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Two-Way Selection for Daily Gain and Feed Conversion in a Composite Rabbit Population[1]

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ABSTRACT: We conducted a two-way selection experiment in a composite rabbit population to investigate the responses to selection for postweaning ADG and feed conversion (FC). Two generations of crossing, followed by four generations of random pair matings, preceded three generations of selection. Selection was practiced within four lines: high-feed conversion (HFC), low-feed conversion (LFC), high gain (HG), and low gain (LG). Data on 1,446 rabbits from the random mating and selection generations were fitted to an animal model to estimate heritabilities of and the genetic correlation between ADG and FC. The two-trait model included rabbit and common litter random effects and line, generation, and sex fixed effects. Estimates of heritability of ADG and FC were .48 and .29, respectively, and the genetic correlation between them was −.82. Common litter environmental effects accounted for a proportion of .11 and .13 of the phenotypic variation of the two traits, respectively. For ADG (in g/d) the regressions of mean breeding values on generation number during the selection period were $1.23 \pm .12$ ($P < .01$) in the HG line and $−.86 \pm .12$ ($P < .01$) in the LG line; the regressions for FC (in g feed/g gain) were $−.07 \pm .01$ ($P < .01$) in the HFC line and $.03 \pm .01$ ($P < .05$) in the LFC line. Selection for ADG was effective in improving ADG and FC.

Key Words: Rabbits, Selection, Growth, Feed Conversion, Genetic Parameters

Introduction

An important economic objective of rabbit production is the rapid attainment of slaughter weight. Average daily gain has been indicated as the preferred trait for selection in the postweaning period, especially in unimproved populations, because it is less affected by common litter effects than the individual weights at specific ages (Rochambeau et al., 1989; Estany et al., 1992; McNitt and Lukefahr, 1996). Previously reported heritability estimates for ADG varied in magnitude from .13 to .48 (Rochambeau et al., 1989; Moura et al., 1991; Estany et al., 1992; Ferraz and Eler, 1994; Krogmeier et al., 1994; Lukefahr et al., 1996; McNitt and Lukefahr, 1996), suggesting that mass selection could be successfully used to improve this trait. In fact, selection for ADG and slaughter weight has been effective in rabbits (Mgheni and Christensen, 1985; Rochambeau et al., 1989; Estany et al., 1992; Lukefahr et al., 1996), although in some cases the response was less than expected (Rochambeau et al., 1989; Estany et al., 1992).

Feed cost represents over 70% of rabbit meat production cost, so that feed conversion (**FC**; i.e., the ratio of feed consumed to body weight gain attained) is a critical economic factor. However, no reference was found on heritability estimates or on direct or correlated responses to selection for this trait.

Vogt (1979) presented results on genetic parameters of ADG and FC from partial data on this population. Within-generation estimates of heritability, obtained from the regression of offspring on midparent value, ranged from .13 to .54 for ADG and from .08 to .54 for FC. Response to subsequent selection was not reported. The objectives of this study were to evaluate the direct and correlated responses to three subsequent generations of divergent selection for ADG and FC in the same composite rabbit population and also to obtain overall estimates of genetic and environmental parameters from combined random mating and selection generations.

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Table 1. Number of records, means and standard deviations of average
daily gain (ADG), feed conversion (FC), and average feed
disappearance (AFD) in the random mating generations

Generation	No. litters	No. animals	ADG, g/d		FC, g feed/g gain		AFD, g/d	
			Mean	SD	Mean	SD	Mean	SD
3	19	111	29.0	5.7	5.55	.92	158	23
4	19	98	30.0	6.0	5.65	.94	165	24
5	27	143	29.9	4.5	4.46	.74	132	17
6	30	180	30.8	5.2	4.46	.53	136	20

Materials and Methods

Animals and Management. Two sequential generations of crossing involving four rabbit breeds (New Zealand White, Siamese Satin, Dutch, and Flemish Giant) were conducted at the University of Hawaii from 1970 to 1972 to develop a composite population. The crosses were planned so that all the F2 animals had equal contributions from each breed (for details see Vogt, 1979). Four generations of random single pair matings (generations three to six) were followed by three generations of selection (generations seven to nine) from 1973 to 1977.

