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Original article

A new method aimed at using the dominance variance in closed breeding populations

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Summary – A new method that allows use of part of the dominance effects in a closed population is proposed. In the framework of a progeny test selection scheme, the method basically consists of performing 2 types of matings: a) minimum coancestry matings in order to obtain the progenies that will constitute the commercial population and that will also be utilized for testing purposes, and b) maximum coancestry matings from which the population will be propagated. The performance of the new method has been checked by computer simulation and results show a superiority over the standard progeny test in all cases where unfavourable alleles are recessive, especially when they are at low frequency.

artificial selection / dominance variance / mating strategy / computer simulation

Résumé – Une nouvelle méthode visant à utiliser la variance de dominance dans des populations fermées en sélection. Une nouvelle méthode est proposée pour utiliser les effets de dominance dans des populations fermées. Dans le cadre d'un schéma de sélection sur descendance, la méthode consiste à réaliser 2 types d'accouplements: a) accouplements avec parenté minimale afin d'obtenir les descendants qui constituent la population commerciale et qui en même temps servent à l'épreuve de descendance, et b) accouplements avec parenté maximale servant à propager la population. La valeur de la nouvelle méthode a été vérifiée par simulation sur ordinateur, et les résultats montrent qu'elle est supérieure à l'épreuve de descendance classique dans tous les cas où les allèles défavorables sont récessifs, et surtout si leurs fréquences sont faibles.

sélection artificielle / variance de dominance / système d'accouplement / simulation sur ordinateur

INTRODUCTION

Traditionally, livestock breeders select on an intrapopulation basis, choosing those individuals with highest additive genetic values. And in order to obtain benefits derived from dominance effects this selection is carried out separately in each of 2 or more populations hoping that the value of the cross is increased in addition as a result of heterosis.

The justification of this approach is, in principle, quite simple. The additive genetic merit of candidates for selection is estimable and its mean value can be increased by selecting those individuals with the most desirable values. The dominance value is also estimable from pedigree data, at least in non-inbred populations (Henderson, 1985), but it cannot be accumulated by standard selection procedures. Even if we had estimated the dominance value, it would not be worthwhile to select those individuals with the most desirable values because its average value will regress towards zero, as consequence of random mating.

The reciprocal-recurrent selection (RRS) proposed by Comstock *et al* (1949) is the only available methodology designed to overcome this situation and when applied to a single population it involves arbitrarily subdividing the population in 2, each part being tested against the other. This last situation has been scarcely studied (Wei and Van der Steen, 1991).

In this paper we propose a new methodology of selection that can be used in a closed population and that allows use of dominance variance, at least partially. Its performance in a progeny test scheme is evaluated by computer simulation.

THEORY

As emphasized by Hoeschele and VanRaden (1991) the utilization of dominance effects in a breeding programme require working with pairs of individuals. If the offspring of a particular sire (S_1) and dam (D_1) have high average dominance effects, the mating of a close relative of sire S_1 to a close relative of dam D_1 would also produce offspring with high dominance effects. This implies that we should try to accumulate genes of the sire (S_1) for one side and genes of the dam (D_1) for the other side and to combine them in successive generations.

Intuitively, it seems that the process of accumulation of genes requires inbreeding while to combine genes requires some form of mating between individuals distantly related in the pedigree. Both processes are contradictory and for this reason the more obvious solution is to apply a different mating system for the process of propagation of the population and for the process of testing and obtaining commercial animals. We therefore suggest a methodology that basically consists of performing alternatively 2 types of matings: (1) minimum coancestry matings between the candidates for selection for progeny testing and replacement matings in the commercial population and (2) maximum coancestry matings between the selected sires and dams from which progeny the population will be propagated.

In the next section simulation results are presented focused on testing if the proposed method can exploit dominance variance in a better way than classical selection schemes although a systematic study of its properties is not intended.

SIMULATION

Breeding population

The simplest way to implement the proposed method is in the progeny test scheme. Here, M candidates for selection of each sex are mated with a criterion of minimum coancestry. From the progeny of each of the M matings, n individuals are measured and on the basis of the progeny means the best N individuals from the M parents of each sex are selected. These individuals are mated following a criterion of maximum coancestry in order to obtain the $2M$ candidates for selection in the next generation. The values for M , n and N were 64, 5 and 16 respectively. The breeding scheme is shown in figure 1.

