given line were selected and mated in pairs, avoiding sibmatings; the selected proportion was therefore 20%. The selection criteria were based on individual performance for egg mass in females and on full-sister family information in males. Selection for adult weight was based on individual values also. The linear index (line L) in females was $I = b_1 x_1 + b_2 x_2$, where x_1 and x_2 are the phenotypic values for egg mass and adult weight, respectively. The coefficients b_1 and b_2 are given by approximating the ratio by a linear function and using the partial derivatives of the ratio evaluated at the means (m_2/m_2^2 and $-m_1/m_2^2$) as economic weights (Harris 1970). Since $1/m_2^2$ is a common factor, it can be dropped, and the economic weights become m_2 and $-m_1$. Finally,

$$\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} = \begin{bmatrix} P_{11} & P_{12} \\ P_{12} & P_{22} \end{bmatrix}^{-1} \begin{bmatrix} G_{11} & G_{12} \\ G_{12} & G_{22} \end{bmatrix} \begin{bmatrix} m_2 \\ -m_1 \end{bmatrix} \quad (1)$$

where P_{ij} and G_{ij} are the phenotypic and genetic covariances betwen traits i and j. The linear index in males was $I = b_1 \bar{x}_1 + b_2 x_2$, where $\bar{x}_1$ is the mean of the male's full sisters for egg mass, and the coefficients b_1 and b_2 are given by:

$$\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} = \begin{bmatrix} W_{11} & 0.5 G_{12} \\ 0.5 G_{12} & P_{22} \end{bmatrix}^{-1} \begin{bmatrix} 0.5 G_{11} & 0.5 G_{12} \\ G_{12} & G_{22} \end{bmatrix} \begin{bmatrix} m_2 \\ -m_1 \end{bmatrix} \quad (2)$$

where $W_1 = [P_{11} + 0.5(n-1) G_{11}]/n$, and n is the family size for egg mass. The nonlinear index (line NL) was: $(m_1 + \hat{G}_1)/(m_2 + \hat{G}_2)$, where $\hat{G}_1$ and $\hat{G}_2$ are the selection indices for each

breeding value estimated on information from both traits (Henderson 1963). The nonlinear index in females was $[m_1 + (a_1 x_1 + a_2 x_2)]/[m_2 + (c_1 x_1 + c_2 x_2)]$, where the coefficients a_1, a_2, c_1, and c_2 are given by:

$$\begin{bmatrix} a_1 \\ a_2 \end{bmatrix} = \mathbf{P}^{-1} \begin{bmatrix} G_{11} \\ G_{12} \end{bmatrix}; \quad \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} = \mathbf{P}^{-1} \begin{bmatrix} G_{12} \\ G_{22} \end{bmatrix} \quad (3)$$

and $\mathbf{P}^{-1}$ is the inverse matrix of phenotypic covariances in Eq. (1). Similarly, the nonlinear index in males was $[m_1 + (a_1 \bar{x}_1 + a_2 x_2)]/[m_2 + (c_1 \bar{x}_1 + c_2 x_2)]$, where the coefficients are given by:

$$\begin{bmatrix} a_1 \\ a_2 \end{bmatrix} = \mathbf{P}^{-1} \begin{bmatrix} 0.5 G_{11} \\ G_{12} \end{bmatrix}; \quad \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} = \mathbf{P}^{-1} \begin{bmatrix} 0.5 G_{12} \\ G_{22} \end{bmatrix} \quad (4)$$

and $\mathbf{P}^{-1}$ is the inverse matrix in Eq. (2).

Estimates of phenotypic and genetic variances and covariances for both traits in the base population were obtained from full-sib families (Table 1). The selection criteria in each line are included in Table 2.

Expected responses to selection for each trait in line E are, in females

$$\Delta G_1 = i G_{11}/\sqrt{P_{11}}; \quad \Delta G_2 = i G_{12}/\sqrt{P_{11}} \quad (5)$$

and, in males

$$\Delta G_1 = 0.5 i G_{11}/\sqrt{W_{11}}; \quad \Delta G_2 = 0.5 i G_{12}/\sqrt{W_{11}}, \quad (6)$$

where i is the standardized selection differential for the selection criterion. Expected responses in line W are

$$\Delta G_1 = i G_{12}/\sqrt{P_{22}}; \quad \Delta G_2 = i G_{22}/\sqrt{P_{22}}. \quad (7)$$

