

BREEDING AND GENETICS

Selection Strategies for Limiting the Increase in Ascites While Increasing Growth in Broilers

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ABSTRACT The objective of the current study was to compare the changes in a fitness trait when selection is performed for 5, 10, and 20 generations on a production trait that influenced its expression. Responses to single-trait selection for growth based on phenotype or animal model predictions were compared by computer simulation. Two-trait index selection was performed when a trait, related to the fitness trait, was included in the index with the production trait. The phenotypic expression of the fitness trait among the sibs was also considered as a

selection factor for single-trait and two-trait index selection.

For a fixed increase in the expression of the fitness trait, mass selection produced a larger increase in the production trait than did use of standard animal model best linear unbiased prediction under single-trait selection. The reduction in the genotypic mean of the fitness trait was accompanied by an increase in its phenotypic expression. The use of sib information and an indicator trait reduced the level of expression reached by the fitness trait.

(Key words: selection, ascites, growth, fitness, inbreeding)

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INTRODUCTION

Genotype by environment interaction is usually considered in terms of a change in the difference between the phenotypic values of two or more genotypes measured in two or more external environments. It is becoming more apparent that the internal environment plays an equally important role in the expression of alternate genotypes. The ascites syndrome (AS) in broiler chickens is an example in which genotypes selected for rapid growth often exhibit difficulty meeting the increased metabolic demand for oxygen. The condition is thought to be caused by pulmonary hypertension due to the forced higher blood flow, which often results in a leaking of the right heart valve into the inter-peritoneal space (Julian, 1993). The phenotypic correlation observed, by noting the increase in the ascites frequency as the growth rate is increased, suggests that a genetic correlation must be present. However, when the weight is held at a constant level, the fastest growing birds are not necessarily those that develop the condition (Wideman, 1997).

Julian (1998) has suggested using a genetic approach to reduce the levels of occurrence that ascites has reached in today's broilers. Ascites might be considered as a polygenic condition, produced through the action of a few

or several, loci (Wideman, 2001) each affecting the same, or different, metabolic functions that depend on an adequate supply of oxygen. The incidence of ascites has increased because of the physiological stress caused by selection for rapid growth. The condition manifests itself in those birds not able to make available the oxygen required to meet a higher demand (Julian, 1993). The degree of this stress could be considered as an internal environment specific to the individual. The external environment is still a part of the process, as fast growth is often encouraged by a change to a higher energy diet (Julian, 1993). Other types of environmental alteration, such as a change in altitude, also produce a challenge in obtaining enough oxygen to meet the requirement of the metabolic system (Julian, 1993). External environmental change often challenges the fitness of the bird.

In poultry, there are many cases in which the relationship between the phenotypes and genotypes of a production trait has been found to be affected by the management (Sheridan, 1990). Feed restriction, for example, reduces growth rate and, hence, physiological stress. Such interactions also occur when an internal environment determined by the genotypes at one set of loci of the individual causes a difference in the phenotypic expression of a second trait controlled by another part of the genome. This condition is common in many species, particularly when the level of production is involved. For example,

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Abbreviation Key: AS = ascites syndrome; BLUP = best linear unbiased prediction.

Smith et al. (1983) cite the effect of genetic litter size on preweaning survival in swine, and Boettcher et al. (1997) found that the relationship between confirmation traits and herd life for Holstein dairy cows depended on the milk production level. Stress resistance is also likely to affect, but not to be genetically correlated with, production. The genotype by environment interaction involving ascites was noted in a study by Scheele et al. (1991) that showed birds with a low feed to gain ratio are more likely to develop the condition under environmental pressure delivered through temperature and diet.

Management techniques to reduce ascites have been used by controlling such things as the temperature in which birds are raised or by feed restriction of some type (Julian, 1993). However, such procedures usually result in a reduction of potential weight gain. Rather than altering the external environment and thereby affecting production traits as well as AS, it would be more promising if birds that are predisposed to developing the condition could be identified and culled from the population.

Odom et al. (1991) found that chicks that are at risk of developing ascites can be identified at 1 wk of age by electrocardiograph analysis. The relative hematocrit value has been suggested as an indicator of AS susceptibility (Shlosberg et al., 1996, 1998). Troponin T levels in blood have also been found to be associated with heart damage (Maxwell et al., 1994; Grashorn et al., 1998), but conflicting results concerning such physiological markers are not uncommon. Buys et al. (1999), for example, concluded from their research that a high hematocrit count is not a reliable candidate for use in detecting birds that will become ascitic.