Matings occurred at 5.5 to 6.5 mo of age, and only one litter was obtained from each mated pair, eliminating variation due to age of dam or parity. Sib matings were avoided at all times during the experiment. In each generation all litters were born within a 6-wk period, minimizing variation due to seasonal effects. Weaning took place at 56 to 60 d of age. At weaning, at least four animals from each litter (two males and two females, if available) were chosen randomly and placed in individual cages to undergo a 4-wk evaluation of ADG and FC. The latter trait was measured as the ratio of feed disappearance to weight gain. Average feed disappearance (**AFD**) was measured as the ratio of feed disappearance to number of days in the corresponding period. Animals consumed a commercial pelleted diet containing 18% crude protein, 2% crude fat, and 16% crude fiber on an ad libitum basis throughout the experiment.

Numbers of litters and animals tested and means and standard deviations of ADG, FC, and AFD for the random mating generations are given in Table 1. Generation six was the foundation population for bidirectional selection for ADG and FC. From this foundation population, approximately 15 males and 15 females were selected to initiate each of the four selection lines according to the following criteria: high ADG (**HG**), low ADG (**LG**), high FC (**HFC**), and low FC (**LFC**). High FC is defined as high efficiency (i.e., less feed consumed per unit of gain). For three generations mass selection was practiced within lines and according to the respective criteria. Lines were maintained with 15 to 20 mating pairs per generation.

Genetic Parameter Estimations. Performance records on 1,446 animals from generation three to nine were

fitted to a two-trait animal model for estimation of heritabilities and genetic correlations. Performance records on the purebred ancestors and first two crossbred generations were ignored because additive genetic variance could not be assumed to be homogeneous across all generations. The additive genetic relationship matrix included untested animals as well as those from the crossbred generations (n = 2,816). The REML procedure was used with the same design matrix applied for both traits. Maternal effects were fitted in a preliminary analysis. Estimates of maternal additive variance were .11 and .00 for ADG and FC, respectively, which resulted in estimates of maternal heritabilities at .00 for both traits. Therefore, maternal effects were omitted from the final model, which was assumed to be

$$\mathbf{Y} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{Z}_2\mathbf{u}_2 + \epsilon$$

where $\mathbf{Y}$ = vector of observations, β = vector of fixed effects of line, generation, and sex, $\mathbf{u}_1$ = random vector of additive genetic animal effects, $\mathbf{u}_2$ = random vector of common litter environmental effects, $\mathbf{X}$, $\mathbf{Z}_1$, and $\mathbf{Z}_2$ = incidence matrices relating β, $\mathbf{u}_1$, and $\mathbf{u}_2$ to $\mathbf{Y}$, and ϵ = random vector of residual effects.

Animal, common litter, and residual effects were treated as random with variances $\mathbf{A} \otimes \mathbf{G}$, $\mathbf{I} \otimes \mathbf{P}$, and $\mathbf{I} \otimes \mathbf{R}$, respectively, where $\mathbf{G}$, $\mathbf{P}$, and $\mathbf{R}$ denote covariance matrices among two traits for each animal, common litter, and residual effects, respectively. The relationship matrix is $\mathbf{A}$, the identity matrix is $\mathbf{I}$ and $\otimes$ stands for Kronecker product. Variance and covariance components were computed using the Multiple Trait Derivative Free Restricted Maximum Likelihood Program (Boldman et al., 1993).

Measurement of Response to Selection. Selection differentials were calculated as the differences in ADG or FC between the mean of the selected individuals and the mean of their sex in each line each generation. The selection differentials were weighted by the number of offspring alive at 8 wk of age to give an estimate of the joint effect of natural and artificial selection. Standardized selection differentials were calculated by dividing the measured selection differential by the phenotypic standard deviation each generation. Expected selection intensities were obtained from the table for small populations (Becker, 1992). Values

for males and females were averaged to give the intensity in each line-generation combination.

Breeding values for ADG and FC of animals from generation six to generation nine (foundation and selection generations) were estimated from a second analysis using the same two-trait animal model. Average values were calculated for each line-generation combination and plotted against generation number to illustrate genetic trends. The same average values were then regressed on generation number to estimate linear genetic trends. The regression coefficients were compared with zero using Student's t tests.

Results and Discussion

The number of records, means, and standard deviations for ADG, FC, and AFD by line and generation for the selection generations are presented in Table 2.