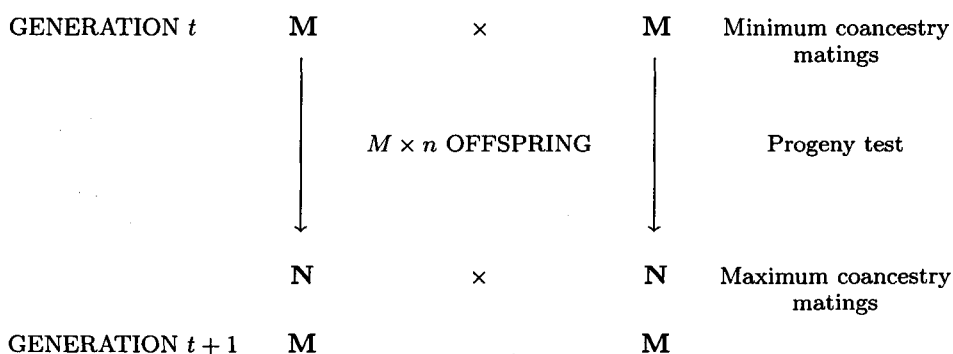


Fig 1. Breeding scheme of the proposed new selection method.

This new method is compared with a classical progeny test that follows the same scheme of figure 1 but where both types of matings were at random. The comparison criterium is the performance of the commercial population, that is the mean value of the progenies coming from the M minimum coancestry matings (or from the equivalent random mating of the classical progeny test).

Mating method

Maximum and minimum coancestry matings were obtained applying linear programming techniques as in Toro and Pérez-Enciso (1990). If the matrix of coancestries $\mathbf{C} = \{c_{ij}\}$ among selected sires and dams are known, the problem of maximum coancestry matings reduces to finding a $\mathbf{X} = \{x_{ij}\}$ matrix where x_{ij} represents a decision variable indicating whether the i -sire and the j -dam are ($x_{ij} = 1$) or are not ($x_{ij} = 0$) to be mated. Such a matrix is chosen to maximize $\sum_{ij} x_{ij}c_{ij}$ subject to the following restrictions.

(i) $x_{ij} = 0$ or 1 (for all values of i, j)

$$(ii) \sum_{i=1}^M x_{ij} = 1$$

$$(iii) \sum_{i=1}^M x_{ij} = 1$$

Obviously the minimum coancestry matings are solved in a similar way.

Genetic models

The trait of interest was simulated as controlled by 64 equal independent loci. Genotypic values of each locus were $1, d, -1$ for the allelic combinations BB, Bb and bb , respectively. Values of $d = 0, 0.25, 0.5, 0.75, 1$ and 1.125 were considered, representing different degrees of recessivity of the unfavourable allele. The initial frequency of the b allele was $0.8, 0.5$ or 0.2 .

A 2 locus additive \times additive epistatic model was also tested. The genotypic values for this model are given in table I. Thirty-two pairs of such loci were simulated with an initial frequency of alleles b and c of 0.8 .

Table I. Genotypic values for the epistatic model.

	<i>BB</i>	<i>Bb</i>	<i>bb</i>
<i>CC</i>	4.0	1.0	-2.0
<i>Cc</i>	1.0	0.25	-0.50
<i>cc</i>	-2.0	-0.50	1.0

In all cases the phenotypic values were obtained adding a random normal deviate to the genotypic value such that heritability in the narrow sense was 0.20 . The number of runs was 100 .

RESULTS

The mean values of the trait of the individuals in the commercial population (deviated from the base population) after 5 and 10 generations using the classical progeny test (R_P) and the new method (R_N) are presented in table II, for different degrees of recessivity and different initial gene frequencies of unfavourable alleles together with the mean inbreeding coefficients of these individuals. The last column shows the effectiveness of the new method with respect to the standard one.

Results after 5 generations of selection indicate a clear superiority of the new method when unfavourable alleles are recessive, especially if they are at low frequency. With complete recessivity and the lowest frequency considered, the advantage is up to 68% . After 10 generations of selection the new method behaves worse for additivity or partial recessivity but the advantage for complete recessivity is still

Table II. Response and inbreeding coefficient of the commercial population after 5 and 10 generations of selection using the classical progeny test ($R_P F_P$) and the new method ($R_N F_N$).