The present study was a simulation exercise to examine the effects of selecting for a production trait, such as growth rate, on a binary fitness trait, such as ascites. Best linear unbiased prediction (BLUP; Henderson, 1975) or mass selection techniques were the two principle procedures used. Attention was also paid to the use of an indicator trait that was weakly or strongly genetically correlated with the AS condition when BLUP was the method used. In addition, use of the incidence of the fitness phenotype among the sibs of an individual was examined as a possible tool to limit the increase in the expression of the trait in the progeny.

MATERIALS AND METHODS

The base populations simulated for use in the various selection strategies considered were based on the infinitesimal model and included genotypes for growth, AS, and an indicator trait correlated with AS (McMillan, 2000). The traits were standardized to mean zero and unit phenotypic variance in the base population. Subsequent changes in the mean were expressed in phenotypic standard deviation units.

Phenotypes for growth and the indicator trait were assigned to be the sum of the genetic component and an independent standard normal deviate representing random environmental effects. The phenotype for growth

was 1 U higher in males than females. The phenotype for ascites was assigned by

$$\begin{aligned} Y_3 &= 1 \text{ if } g_1 + e_1 + g_3 + e_3 \geq C \\ Y_3 &= 0 \text{ if } g_1 + e_1 + g_3 + e_3 < C \end{aligned}$$

where g_1 and g_3 = genetic components, and e_1 and e_3 = environmental components of growth and acites, respectively; C = a value on the underlying distribution of susceptibility that separates the ascitic from the nonascitic genotypic states. The phenotype, $Y_3 = 1$, is an individual that develops ascites; $Y_3 = 0$ is an individual that will not become ascitic. Two values were used for C , representing flocks with a high or low incidence of ascites prior to selection. The expression

$$g_1 + e_1 + g_3 + e_3$$

is the liability for ascites and depends on the phenotype for growth rate as well as genetic and random components of ascites.

The genetic components of an individual in a subsequent generation were given by

$$g_s/2 + g_d/2 + m((1 - F)/2)^{1/2}$$

where g_s = the genetic component of its sire, g_d of its dam; F = the average inbreeding coefficient of the sire and dam, and m = a normally distributed Mendelian sampling component, with (co)variances as given for the genetic components in the base population.

The AS phenotype was, basically, a susceptibility phenotype that included genetic and environmental components for the growth and ascites factors. It was treated as a threshold trait. If the resulting phenotype exceeded a given value C , ascites would occur. In other words, the expression of the genetic predisposition to developing ascites required the necessary genotypic growth rate and the appropriate environmental deviation. If ascites did result, the individual was automatically excluded from the parental group, but its growth was nevertheless recorded.

Two basic situations were considered. One was selection for growth as a single trait. The other included the indicator trait to be combined with the growth trait in an index for two-trait selection. Selection for growth alone was performed as a simple mass selection or on the basis of estimated breeding values derived from an animal model BLUP procedure, which incorporates all family information. When the indicator trait was included, BLUP alone was used with an index that gave equal weight to the growth and indicator phenotypes. The initial correlation between the indicator trait and the AS trait was set at 0.3, 0.5, or 0.7. For both situations, the incidence of AS in the sibs of an individual was used or was not considered, to exclude potential parents before selection.

Each of the selection strategies outlined above was run with low (0%) and high (4%) starting AS incidences. For each generation of 256 males and 256 females, half the

females were selected and mated with 8, 16, 32, 64, or 128 selected males. Mates were assigned at random, and selection was continued without mutation for 20 non-overlapping generations. Inbreeding levels for each generation were recorded, and 100 replicates of each population were run.

The ANOVA was performed to compare the effects of the selection strategies on the average genetic response of each population for growth and AS% reached in Generations 5, 10, and 20. Model 1, used for the analysis of the results for single-trait selection, was

$$y_{ijkl} = \mu + a_i + b_j + ab_{ij} + c_k + ac_{ik} \\ + bc_{jk} + abc_{ijk} + d_l + e_{ijkl}$$

where y_{ijkl} = a trait to be selected; μ = the overall mean; a_i where $i = 1,2$ is the fixed effect of mass vs. BLUP based selection; b_j where $j = 1,2$ is the fixed effect of sib culling vs. no sib culling; c_k where $k = 1,5$ represents the fixed effect of numbers of sires selected; ab_{ij} , ac_{ik} , bc_{jk} , and abc_{ijk} = interactions among these effects; d_l where $l = 1,100$ represents the random effect of the l th replicate; and e_{ijkl} = a normally distributed random deviation.