Expected responses to selection in line R are obtained by approximating the ratio (selection criterion) by a linear function using the partial derivatives evaluated at the means (m_2/m_2^2 and $-m_1/m_2^2$ or, equivalently, m_2 and $-m_1$); in females

$$\Delta G_1 = i \frac{m_2 G_{11} - m_1 G_{12}}{\sqrt{m_2^2 P_{11} + m_1^2 P_{22} - 2 m_1 m_2 P_{12}}}; \quad (8)$$

$$\Delta G_2 = i \frac{m_2 G_{12} - m_1 G_{22}}{\sqrt{m_2^2 P_{11} + m_1^2 P_{22} - 2 m_1 m_2 P_{12}}} \quad (9)$$

and, in males

$$\Delta G_1 = i \frac{m_2 0.5 G_{11} - m_1 G_{12}}{\sqrt{m_2^2 W_{11} + m_1^2 P_{22} - m_1 m_2 G_{12}}}; \quad (10)$$

$$\Delta G_2 = i \frac{m_2 0.5 G_{12} - m_1 G_{22}}{\sqrt{m_2^2 W_{11} + m_1^2 P_{22} - m_1 m_2 G_{12}}} \quad (11)$$

Gunsett (1984) and Mather et al. (1988) have presented equivalent equations employing expressions for the selection differentials of the numerator and denominator traits. Expected responses in line L are as those in line R, using b_1 and b_2 instead of m_2 and $-m_1$. Finally, expected responses to selection in line NL are those in line L using partial derivatives of the selection criteria (Table 2) evaluated at the population means instead of b_1 and b_2. These are 0.0018 and -0.0014 in females and, in males, 0.0021 and -0.0009. In all five lines, expected response for the egg mass/adult weight ratio is approximately

$$\begin{aligned} \Delta G_3 &= \frac{m_1 + \Delta G_1}{m_2 + \Delta G_2} - \frac{m_1}{m_2} \\ &= \frac{m_2}{m_2(m_2 + \Delta G_2)} \Delta G_1 - \frac{m_1}{m_2(m_2 + \Delta G_2)} \Delta G_2. \end{aligned} \quad (12)$$

For line L, this expected response must be divided by m_2^2.

Mean response observed per generation was calculated as the regression coefficient of generation means on generation number. Standard errors of observed responses were calculated from the square root of the variance among replicate slopes divided by the number of replicates. Mean responses were adjusted using line R as a covariate (Muir 1986a, b); this method provides information on the relative response of the two lines to common intrageneration environmental factors (genotype-environment interaction).

Results

As shown in Table 1, the mean value for egg mass was less than that for adult weight, but egg mass was more variable than adult weight, with a coefficient of variation (46%) more than four times that for adult weight (10.5%). This variation is similar to that estimated for egg number (one of the two components of egg mass) in the Consejo pupulation (43.6%, Campo and Rodríguez 1985). Heritability estimated for egg mass was greater than that for adult weight; nonadditive genetic variance would affect egg mass estimates of heritability more than adult weight estimates. The heritability estimates for adult weight of Campo and Rodríguez (1985) and Campo and Velasco

(1989) agree well with the value in Table 1. Phenotypic correlation between egg mass and adult weight was small and positive, and the genetic correlation was near zero. The estimate of heritability obtained by offspring-parent regression for adult weight (0.39 ± 0.06) was similar to that in Table 1; however, the estimate obtained by regression for egg mass (0.35 ± 0.06) was less than that obtained by analysis of full-sib families, indicating the action of nonadditive effects for this trait. A positive and small value for the genetic correlation was found by analysis of regression (0.19 ± 0.02). The egg mass/adult weight ratio had estimates of heritability greater by analysis of full-sib families (0.50) than by offspring-parent regression (0.34) (Table 2). Expectation of the heritability of the ratio (Sutherland 1965) was 0.57. The correlations between the ratio and its components were asymmetrical; expectations for the phenotypic and genetic correlations (Sutherland 1965) were much greater between the ratio and egg mass (0.97 and 0.98, respectively) than between the ratio and adult weight (−0.08 and −0.14), suggesting that the ratio was influenced more by its numerator than by its denominator.