Estimates of heritabilities of and genetic correlations between ADG and FC are presented in Table 3. The heritability estimates were high, especially for ADG (.48), suggesting that response to mass selection would be particularly effective for this trait. Published estimates of heritability of postweaning gain in rabbits were variable, ranging from .13 to .48 (Rochambeau et al., 1989; Moura et al., 1991; Estany et al., 1992; Ferraz and Eler, 1994; Krogmeier et al., 1994; Lukefahr et al., 1996; McNitt and Lukefahr, 1996). Variability may be due to the variety of breeds,

environmental conditions, and methodology involved in these studies. Estimates of heritability of ADG specifically using animal models varied nearly as widely, from .17 (Lukefahr et al., 1996) for a synthetic population, to .35 and .36 (Ferraz and Eler, 1994) for purebred animals, to .48 (Krogmeier et al., 1994) for crossbred rabbits. The latter estimate, based on reciprocal New Zealand White and Helle Grossilber crossbred rabbits, was of the same magnitude as that obtained in the present study. These high estimates could be partially attributed to the fact that ADG was evaluated later in life (up to 84 d of age) than in the other studies (28 to 77 d of age). Accordingly, Lukefahr et al. (1992) estimated the heritability of a related trait, body weight at 90 d of age, in rabbits from tropical Ghana to be .42.

The estimate of heritability for FC was .29, suggesting that response to mass selection would be less effective for this trait. Previously published results involving partial data from the present population (Vogt, 1979) gave estimates of heritabilities of FC ranging from .08 ± .05 to .60 ± .13. Those estimates were computed within generation and based on the regression of offspring on mid-parent value.

Litter common environment effects accounted for similar amounts of variation for each trait (Table 3), indicating that these effects are carried on to the postweaning period. This finding was previously documented in rabbits (Ferraz and Eler, 1994; Lukefahr et al., 1996). The estimate of phenotypic variance for ADG in the present study (27.43) is comparable to previously reported estimates (Ferraz and Eler, 1994; Lukefahr et al., 1996).

Table 2. Number of records, means, and standard deviations for average daily gain (ADG), average feed disappearance (AFD), and feed conversion (FC) by line and generation[a]

Generation	No. animals	ADG, g/d		FC, g feed/g gain		AFD, g/d	
		Mean	SD	Mean	SD	Mean	SD
				HG			
7	118	30.0	5.2	4.85	.95	142	17
8	83	33.0	6.0	3.89	.55	127	17
9	67	31.0	8.8	4.73	.66	140	19
				LG			
7	69	26.7	5.8	5.20	1.40	132	15
8	80	26.7	4.5	4.39	.63	115	15
9	43	22.6	4.4	5.79	1.08	128	17
				HFC			
7	73	26.8	4.6	5.09	.90	134	17
8	77	27.5	3.8	4.36	.57	119	15
9	60	25.6	4.9	5.39	.87	134	14
				LFC			
7	88	29.2	4.8	4.79	.62	138	18
8	85	28.8	4.2	4.17	.60	118	14
9	71	25.7	9.1	5.59	1.17	133	16

[a]HG = line selected for high average daily gain. LG = line selected for low average daily gain. HFC = line selected for high feed conversion. LFC = line selected for low feed conversion.

Table 3. Genetic, environmental, and phenotypic parameters
for average daily gain (ADG) and feed conversion (FC)

Trait	Parameter[a]						
	h^2	c^2	e^2	$\sigma^2 p$	r_g	r_c	r_e
ADG	.48	.11	.41	27.43			
					−.82	−.42	−.65
FC	.29	.13	.59	.72			

[a]h^2 = direct heritability; c^2 and e^2 = common litter and residual environmental variances as proportions of phenotypic variance ($\sigma^2 p$); r_g = genetic correlation between ADG and FC; and r_c and r_e = common litter and residual environmental correlations between ADG and FC.

The genetic correlation estimate (Table 3) points to a strong negative association between the two traits, so that increasing ADG would cause a reduction in the amount of feed needed per gram of gain achieved. High negative estimates of the genetic correlation between these traits were previously obtained with mice (Sutherland et al., 1970; Brown and Frahm, 1975). In contrast with the present study, in the mouse studies the genetic correlation between average daily gain and feed conversion was defined as the amount of gain per feed consumed; therefore the sign of the correlation was positive.