Model 2, used for the statistical analysis of results from two-trait selection, was

$$y_{ijkl} = \mu + r_i + b_j + c_k + ab_{ij} + ac_{ik} \\ + bc_{jk} + abc_{ijk} + d_l + e_{ijkl}$$

where r_i , $i = 1,3$ represents the fixed effect of a genetic correlation between growth and an indicator trait of 0.3, 0.5, or 0.7, and other terms are as described for Model 1.

Linear and quadratic orthogonal polynomial contrasts were used to examine factor effects on the trends for growth observed across the numbers of males selected, which was done separately for the two initial AS incidences for single- and two-trait selection methods. When two traits were involved, these comparisons were made for each of the three genetic correlations arranged between the ascites and indicator traits. In order to account for the heterogeneity of group variances due, in part, to different levels of inbreeding, the data were weighted by the reciprocal of twice the inbreeding levels attained in each replicate, prior to analysis (Snedecor and Cochran, 1967). The analyses were performed with the PROC GLM procedure of SAS software (SAS Institute, 1999).

RESULTS

Single-Trait Selection

Table 1 provides a summary of the ANOVA for growth and AS% traits using Model 1. For growth, most single- and two-factor terms in were significant after 5, 10, and 20 generations of single-trait selection. Within each procedure, the shape of the response across numbers of males selected was affected by the prior selection of sires on the incidence of ascites among their sibs (Table 2). At Generation 20, the three-factor interaction was significant

($P < 0.05$) for high initial AS% and marginally significant ($P = 0.056$) for low initial AS%. This finding suggests that differences between the BLUP-based and mass selection procedures followed a different pattern across the numbers of males chosen when culling on sib ascites information was performed compared to when such culling was not used. Table 2 shows significant interactions for the linear and quadratic contrasts across numbers of sires selected, whether or not sib information was used, for both selection procedures. Table 3 lists the genotypic means for growth reached by Generation 20 for the various selection strategies. The phenotypic means were almost identical and were not included. The differences between BLUP and mass selection means were always positive. They showed a positive linear trend ($P < 0.05$) as the numbers of sires were reduced but only when culling on sib information took place.

Analysis of AS% data showed a similar pattern to that found for growth (Table 4). There were fewer significant two-factor terms, except in Generation 20. The three-factor term was again significant ($P < 0.05$) only in this generation when the initial AS% was high and marginally significant ($P = 0.07$) when it was low. Phenotypic and genotypic means at Generation 20 are given for ascites in Table 3. There was a small, significant ($P < 0.05$) difference between the results of using BLUP or mass selection procedures and a reduction in numbers of sires chosen results in a larger response. The genetic means have been reduced after 20 generations for all selection schemes employed, whereas the phenotypic expression of the trait increased. The highest incidence (49%) occurred when eight males were selected with the BLUP procedure and the sib information was not used for culling. The larger increase in growth with BLUP compared to that using mass selection was generally accompanied by a higher incidence of ascites.

Inbreeding coefficients reached by Generation 20 are also included in Table 3. As expected, they were larger when fewer males were chosen. They did not seem to be affected by culling on sib ascites information and BLUP always produced a higher level of inbreeding than did mass selection.

Two-Trait Selection

The results of the analysis for two-trait selection on growth showed no significant three-factor interaction (Table 4) for Model 2. Thus, there was no evidence from these simulations that the genetic correlation between growth and the indicator trait for ascites had any effect on the difference in response for culled and nonculled birds, as the number of sires chosen was changed. There were significant single- and two-factor terms that showed the change in selection response to altered sire number was affected by the correlation and also by whether or not culling on sib information was performed (Table 5). Growth response was greater when there was no culling and increased with stronger correlation, given the number of sires selected (Table 6). However, trends in re-

TABLE 1. ANOVA mean squares for weight and ascites percentage (AS%) by using single-trait selection