Mean values per generation for the egg mass/adult weight ratio are given in Table 3 (replicates pooled) for all five lines, with regression coefficients of means on generation number and expected responses. Observed responses were significant in the nonlinear (NL) and linear (L) index lines; response was important in the line selected for increased egg mass (E), although the observed response was only twice its standard error and was not significant. In generation zero, there was a large difference between the E and NL and L line means for egg mass/adult weight, as a consequence of the large variation for egg mass. This might have influenced the rate of change in line E. Neither the line selected for increased egg mass/adult weight ratio (R) nor the line selected for decreased adult weight (W) responded significantly over the three generations. The expected response of line NL was greater than that of lines L, E, and R; the ratio of expected response in these three lines versus expected response in line NL ranged from 0.91 to 0.95. The expect-

Table 1. Parameter estimates of the base population

Parameter	Trait[a]	
	Egg mass	Adult weight
Mean	152.06 ± 2.66	224.49 ± 0.64
Variance:		
Phenotypic	4,895.20	564.13
Genetic	2,704.61	227.18
Heritability	0.55 ± 0.08	0.40 ± 0.06
Covariance:		
Phenotypic	245.24	
Genetic	40.73	
Correlation:		
Phenotypic	0.14 ± 0.04	
Genetic	0.05 ± 0.12	

[a] Hundredths of milligrams

Table 2. Selection criteria for each sex and line[a]

Line	Selection criterion	
	Females	Males
E	x_1	$\bar{x}_1$
W	x_2	x_2
R	x_1/x_2	$\bar{x}_1/x_2$
L	$127.81\,x_1 - 100.59\,x_2$	$146.65\,\bar{x}_1 - 50.32\,x_2$
NL	$\dfrac{152.06 + (0.5611\,x_1 - 0.1717\,x_2)}{224.49 + (-0.0121\,x_1 + 0.4080\,x_2)}$	$\dfrac{152.06 + (0.6573\,\bar{x}_1 + 0.0485\,x_2)}{224.49 + (0.0059\,\bar{x}_1 + 0.4025\,x_2)}$

[a] x_1: individual egg mass; $\bar{x}_1$: full-sib mean egg mass; x_2: adult weight

Table 3. Egg mass/adult weight ratio ($\times 100$): mean values per generation, mean observed responses $\pm$ standard errors, and expected responses

Line	Generations				Mean response	Expected response
	0	1	2	3		
E	71.08	64.23	71.39	87.36	5.60 ± 2.78	21.01
W	58.23	73.23	57.74	59.00	-1.32 ± 5.13	3.18
R	73.93	88.62	70.64	82.67	0.82 ± 1.56	21.88
L	63.22	57.21	67.88	66.07	1.92 ± 0.44	21.95
NL	49.55	49.68	51.64	68.69	5.94 ± 1.52	23.06

Table 4. Egg mass (10^{-2} mg): mean values per generation, mean observed responses $\pm$ standard errors, and expected responses

Line	Generations				Mean response	Expected response
	0	1	2	3		
E	167	149	164	201	11.7 ± 6.44	47.81
W	126	151	114	115	-7.0 ± 9.36	-2.30
R	166	202	156	182	0.2 ± 3.81	46.37
L	141	128	152	151	5.4 ± 2.61	47.24
NL	110	112	112	159	14.7 ± 3.75	49.37

Table 5. Adult weight (10^{-2} mg): mean values per generation, observed responses $\pm$ standard errors, and expected responses

Line	Generations				Mean response	Expected response
	0	1	2	3		
E	231	229	226	228	-1.2 ± 0.30	0.71
W	220	209	198	195	-8.6 ± 1.85	-13.30
R	224	223	219	214	-3.4 ± 1.15	-3.09
L	222	218	222	225	1.6 ± 2.82	-2.26
NL	217	219	211	222	0.7 ± 1.69	-2.65

Table 6. Regression coefficients using line R as a covariate

Line	Adjusted mean response			Genotype-environment interaction		
	Ratio	Egg mass	Adult weight	Ratio	Egg mass	Adult weight
E	5.73	11.74	-3.95	-0.16	-0.20	-0.81
W	-1.97	-7.14	-14.43	0.80	0.70	-1.71
L	2.31	5.48	-5.10	-0.48	-0.40	-1.97
NL	5.81	14.66	-4.24	0.16	0.20	-1.45

ed response of line W was the least. Observed responses were less than expected in all five lines.

Generation means for egg mass are shown in Table 4. Observed response was significant in line NL; mean response in lines E and L was only twice its standard error and was not significant; selection was not effective for egg mass in lines R and W. The expected response was similar in lines NL, E, L, and R, being negative in line W. The

selection results for adult weight are given in Table 5. Selection significantly decreased adult weight in lines W, R, and E; selection was not effective in decreasing adult weight in lines NL and L. The expected response of the W line was greater than that of the R, L, and NL lines. The observed response was less than expected in line W and it was slightly greater than expected in line R. For adult weight, neither the expected decrease in both index lines (NL and L) nor the expected increase in line E were observed.

