

SELECTION FOR A QUANTITATIVE TRAIT WITH AND WITHOUT CULLING ON LOW FITNESS WHEN SEPARATE LOCI AFFECT THE TRAIT AND FITNESS

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SUMMARY

Selection for a quantitative trait with and without culling of families with low fitness was simulated assuming different loci affected the quantitative trait and fitness, with unlinked and with linked loci. Culling on fitness reduced the number of genetic deaths and also reduced response in the selected trait. The reduction in response due to culling was greatest when heritability was low, natural selection was present and initial frequency of favourable alleles was low.

INTRODUCTION

Culling families of low fitness during selection for another trait has been suggested (Frankham et al 1988; Frankham 1990a, 1990b) as a way to prevent fitness decline. Generally, selection for a quantitative trait may be opposed by natural selection for two reasons: (1) direct or pleiotropic effects; (2) hitch-hiking or linkage effects (Sved 1977). Simulations of selection for a quantitative trait with and without culling on low fitness assuming pleiotropic effects were reported by Li and James (1991), and showed that prior culling of families with poor fitness reduces response to selection, especially when combined with strong natural selection. This paper considers the hitch-hiking effect, where loci affecting the quantitative trait are distinct from loci affecting fitness.

METHODS

Two selection regimes are compared which are denoted HO, with no culling, and HS with culling on fitness. The computer simulation method is the same as that described by Li and James (1991). Twenty pairs of parents with highest phenotypic values are selected each generation. In HO these are selected from 80 progeny of each sex (20 families with 4 male and 4 female progeny per family), but in HS these are chosen from 64 progeny of each sex (the 4 families with lowest fitness are culled prior to selection). The mass selection is carried on for 25 generations. Each selection regime has 15 replicates.

In the model discussed here, the quantitative trait is controlled by 20 diallelic neutral loci (with no effect on fitness) which are completely additive, all with the same effect and gene frequency P_a in the base population, giving a range of genotypic values from zero to 40. Fitness is determined by 20 other loci, the effects being recessive at each locus and multiplicative between loci, all with the same gene frequency P_f in the base population. All loci are unlinked in some runs. In other runs they are linked and equally spaced along one chromosome with a recombination rate of 0.05 between adjacent loci. The natural selection coefficient S is the same at all fitness loci, being either 0 or 0.05. The values of P_a were 0.1 or 0.5, and the values of P_f were 0.05 or 0.1. The heritability of the quantitative trait was either 0.1 or 0.3. Two parameters were measured: one was response ratio (HS/HO), which was

calculated as average response from 15 replicates in HS lines divided by average response in HO lines; the other was number of genetic deaths due to natural selection, which was the number of individuals out of the 400 produced each generation which did not survive.

RESULTS AND DISCUSSION

Unlinked loci

Table 1 shows the response ratios and numbers (out of 400) of genetic deaths after 20 generations for different P_t , P_s and S values in the absence of linkage.

Table 1. Comparison of response ratios and genetic deaths for two selection regimes without linkage (generation 20)

S	$h^2 = 0.1$				$h^2 = 0.3$			
	P_t	P_s	Response HS/HO (%)	Deaths HO	Response HS	Deaths HS/HO (%)	HO	HS
0	.05	.1	90±3.6			93±2.1		
		.5	97±3.1			99±0.9		
	.1	.1	93±3.9			94±2.7		
		.5	98±3.2			98±1.1		
.05	.05	.1	92±4.3	4.3±1.3	1.4±0.6	97±2.9	5.3±1.2	1.2±0.6
		.5	94±2.8	3.2±0.7	1.6±0.6	97±1.2	4.4±1.1	1.7±0.5
	.1	.1	88±3.8	13.2±1.9	2.8±0.5	92±2.9	13.9±2.5	3.5±0.8
		.5	96±3.2	9.8±1.7	3.5±0.8	98±1.2	10.7±1.8	2.8±0.8

With no linkage and no natural selection, responses obtained using the two selection regimes are determined by the selection intensity for the quantitative trait, so this has been taken as the standard for comparison. As expected there were always significantly fewer genetic deaths in the HS line, and the response was lower than in the HO lines. The reduction in response was greater with natural selection except when both P_t and P_s were small, and was significantly greater with low heritability. Thus, in general, conditions favouring random loss of favourable quantitative genes gave lower HS/HO ratios.

Linked loci

The hitch-hiking effect involves associations between genes favoured by artificial selection and fitness genes. These would be established by random formation of linkage disequilibrium in finite populations. Table 2 shows the results for the model with linkage which we simulated. A comparison with the HS/HO ratios in Table 1 shows no clear indication of an effect of linkage. On the other hand there are clearly more genetic deaths in the case of linkage, which has a highly significant effect on genetic deaths in the HO lines but not HS lines. This occurred because with linkage some deleterious genes were carried along with genes favourable for the quantitative trait. Culling of families with low fitness can prevent this hitch-hiking effect, without significant extra loss of response.

Table 2. Comparison of response ratios and genetic deaths for two selection regimes with linkage (generation 20)

S	$h^2 = 0.1$				$h^2 = 0.3$			
	Response		Deaths		Response		Deaths	
	P_t	P_s	HS/HO (%)	HO	HS	HS/HO (%)	HO	HS
.0	.05	.1	94±4.7			95±3.1		
		.5	98±3.8			99±1.3		
	.1	.1	90±4.2			96±3.5		
		.5	96±3.2			100±1.4		
.05	.05	.1	89±4.9	9.1±2.2	1.0±0.3	95±2.9	16.0±4.0	2.1±0.8
		.5	94±3.5	4.3±1.0	0.7±0.4	95±1.6	6.7±1.8	1.6±0.5
	.1	.1	88±4.7	15.2±3.6	3.8±1.03	91±2.6	16.9±3.1	6.8±1.8
		.5	91±3.8	13.2±2.2	.1±0.8	95±1.5	16.0±2.8	4.4±1.0

The response ratio was not significantly affected by linkage, or P_t , or interactions, but was significantly reduced by low h^2 , presence of natural selection, and low initial frequency of favourable alleles. Thus with linked loci the fitness advantage of HS over HO was greater, while the disadvantage in selection response was not greater than with no linkage, so the overall merit of HS was higher for linked than for unlinked loci. To get further information on the response pattern, similar analyses were done on data from generation 10. The results were similar to those described above, but the effect of heritability was not significant for HS/HO or for genetic deaths in HO. This suggests that both systematic effects (due to h^2) and random drift effects are involved, but drift plays a more important part in the difference between the two regimes.

The models simulated were chosen to give indications of which factors might be important in governing the relative merits of the HS and HO regimes. In practice, one does not usually know gene frequencies, linkage relations, or gene effects, so our results cannot be applied directly. However, they do show that culling on low fitness can lead to less fitness loss without substantial reduction in response, especially when random drift is not very important.

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