Source ¹ of variation	Trait	df	Initial AS%					
			High (4%)			Low (0%)		
			Gen ² 5	Gen 10	Gen 20	Gen 5	Gen 10	Gen 20
Procedure	Growth	1	90.4*	95.6*	83.7*	109.1*	97.1*	63.1*
	AS%	1	1.3*	3.8*	5.0*	0.1	1.1*	1.1*
Sib	Growth	1	859.7*	1,578.7*	1,678.5*	38.5*	464.3*	1,228.6*
	AS%	1	28.7*	8.4*	11.5*	4.1*	16.6*	0.3
Procedure × sib	Growth	1	1.3*	0.2	2.1*	0.1	2.6*	0.2
	AS%	1	0.5	1.3*	3.0*	0.5	0.5	2.9*
Sire	Growth	4	921.5*	956.3*	1,158.0*	1,164.7*	1,062.6*	1,053.8*
	AS%	4	77.3*	213.5*	492.8*	18.0*	119.7*	402.3*
Procedure × sire	Growth	4	2.3*	2.4*	1.2*	2.5*	1.8*	1.0*
	AS%	4	0.2	0.3	0.9*	0.2	0.8*	2.2*
Sib × sire	Growth	4	2.4*	4.9*	5.9*	0.6*	9.2*	6.8*
	AS%	4	0.1	0.3	1.5*	0.2	0.2	1.1*
Procedure × sib × sire	Growth	4	0.1	0.1	0.7*	0.1	0.2	0.3
	AS%	4	0.0	0.2	0.4*	0.2	0.1	0.3
Replicate	Growth	99	0.4*	0.3*	0.2*	0.5*	2.5*	0.2*
	AS%	99	0.4*	0.3*	0.2*	0.5*	0.3*	0.2*
Error	Growth	1,881	0.2	0.1	0.1	0.3	0.2	0.1
	AS%	1,881	0.2	0.2	0.1	0.2	0.2	0.1

¹Procedure = selection technique employed; Sib = culling on AS occurrence among sibs; Sire = number of sires selected.

²Gen = generation.

*P < 0.05.

sponse across decreasing numbers of sires chosen differed significantly ($P < 0.05$) for culled versus nonculled populations, and also between correlation levels, as shown by the significant two-factor interactions (Table 5).

The statistical analysis of AS% (Table 4) in the two-trait selection populations also failed to show significant three-factor interactions but did show a significant difference in the incidence of ascites across levels of correlation for any given number of sires chosen. The high initial AS% incidence populations also demonstrated a significantly ($P < 0.05$) different linear trend across sire number between culled and nonculled situations, but this result was not observed for the low initial incidence populations.

The indicator trait genetic means were, like those for growth, similar to the phenotypic means and were reduced by each selection procedure (Table 6). As was ob-

served for the single-trait selection (Table 3), the genetic means for ascites were also reduced while their phenotypic expression was increased. Inbreeding was unaffected by initial ascites incidence or by culling on sib information. It was also unaffected by the level of correlation between the two index traits, but it was strongly affected by the number of sires chosen. A comparison of growth means listed in Tables 3 and 6 showed that inclusion of the indicator trait tended to increase the inbreeding levels reached and decreased the growth response, for all numbers of sire chosen, whether or not culling had been performed on sib information.

Figures 1 and 2 show data on the genotypic means for growth plotted against the proportion of the population exhibiting ascites in Generation 20 for each of the selection strategies. Figure 1 pertains to single-trait selection procedures. Figure 2 includes only those for two-trait selection.

TABLE 2. Contrast mean squares from ANOVA for growth by using single-trait selection

Source ¹	Initial ascites percentage (AS%)					
	High (4%)			Low (%)		
	Gen ² 5	Gen 10	Gen 20	Gen 5	Gen 10	Gen 20
BLUP: sib × linear	3.05*	1.0*	0.02	1.39*	10.70*	1.01*
BLUP: sib × quadratic	0.01	1.91*	4.10*	0.11	0.16	1.88*
MASS: sib × linear	1.75*	4.18*	5.05*	0.66	8.63*	6.93*
MASS: sib × quadratic	0.32	1.23*	2.95*	0.11	0.21	2.57*

¹BLUP = best linear unbiased prediction; Sib = culling on AS occurrence among sibs; linear = linear contrast across numbers of males selected; quadratic = quadratic contrast across numbers of males selected; MASS = mass selection.

²Gen = generation.

*P < 0.05.