Mean observed responses adjusted using the line selected to increase the ratio (line R) as a covariate are presented in Table 6. Regression coefficients to check the genotype-environment interaction between lines E, W, L, or NL, and line R are also included in this table. Mean responses for the egg mass/adult weight ratio were positive in lines L, E, and NL, suggesting that index selection and indirect selection for egg mass are more efficient than ratio-based selection. Adjusted mean responses for egg mass were, as for the ratio, positive in lines E, L, and NL, and negative in line W. Adjusted estimates of selection responses for adult weight were negative in all four lines. The environment had a greater effect on the R than on the W and NL lines for the ratio and for egg mass, since the regression coefficient measuring genotype-environment interaction was >0 and <1. Common environmental fluctuations caused the E and R lines to respond in opposite directions for the ratio and for egg mass; the regression coefficient estimating the effects of the genotype-environment interaction was less than zero. The same was true for both traits in line L, and for adult weight in all four lines.

The realized heritability for egg mass (0.43 ± 0.16), calculated in the E selected line as the regression of means on cumulative realized selection differentials, was similar to the heritability estimate in the base population (0.55). Realized heritability for adult weight in line W was 0.23 ± 0.06; it did not differ appreciably from the estimate in the base population (0.40). Realized heritability for the egg mass/adult weight ratio in line R (-0.03 ± 0.18) was very small and negative, differing greatly from the estimate of 0.50 in the base population. This discrepancy indicates that the heritability of the ratio cannot be used to predict selection response for that ratio. Secondary selection differentials for egg mass in the nonlinear and linear index lines (56.52 and 54.25, respectively) were very close to the selection differential realized in line E (60.01); however, secondary selection differentials for adult weight (-1.04 in line L and -0.50 in line NL) differed substantially from that realized in line W (-29.62), suggesting that index lines placed the majority of selection pressure on increasing egg mass. On the other hand, secondary selection differentials for the egg mass/adult weight ratio in the linear (25.60) or nonlinear (24.36) index lines agree well with that observed in line R (32.13).

Discussion

Theoretical expectations for the egg mass/adult weight ratio have been partially observed in the experiment, since the nonlinear index, the linear index, and the egg mass lines had the greatest responses, and response observed in the adult weight line was the least. However, the ratio-based selection line was not effective in changing the egg mass/adult weight ratio, and there was very large deviation from expected response in all five lines. The observed efficiency of the linear index relative to the nonlinear index was less than expected. A superiority of the nonlinear over the linear index was obtained by Campo and Sánchez (1988), selecting for a trait (biomass) defined as the product of two component traits (pupal weight and family size) in Tribolium. Thus, the usefulness of nonlinear indices as selection criteria to improve a nonlinear trait appears to hold also for selection of ratios of two traits.

The observed superiority of the linear index over direct selection for increasing the egg mass/adult weight ratio agrees very well with conclusions of Gunsett (1984, 1986, 1987). Gunsett (1984) reported that with unequal heritabilities of component traits, the linear index is always more efficient in changing a ratio than direct selection. When the component traits have equal heritabilities, the methods give similar responses. On the other hand, the observed discrepancy between the realized heritability of the egg mass/adult weight ratio and the estimates obtained from the correlation among relatives agrees with the general trend obtained from selection experiments (Gunsett 1986), and suggests that the phenotype and genotype of the ratio are not bivariate normal in their distribution. In this way, the heritability estimated from analysis of covariance among relatives would not provide an accurate method of determining expected response for the ratio and would explain the discrepancy between expected and observed response in line R.

Gunsett (1987) suggests that the difference between realized and estimated heritabilities supports the idea of utilizing the components of the ratio in a linear index, when the selection goal is to maximize the response in a ratio. On the other hand, direct selection on the ratio is complicated by the disproportionate fashion by which selection pressure is exerted on the component traits (Gunsett 1984); one advantage that the linear index provides is the predictability of the selection pressure placed on the components. A majority of selection pressure on increasing the numerator seems to represent the optimal strategy for the egg mass/adult weight ratio to be improved. The behavior of the index line is consistent with this optimal strategy, but direct selection on the ratio gave greater weight for decreasing the denominator. Pym (1985) suggests that since it is not possible to assign an economic weighting to food efficiency, since change in

the ratio can be affected by change in the numerator and/or denominator, selection should incorporate both component traits. Obviously, the superiority of the linear index over direct selection for the ratio will depend on the values of the index coefficients; if the index coefficient of one component trait were smaller than that of the other, the efficiency of the ratio-based selection relative to that of the index selection could be increased. Davis (1987) found little advantage in using an index of feed intake and gain (two traits with equal heritabilities) in place of the feed/gain ratio in beef cattle; the index coefficients of feed intake and gain were approximately $-1:4$.