	Progeny test		New method		100 (R _N - R _P)/R _P
	R _P	F _P	R _N	F _N	
5 generations					
f(b) = 0.80					
d = 0	11.69	0.08	11.78	0.004	0.77
d = 0.25	12.39	0.08	13.23	0.004	6.78
d = 0.50	13.25	0.08	14.58	0.003	10.04
d = 0.75	13.97	0.08	15.87	0.004	13.60
d = 1	14.21	0.08	17.61	0.004	23.93
d = 1.125	15.12	0.08	18.02	0.004	19.18
f(b) = 0.50					
d = 0	13.50	0.08	13.47	0.004	-0.22
d = 0.25	12.32	0.08	13.20	0.005	7.14
d = 0.50	10.85	0.08	12.32	0.004	13.55
d = 0.75	9.75	0.08	11.81	0.005	21.13
d = 1	8.71	0.07	11.55	0.005	32.61
d = 1.125	8.06	0.07	11.49	0.004	42.56
f(b) = 0.20					
d = 0	9.61	0.08	9.87	0.004	2.70
d = 0.25	7.73	0.08	8.03	0.004	3.88
d = 0.50	5.78	0.08	6.31	0.003	9.17
d = 0.75	3.70	0.08	4.66	0.004	25.95
d = 1	1.89	0.08	3.17	0.005	67.72
d = 1.125	0.91	0.08	2.77	0.006	204.40
10 generations					
f(b) = 0.80					
d = 0	23.98	0.16	22.10	0.06	-7.84
d = 0.25	24.37	0.16	23.63	0.05	-3.04
d = 0.50	24.90	0.16	25.68	0.05	3.03
d = 0.75	25.76	0.15	27.61	0.05	7.18
d = 1	26.19	0.15	30.18	0.04	15.23
d = 1.125	26.77	0.16	30.94	0.04	15.58
f(b) = 0.50					
d = 0	24.74	0.16	23.71	0.06	-4.16
d = 0.25	22.25	0.15	21.90	0.06	-1.57
d = 0.50	19.30	0.15	20.24	0.05	4.87
d = 0.75	17.07	0.15	18.98	0.04	11.19
d = 1	14.71	0.15	18.85	0.04	28.14
d = 1.125	13.42	0.13	18.84	0.04	40.39
f(b) = 0.20					
d = 0	15.94	0.16	15.49	0.06	-2.82
d = 0.25	12.61	0.16	12.62	0.05	0.01
d = 0.50	9.58	0.15	9.59	0.05	0.10
d = 0.75	6.17	0.15	6.70	0.05	8.59
d = 1	3.16	0.15	4.30	0.04	36.08
d = 1.125	1.60	0.15	3.99	0.04	149.37

$f(b)$: initial frequency of the unfavourable allele at each locus; d : degree of recessivity of the unfavourable allele at each locus; standard errors of R_P and R_N range from 0.06–0.16.

very important (up to 36%). Obviously the overdominance situation would allow a dramatic superiority for the new method.

For a better understanding of how the new method is working, table III presents the evolution of genotypic frequencies showing that, with respect to the standard selection procedure, a higher frequency of heterozygotes and a lower frequency of unfavourable homozygotes is maintained.

The epistatic situation has not been analyzed in detail but in the additive \times additive example studied the new method leads to an advantage of 14 and 4% after 5 and 10 generations of selection which indicates that it could also be useful in at least some epistatic situations.

The inbreeding of commercial animals is lower with the new method because they are produced by minimum coancestry matings. On the contrary, the inbreeding of the candidates for selection is quite high, because they are the result of maximum coancestry matings. The inbreeding coefficient of these individuals is shown in table IV and attains values as high as 0.39 and 0.59 after 5 and 10 generations respectively. In order to visualize the inbreeding depression that would occur in the candidates to selection table IV also presents the performance of the offspring coming from the maximum coancestry matings (R'_N) compared with the offspring of the equivalent random mating of the standard progeny test (R'_P).

The level of inbreeding can be reduced if, in setting up the linear programming problem, we introduce the additional restriction that not all possible brother-sister matings are allowed, but rather a proportion of them ($p = 0.75, 0.50, 0.25$ and 0.00). Here, the decision if whether a particular brother-sister mating is possible is taken at random. Table V presents the results obtained with $d = 1$, indicating that a lower inbreeding and, therefore, a better performance of the candidates for selection, can be obtained maintaining at the same time an important selection response for the commercial population.

DISCUSSION

Several authors have suggested that if there is evidence that dominance effects are important for a trait of interest, the animals that constitute the final commercial product should be obtained from a type of mating different from that involved in the maintenance of the breeding population (Jansen and Wilton, 1985; Kinghorn, 1987). The idea is that selection should be done according to the estimated additive breeding value but the animals going to the market should be the product of planned matings that maximize the overall (additive plus dominance effects) genetic merit of the offspring. More recently a mating strategy for utilization of dominance effects within a breed, based on predicted sire-maternal grandsire combining abilities was investigated via simulation by DeStefano and Hoeschele (1991) and applied to cattle data of conformation traits by Lawlor *et al* (1991).