TABLE 3. Means for the growth expressed as units of phenotypic standard deviation units and ascites percentage (AS%) traits and inbreeding levels reached in Generation 20 by using single-trait selection¹

Initial AS%	Sib	Sire	Trait								
			Growth genotypic			AS genotypic values		AS % phenotypic		Inbreeding	
			BLUP	MASS	BLUP-MASS ²	BLUP	MASS	BLUP	MASS	BLUP	MASS
High (4%)	No	8	5.12	4.91	0.21	-2.50	-2.58	49	41	0.40	0.29
		16	4.88	4.71	0.18	-2.45	-2.51	44	38	0.23	0.17
		32	4.43	4.22	0.20	-2.21	-2.18	38	34	0.13	0.09
		64	3.77	3.57	0.20	-1.80	-1.72	32	29	0.07	0.05
		128	2.90	2.72	0.18	-1.26	-1.17	24	23	0.04	0.03
	Yes	8	4.23	3.80	0.43	-2.46	-2.40	26	19	0.40	0.31
		16	3.88	3.57	0.32	-2.41	-2.35	21	16	0.24	0.18
		32	3.33	3.08	0.24	-2.15	-2.01	15	14	0.14	0.11
		64	2.73	2.54	0.20	-1.75	-1.61	12	12	0.08	0.07
		128	2.00	1.85	0.15	-1.26	-1.15	10	9	0.05	0.04
Low (%)	No	8	6.19	6.04	0.15	-1.85	-2.06	49	39	0.42	0.30
		16	6.01	5.80	0.20	-1.88	-1.95	43	36	0.25	0.17
		32	5.55	5.31	0.23	-1.68	-1.61	37	32	0.14	0.10
		64	4.91	4.72	0.18	-1.28	-1.22	30	27	0.07	0.05
		128	4.05	3.88	0.17	-0.79	-0.72	23	21	0.04	0.03
	Yes	8	5.32	5.08	0.24	-1.89	-1.97	25	19	0.41	0.31
		16	5.08	4.80	0.28	-1.93	-1.86	20	16	0.25	0.18
		32	4.61	4.36	0.25	-1.74	-1.57	15	14	0.14	0.11
		64	4.03	3.85	0.18	-1.34	-1.21	12	12	0.08	0.06
		128	3.31	3.19	0.12	-0.88	-0.80	9	9	0.05	0.04

¹Sib = culling on AS occurrence among sibs; Sire = number of sires selected; BLUP = best linear unbiased prediction; MASS = mass selection.

²Significant ($P < 0.05$) linear trend of BLUP-MASS growth values across numbers of sires selected when prior selection on sib ascites incidence is made.

It is clear from both graphs that when the initial selection with sib information was applied, the growth and AS% levels attained for each number of sires chosen was much reduced, compared to those reached when this initial

selection was not implemented. Figure 1 also illustrates, for single-trait selection, that for any level of AS% reached, the corresponding growth rate was equal or improved when mass selection was used instead of BLUP.

TABLE 4. ANOVA mean squares for growth and ascites percentage (AS%) by using index selection

Source ¹	Trait	df	Initial AS%					
			High (4%)			Low (%)		
			Gen ² 5	Gen 10	Gen 20	Gen 5	Gen 10	Gen 20
r	Growth	1	6.6*	39.8*	134.7*	1.5*	19.1*	131.6*
	AS%	1	119.6*	175.9*	270.9*	148.1*	203.3*	291.0*
Sib	Growth	1	612.6*	1,146.9*	1,440.4*	18.4*	204.3*	828.1*
	AS%	1	10.9*	4.0*	6.2*	3.1*	8.8*	2.0*
r × sib	Growth	1	1.0*	1.1*	0.5*	0.1	0.5*	0.9*
	AS%	1	0.4	0.3	0.3	0.0	0.1	0.2
Sire	Growth	4	947.3*	1,111.1*	1,324.0*	1,131.7*	1,248.8*	1,240.8*
	AS%	4	166.8*	317.8*	624.2*	67.8*	192.3*	492.9*
r × sire	Growth	4	0.3	1.1*	2.2*	0.1	0.9*	2.6*
	AS%	4	2.5*	3.1*	4.0*	2.8*	3.1*	3.3*
Sib × sire	Growth	4	0.6*	2.3*	4.2*	0.3	3.5*	5.0*
	AS%	4	0.2	0.3	1.1*	0.1	0.1	0.3
r × sib × sire	Growth	4	0.2	0.1	0.1	0.0	0.1	0.0
	AS%	4	0.0	0.1	0.1	0.1	0.0	0.1
Replicate	Growth	99	0.5*	0.3*	0.2*	0.9*	0.4*	0.3*
	AS%	99	0.6*	0.3*	0.2*	0.9*	0.6*	0.3*
Error	Growth	1,881	0.2	0.1	0.1	0.2	0.1	0.1
	AS%	1,881	0.2	0.2	0.1	0.2	0.1	0.1

¹r = genetic correlation between AS and indicator trait; Sib = culling on AS occurrence among sibs; Sire = number of sires selection.