Observed response of the linear index line was not greater for the ratio than that of the egg mass line as expected, but the change in egg mass/adult weight ratio was not significant in this line. Table 3 shows that selection on the linear index is expected to be 4.5% more effective than selection on egg mass alone. Similarly, Lin (1980) indicated that selection on an index of weight gain and feed intake in mice was 10% more effective than selection on weight gain for improvement of feed efficiency. When the goal was to obtain the largest negative response in fat weight/body weight, Eisen and Prasetyo (1988) found in mice that the linear index was only marginally better (5%) than single selection for decreased fat weight. Pym and James (1979) reported that predicted response to selection based on the linear index of weight and feed consumption in broilers was always greater than predicted response to selection for weight alone. This expected superiority of the linear index over indirect selection for adult weight was observed in our experiment.

The observed superiority of indirect selection for the numerator trait over direct ratio-based selection agrees with the results reported by Clayton and Powell (1979) in ducks, in which the simplest and most effective way of improving feed efficiency is by selection for final body weight. They emphasized that increasing relative fatness is the main disadvantage of this procedure. Leenstra and Pit (1987) selected for feed conversion (feed consumed/ weight gain) and for body weight in a broiler sire strain; the line selected for feed conversion had better feed conversion and less abdominal fat. Finally, the expected superiority of the line selected for the numerator trait (egg mass) over that selected for the denominator (adult weight) was confirmed in our study. The high and positive value for the genetic correlation between the ratio and egg mass, and the small and negative value between the ratio and adult weight, are consistent with the behavior of both lines. According to Yüksel (1979), feed efficiency and gain are positively correlated in some farm and laboratory animals, while the correlation between efficiency and feed consumption is either zero, or negative and small. In agreement with these observed results, Nestor and Bacon (1986) found that biological efficiency

(egg mass/metabolic body weight), an indirect estimate of feed efficiency, of turkeys increased in the line selected for egg production and decreased in the line selected for body weight.

Given the conditions of this experiment (numerator trait much more variable than denominator trait, mean values and heritabilities not very different for the component traits, small phenotypic and genetic correlations between numerator and denominator, and asymmetrical correlations between the ratio and its components), non-linear index, linear index, and selection for the numerator trait are the most efficient methods to improve a ratio of two traits, while direct ratio-based selection and selection for the denominator trait appear to be inappropriate for the selection of a ratio.

References

Campo JL, Rodríguez MC (1985) Experimental comparison of methods for simultaneous selection of two correlated traits in *Tribolium*. 1. Empirical and theoretical selection indexes. Theor Appl Genet 71:93–100

Campo JL, Sánchez A (1988) Experimental comparison of selection methods to improve a nonlinear trait in *Tribolium*. Theor Appl Genet 75:569–574

Campo JL, Velasco T (1989) An experimental test of optimum and desired-gains indexes in *Tribolium*. J Hered 80:48–52

Clayton GA, Powell JC (1979) Growth, food conversion, carcass yields, and their heritabilities in ducks (*Anas platyrhynchos*). Br Poult Sci 20:121–127

Davis ME (1987) Divergent selection for post-weaning feed conversion in beef cattle: predicted response based on an index of feed intake and gain vs feed: gain ratio. J Anim Sci 65:886–895

Eisen EJ, Prasetyo H (1988) Estimates of genetic parameters and predicted selection response for growth, fat, and lean traits in mice. J Anim Sci 66:1153–1165

Fairfull RW, Friars GW, Wilton JW (1977) An empirical comparison of selection methods for the improvement of biomass. Theor Appl Genet 50:193–198

Gunsett FC (1984) Linear selection to improve traits defined as ratios. J Anim Sci 59:1185–1193

Gunsett FC (1986) Problems associated with selection for traits defined as a ratio of two components traits. In: Proc 3rd World Congr Genet Appl Livestock Prod, vol 11, Lincoln/NE, pp 437–442