Average expected selection intensity was comparable in the four lines (Table 4) because similar proportions of males and females were selected per line each generation. Average values were 1.14 and −1.22 for the HG and LG lines, respectively, and −1.23 and 1.14 in the HFC and LFC lines. Selection differentials tended to be greater in the upper direction compared with the lower direction for both traits. It can be speculated that natural selection working against artificial selection contributed to this trend. Moreover, the magnitude of the standardized selection differentials (alternatively referred to as realized selection intensities) revealed that, in every line and generation, selection was less than expected. Poor fertility and mortality of selected animals are

possible causes of this discrepancy (Rochambeau et al., 1989). The average selection differentials obtained for the HG and LG lines were lower than the average selection differential of 4.45 obtained in eight generations of unidirectional selection for the same trait by Rochambeau et al. (1989). This difference could be partially explained by the lower selection intensity on males in the present study, where the proportion of males to females was 1:1, compared with approximately 1:5 in that study. Also, only a limited sample of progeny was tested in the present study.

The phenotypic divergence in ADG after three generations of bidirectional selection amounted to 8.4 g/d, which corresponds, on average, to 4.5% of the population mean of this trait before selection was initiated, per generation. This response is high when compared with results of similar studies but is in agreement with the high estimated heritability. Estany et al. (1992) reported realized responses to unidirectional selection for total gain in the postweaning period in two lines of rabbits to be 2.0 and 1.6% per generation over 12 and nine generations of selection, respectively. Estimated breeding values for ADG increased over generations for the HG line and decreased for the LG line following the expected trends (Figure 1). Phenotypic selection for high gain resulted in a predicted increase of 1.23 ± .22 g/d ($P <$ .001) in the breeding value for ADG per generation.

Table 4. Selection intensities and realized selection differentials for average
daily gain (ADG) or feed conversion (FC) in the respective lines[a]

Generation	Expected selection intensity	Selection differential, g/d	Standardized selection differential	Expected selection intensity	Selection differential, g feed/g gain	Standardized selection differential
	HG			HFC		
6	1.36	4.95	.96	−1.56	−.47	−.89
7	1.11	3.59	.69	−1.01	−.27	−.30
8	.95	1.37	.23	−1.13	−.26	−.46
	LG			LFC		
6	−1.56	−4.13	−.80	1.39	.44	.83
7	−.82	−1.02	−.20	1.02	.22	.36
8	−1.28	−2.44	−.56	1.01	.10	.17

[a]HG = line selected for high average daily gain. LG = line selected for low average daily gain. HFC = line selected for high feed conversion. LFC = line selected for low feed conversion.
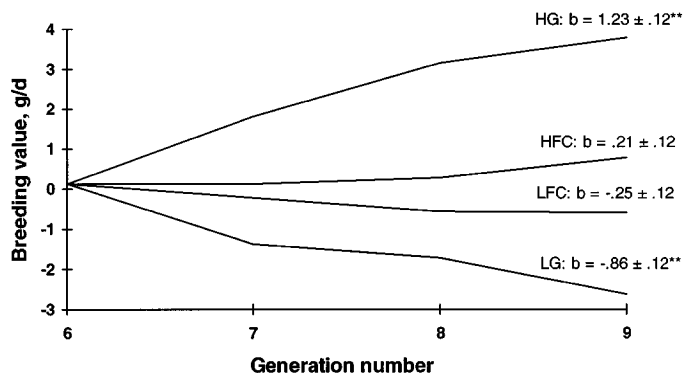
Figure 1. Genetic trends for average daily gain (ADG) in lines selected for high gain (HG), low gain (LG), high feed conversion (HFC), and low feed conversion (LFC). **$P < .01$. b = average response in ADG per generation.

Correspondingly, mass selection for low gain resulted in an average decrease of .86 ± .12 g/d ($P < .001$) in the breeding value for ADG per generation. These trends are in agreement with the higher selection differential in the upper direction compared with the lower direction. In contrast with these results, asymmetry of response to selection for a similar trait, body weight at 112 d in rabbits, was reported by Mgheni and Christensen (1985), where despite the overall higher selection differential on the upward line, response was higher in the downward line. The genetic trends obtained for ADG in the HG line are comparatively higher than previously reported values. Estany et al. (1992) reported .65 and .52 g/d for the B and R closed lines, respectively, and Rochambeau et al. (1989) obtained .85 g/d. The latter studies covered a minimum of eight generations of selection, in contrast to three in our study. It is accepted that the average response tends to be higher in the initial generations of selection (Falconer, 1989), and so the smaller number of selection generations could partially explain the increased overall response. Another factor that could have contributed to the difference was the distinct genetic make-up of the populations in the studies. The first generations after crossings in a composite population may be especially favorable for selection as compared with closed lines.