²Gen = generation.

* $P < 0.05$.

TABLE 5. Contrast mean squares from ANOVA for growth by using index selection

Source ¹	Initial ascites percentage (AS%)					
	High (4%)			Low (0%)		
	Gen ² 5	Gen 10	Gen 20	Gen 5	Gen 10	Gen 20
Sib × linear r = 0.3	0.31	1.47*	1.26*	0.45	2.26*	2.16*
Sib × quadratic r = 0.3	0.00	0.02	1.54*	0.00	0.16	0.53*
Sib × linear r = 0.5	1.32*	1.82*	3.10*	0.11	1.62*	2.13*
Sib × quadratic r = 0.5	0.01	0.25	0.08	0.00	0.62*	0.50*
Sib × linear r = 0.7	0.07	0.39	1.00*	0.19	2.16*	3.09*
Sib × quadratic r = 0.7	0.65	0.39	1.21*	0.8	0.01	0.59*

¹Sib = culling on AS occurrence among sibs; linear = linear contrast across numbers of males selected; quadratic = quadratic contrast across numbers of males selected; r = genetic correlation.

²Gen = generation.

*P < 0.05.

When two-trait selection was used, the data in Figure 2 indicated that the gain in growth rate was increased as the correlation between the indicator trait and the ascites trait increased.

DISCUSSION

Few studies have been performed to estimate the heritability of ascites and its genetic correlation with produc-

tion traits (Lubritz et al., 1995; Moghadam et al., 2001). When a trait such as ascites is affected by a genetic component whose phenotypic expression is altered somewhat by a change in the internal environment caused by selection for a second trait, such as growth, the genetic mean of the trait in question can respond in a direction opposite to that of its phenotypic expression. In the case of AS, the genetic component for developing the condition can remain at a constant level or reach a lower level in re-

TABLE 6. Means for the growth and indicator traits, expressed in phenotypic standard deviation units, and ascites percentage (AS%) in Generation 20 using index selection

Initial AS%	Sib ¹	Sire ²	Trait														
			Growth genotypic values			Indicator genotypic values			Ascites (%) genotypic values			Ascites phenotypic values (%)					
			Genetic correlation (r) between ascites and indicator traits														
High (4%)	No	8	4.68	5.01	5.21	-3.28	-3.54	-3.71	-2.43	-2.89	-3.23	39	35	31	0.46	0.46	0.47
		16	4.58	4.83	5.08	-3.26	-3.51	-3.67	-2.54	-2.92	-3.29	33	30	28	0.28	0.28	0.29
		32	4.18	4.41	4.67	-3.00	-3.22	-3.42	-2.33	-2.67	-3.07	29	26	23	0.15	0.16	0.16
		64	3.54	3.78	3.98	-2.49	-2.69	-2.86	-1.92	-2.25	-2.55	24	22	20	0.08	0.08	0.08
		128	2.77	2.93	3.07	-1.81	-1.98	-2.12	-1.40	-1.67	-1.90	19	18	16	0.04	0.04	0.04
	Yes	8	3.79	4.01	4.34	-3.04	-3.32	-3.54	-2.39	-2.75	-3.21	19	16	14	0.45	0.45	0.47
		16	3.58	3.87	4.17	-2.90	-3.21	-3.49	-2.44	-2.85	-3.21	15	13	12	0.28	0.28	0.29
		32	3.22	3.45	3.74	-2.71	-2.94	-3.16	-2.25	-2.58	-2.93	12	11	10	0.16	0.16	0.17
		64	2.69	2.95	3.15	-2.24	-2.50	-2.71	-1.91	-2.22	-2.52	10	9	8	0.09	0.09	0.09
		128	1.98	2.14	2.32	-1.65	-1.82	-1.99	-1.44	-1.63	-1.88	8	7	7	0.05	0.05	0.05
Low (0%)	No	8	5.76	6.04	6.27	-3.21	-3.30	-3.35	-1.94	-2.39	-2.75	35	30	27	0.47	0.49	0.49
		16	5.66	5.87	6.18	-3.10	-3.22	-3.34	-2.00	-2.37	-2.82	31	27	24	0.29	0.29	0.30
		32	5.26	5.51	5.76	-2.87	-2.96	-3.09	-1.79	-2.20	-2.59	27	23	21	0.16	0.17	0.17
		64	4.68	4.87	5.07	-2.40	-2.50	-2.56	-1.45	-1.78	-2.11	22	19	17	0.09	0.09	0.09
		128	3.90	4.03	4.16	-1.78	-1.87	-1.91	-1.01	-1.28	-1.53	16	14	12	0.05	0.05	0.05
	Yes	8	4.99	5.30	5.56	-2.99	-3.15	-3.33	-1.97	-2.36	-2.76	17	15	13	0.45	0.46	0.47
		16	4.86	5.15	5.45	-2.91	-3.12	-3.30	-2.02	-2.43	-2.80	14	12	12	0.29	0.30	0.29
		32	4.50	4.78	5.08	-2.68	-2.89	-3.01	-1.86	-2.23	-2.59	12	11	10	0.16	0.17	0.17
		64	3.99	4.22	4.46	-2.28	-2.44	-2.55	-1.51	-1.83	-2.14	10	9	8	0.09	0.09	0.09
		128	3.30	3.48	3.66	-1.70	-1.82	-1.91	-1.09	-1.33	-1.60	7	6	6	0.05	0.05	0.05