Gunsett FC (1987) Merit of utilizing the heritability of a ratio to predict the genetic change of a ratio. J Anim Sci 65:936–942

Gunsett FC, Baik DH, Rutledge JJ, Hauser ER (1981) Selection for feed conversion on efficiency and growth in mice. J Anim Sci 52:1280–1285

Harris PC (1969) Effectiveness of egg mass/feed consumption ratio in improving genetic productive efficiency of laying hens. Poult Sci 48:1817

Harris DL (1970) Breeding for efficiency in livestock production: defining the economic objectives. J Anim Sci 30:860–865

Henderson CR (1963) Selection index and expected genetic advance. In: Hanson WD, Robinson HF (eds) Statistical genetics and plant breeding. NAS-NRC, Washington/DC, pp 141–163

Itoh Y, Yamada Y (1988) Linear selection indices for non-linear profit functions. Theor Appl Genet 75:553–560

Leclercq B, Blum JC, Boyer JP (1980) Selecting broilers for low or high abdominal fat: initial observations. Br Poult Sci 21:107–113

Leenstra FR, Pit R (1987) Fat deposition in a broiler sire strain. 2. Comparisons among lines selected for less abdominal fat, lower feed conversion ratio, and higher body weight after restricted and ad libitum feeding. Poult Sci 66:193–202

Lin CY (1980) Relative efficiency of selection methods for improvement of feed efficiency. J Dairy Sci 63:491–494

Manson JM (1973) Genetic change in the egg weight, body weight association in the fowl. In: Proc 4th Europ Poult Conf, London, pp 247–256

Mather DE, Gunsett FC, Allen OB, Kannenberg LW (1988) Estimation of phenotypic selection differentials for predicting genetic responses to ratio-based selection. Genome 30:838–843

Muir WM (1986a) Efficient design and analysis of selection experiments. In: Proc 3rd World Congr Genet Appl Livestock Prod, vol 12. Lincoln/NE, pp 269–282

Muir WM (1986b) Estimation of response to selection and utilization of control populations for additional information and accuracy. Biometrics 42:381–391

Nestor KE, Bacon WL (1986) The influence of genetic increases in egg production and body weight on egg mass production and biological efficiency. Poult Sci 65:1410–1412

Notter DV, Dickerson GE, Deshazer JA (1976) Selection for rate and efficiency of lean gain in the rat. Genetics 84:125–144

Ponzoni RW (1985) Linear approximation of nonlinear selection indices: an example with Australian Merino sheep. J Anim Breed Genet 102:395–399

Pym RAE (1985) Direct and correlated responses to selection for improved food efficiency. In: Hill WG, Manson JM, Hewitt D (eds) Poultry genetics and breeding. British Poultry Science, Oxford, pp 97–112

Pym RAE, James JW (1979) Selection for food conversion in broilers: predicted responses to selection for economic efficiency. Br Poult Sci 20:99–107

Pym RAE, Nicholls PJ (1979) Selection for food conversion in broilers: direct and correlated responses to selection for body-weight gain, food consumption, and food conversion ratio. Br Poult Sci 20:73–86

Sharp GL, William GH, Robertson A (1984) Effects of selection on growth body composition and food intake in mice. I. Responses in selected traits. Genet Res 43:75–92

Smith C (1967) A note on the improvement of a trait by selecting on its components. Anim Prod 9:127–130

Sutherland TM (1965) The correlation between feed efficiency and rate of gain, a ratio and its denominator. Biometrics 21:739–749

Sutherland TM, Biondini PE, Haverland LM, Pettus D, Owen WB (1970). Selection for rate of gain, appetite, and efficiency of feed utilization in mice. J Anim Sci 31:1049–1057

Turner HN (1959) Ratios as criteria for selection in animal or plant breeding with particular reference to efficiency of food conversion in sheep. Aust J Agric Res 10:565–580

Wang CT, Dickerson GE (1984) Selection for rate and for efficiency of lean growth in rats: responses to selection and relaxation of selection. J Anim Sci 58:831–845

Wilson SP (1969) Genetic aspects of feed efficiency in broilers. Poult Sci 48:487–495

Yüksel E (1979) Genetic aspects of the efficiency of food utilization in some farm and laboratory animals. Anim Breed Abstr 47:499–504

Yüksel E, Hill WG, Roberts RC (1981) Selection for efficiency of feed utilization in growing mice. Theor Appl Genet 59:129–137