Correlated responses to selection for ADG are illustrated in Figure 2 and are reflected by the corresponding regression coefficients. Selection for high ADG resulted in a remarkably favorable ($P < .001$) correlated response in feed conversion (−.10 ± .01 g feed/g gain).

Estimated breeding values of FC decreased over generations for the HFC line and increased for the LFC line accompanying selection direction (Figure 2). However, the absolute phenotypic divergence in FC, after three generations of two-way selection, was only .20 g feed/g gain (on average .8% of the population mean of this trait prior to selection, per generation),

indicating a weaker response to direct selection for this trait, when compared with ADG. This result is consistent with the lower heritability estimate for this trait. Reduction in feed intake has been indicated as a limiting factor to improvement of feed conversion in swine (reviewed by Cameron, 1991). Furthermore, selection on ratio traits, such as feed conversion, presents an additional problem. Although the components traits, ADG and feed consumption, are expected to be normally distributed, the ratio between the two may not be, so that responses to selection for ratio traits may actually deviate from expected (Gunsett, 1986). For this reason, selection on residual feed conversion (i.e., the difference between the actual feed intake and that expected given the requirements of the animal) rather than on ratio traits was suggested (Cameron, 1991).

The regression coefficients of FC breeding values on generation number for the HFC line (Figure 2) revealed an average decrease of .03 ± .01 g of feed consumed per gram of gain ($P = .028$) per generation. Phenotypic selection for low feed conversion resulted in an increase in the average breeding value for FC of the order of .03 ± .01 g feed/g gain ($P = .016$) per generation. This symmetry of response was unexpected because the selection differential was larger in the upward direction.

Correlated responses to selection for FC are illustrated in Figure 1 and are reflected by the corresponding regression coefficients. Selection for high FC failed to produce a significant favorable response in ADG ($P = .129$). The regression coefficient (.21 ± .12 g/d per generation) was not different from zero. Selection for high ADG, as already noted, resulted in a remarkably favorable correlated response in FC (−.10 ± .01 g feed/ g gain), even greater than the response to direct selection for high FC (−.03 ± .01 g feed/g gain). This could be at least partially explained by the standardized selection differentials being, on average,
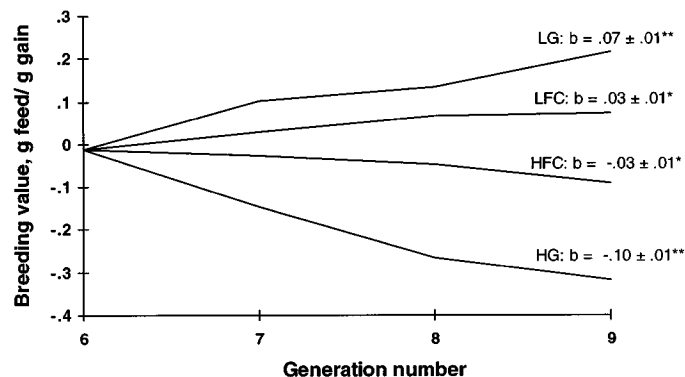

Figure 2. Genetic trends for feed conversion (FC) in lines selected for high gain (HG), low gain (LG), high feed conversion (HFC), and low feed conversion (LFC). *$P < .05$, **$P < .01$. b = average response in FC per generation.

higher for the HG line than for the HFC lines (Table 4). Favorable correlated responses in feed conversion for selection on rate of gain were reported previously for mice (Sutherland et al., 1970; Brown and Frahm, 1975) and explained mainly by the high and negative genetic correlation between the two traits. Similarly, in swine, the selection on a combined index of growth rate and low backfat can result in a substantial improvement of the feed conversion rate (Sather and Freeden, 1978; Vangen, 1980; Cameron, 1991).

In conclusion, ADG and FC are moderately to highly heritable, having the potential to respond effectively to mass selection. The high and negative genetic correlation between the two traits points to favorable correlated responses to selection on either one. The actual selection for ADG produced effective response for this trait, as well as favorable correlated responses for FC. Direct selection for FC improved this trait but failed to improve ADG.

Implications

The present study provides evidence that selection for average daily gain is effective and can be used in rabbit production to improve growth rate and feed conversion, at least in the first generations of selection. This information suggests that a selection program effective in improving average daily gain and feed conversion can be developed without experiencing the difficulties associated with feed consumption measurement.

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