¹Sib = culling on AS occurrence among sibs.

²Sire = number of sires selected.

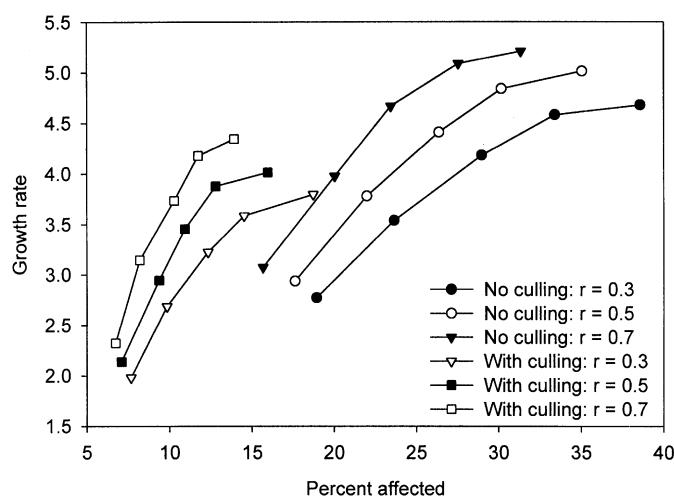
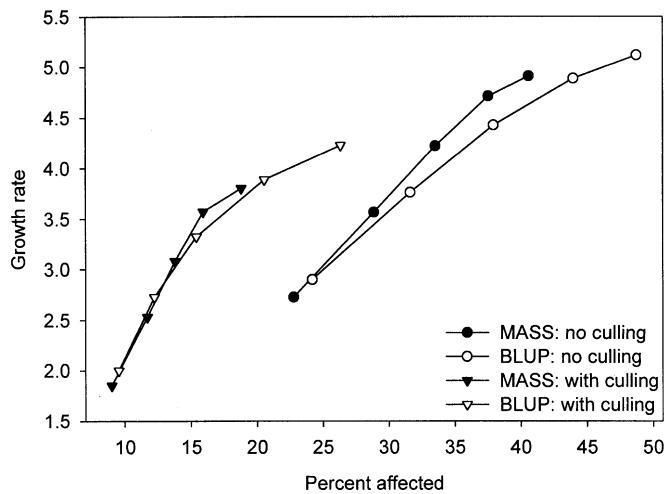


FIGURE 1. Growth rate at Generation 20 vs. percentage affected. Selection on growth. High proportion with ascites in base: 256 hens bred/generation. MASS = mass selection; BLUP = best linear unbiased prediction; no culling = occurrence of ascites among sibs ignored; with culling = occurrence of ascites among sibs used in selection. [AUTH QUERY: Figures were not labeled. Please verify they appear with correct captions.]

sponse to selection in a fixed environment. When the environmental component changes, in response to selection for increased growth, added metabolic pressure causes an increase in the expression of the susceptibility to ascites. Such an outcome was described by Moghadam et al. (2001) in a study on the genetic parameters of ascites and body weight in broiler chickens. They concluded that because there was a positive genetic correlation between these two traits, selection for body weight tended to increase the level of ascites observed. As noted by de Greef et al. (2001), selection against a trait such as ascites is complicated by the interactions it has with productivity and the environment. When organizing a selection program to improve a production trait, the breeder must take into account the effects of the program, not only on the anticipated gain but also on the fitness of the individuals in the population.

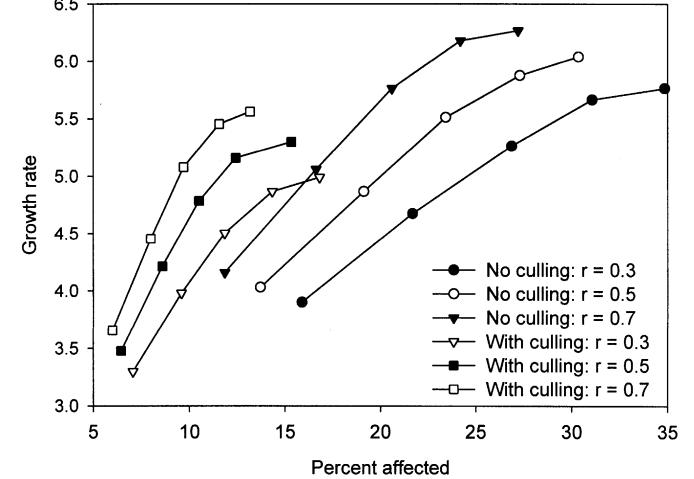
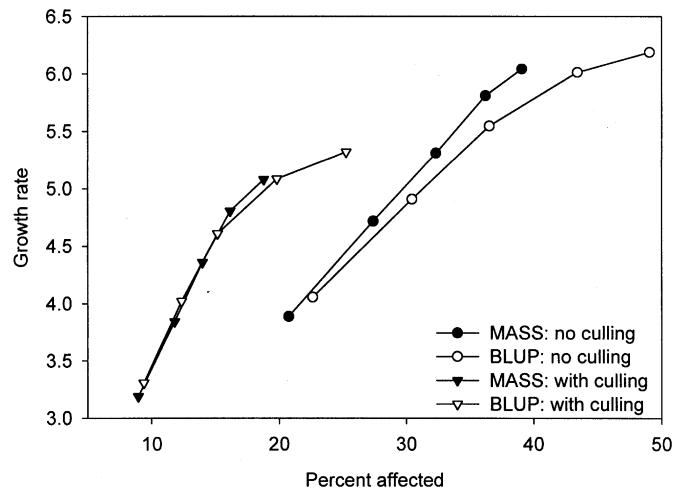


FIGURE 2. Growth rate at Generation 20 vs. percentage affected. Two-trait selection. Low proportion with ascites in base: 256 hens bred/generation. MASS = mass selection; BLUP = best linear unbiased prediction; no culling = occurrence of ascites among sibs ignored; with culling = occurrence of ascites among sibs used in selection.

The results from the current study indicated the potential improvement in a production trait, such as growth, that influences expression of a fitness trait, such as AS, depends upon the level at which the fitness trait appears when selection begins. It was observed that for each selection strategy applied, the higher initial level of AS corresponded to a lower growth rate attained by Generation 20. It was also apparent that using a BLUP procedure resulted in a higher weight gain than that produced by mass selection when only the one trait was considered. When the selection procedure changed from single-trait selection to index selection, inclusion of the indicator trait resulted in further improvement, which was increased as its correlation with AS% increased. Nevertheless, if the level of inbreeding is of concern, mass selection is perhaps the better approach for growth improvement.

Selection for increased growth and reduced ascites through the use of an indicator trait is improved as the genetic correlation between the latter two traits increases. The use of an indicator trait does reduce the increase in

the level of expression reached by the fitness trait. The AS% can be reduced further by selection on sib information prior to selecting for the production trait, but this is accompanied by a cost to the gain achieved. The choice of a procedure for improving a production trait is determined by many considerations, genetic and otherwise. For short-term gain, the results will not differ greatly between the selection strategies considered here, and so simplicity of application is perhaps the criterion to use in making the decision. For longer-term gain, the levels reached in the expression of the fitness trait must be given a higher priority in deciding which route to follow. This and the inbreeding levels that would be reached are jointly important, economically and on an animal welfare basis.

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