Although the above proposal is static, in the sense that the dominance effects are not accumulated, it opens the possibility of the development of new methodologies, once the value of distinguishing between propagation and test matings is accepted. Because dominance effects are interaction effects, the only way of benefiting from them is increasing the frequencies of the "principal effects" that produce more extreme values of interaction. This implies some kind of mating among genetically

Table III. Genotype and gene frequencies in the commercial population after 5 and 10 generations of selection using the classical progeny test and the new method.

	<i>Progeny test</i>			<i>New method</i>		
	Bb	bb	b	Bb	bb	b
<i>5 generations</i>						
<i>f(b) = 0.80</i>						
<i>d = 0</i>	0.374	0.522	0.709	0.412	0.502	0.708
<i>d = 0.25</i>	0.369	0.544	0.729	0.413	0.502	0.709
<i>d = 0.50</i>	0.378	0.522	0.711	0.416	0.502	0.710
<i>d = 0.75</i>	0.377	0.523	0.694	0.416	0.504	0.712
<i>d = 1</i>	0.375	0.529	0.716	0.418	0.502	0.711
<i>d = 1.125</i>	0.377	0.525	0.696	0.416	0.505	0.713
<i>f(b) = 0.50</i>						
<i>d = 0</i>	0.438	0.175	0.394	0.477	0.156	0.394
<i>d = 0.25</i>	0.443	0.175	0.397	0.479	0.154	0.393
<i>d = 0.50</i>	0.447	0.178	0.401	0.483	0.158	0.400
<i>d = 0.75</i>	0.447	0.180	0.404	0.490	0.159	0.404
<i>d = 1</i>	0.452	0.181	0.407	0.494	0.159	0.406
<i>d = 1.125</i>	0.455	0.184	0.412	0.497	0.160	0.408
<i>f(b) = 0.20</i>						
<i>d = 0</i>	0.202	0.023	0.124	0.215	0.015	0.122
<i>d = 0.25</i>	0.205	0.023	0.126	0.218	0.015	0.124
<i>d = 0.50</i>	0.208	0.023	0.127	0.226	0.016	0.129
<i>d = 0.75</i>	0.217	0.024	0.132	0.230	0.015	0.130
<i>d = 1</i>	0.227	0.025	0.138	0.252	0.015	0.141
<i>d = 1.125</i>	0.240	0.028	0.142	0.269	0.015	0.150
<i>10 generations</i>						
<i>f(b) = 0.80</i>						
<i>d = 0</i>	0.385	0.421	0.614	0.436	0.410	0.628
<i>d = 0.25</i>	0.391	0.424	0.620	0.453	0.406	0.633
<i>d = 0.50</i>	0.393	0.428	0.624	0.463	0.404	0.636
<i>d = 0.75</i>	0.399	0.429	0.628	0.469	0.406	0.641
<i>d = 1</i>	0.397	0.436	0.635	0.476	0.405	0.643
<i>d = 1.125</i>	0.397	0.436	0.635	0.477	0.409	0.648
<i>f(b) = 0.50</i>						
<i>d = 0</i>	0.359	0.128	0.308	0.407	0.112	0.315
<i>d = 0.25</i>	0.371	0.125	0.310	0.424	0.108	0.320
<i>d = 0.50</i>	0.384	0.129	0.321	0.446	0.106	0.329
<i>d = 0.75</i>	0.389	0.131	0.325	0.469	0.106	0.341
<i>d = 1</i>	0.390	0.128	0.323	0.495	0.103	0.350
<i>d = 1.125</i>	0.404	0.139	0.341	0.501	0.103	0.354
<i>f(b) = 0.20</i>						
<i>d = 0</i>	0.123	0.013	0.075	0.141	0.009	0.079
<i>d = 0.25</i>	0.129	0.014	0.078	0.144	0.008	0.080
<i>d = 0.50</i>	0.129	0.013	0.077	0.156	0.008	0.086
<i>d = 0.75</i>	0.144	0.014	0.086	0.170	0.007	0.092
<i>d = 1</i>	0.161	0.015	0.096	0.226	0.007	0.120
<i>d = 1.125</i>	0.182	0.019	0.110	0.318	0.009	0.168

f(b) and *d* defined in table I.

similar individuals in order to obtain the next generation although the commercial animals should be produced by other planned matings that will benefit from the interaction.

In this article we have shown that the combination of maximum and minimum coancestry matings can be an effective way to profit from dominance effects. In the simulation, these effects come from the existence of recessive alleles unfavourable to the direction of selection practised. The logic of this assumption is based on 2 pieces of evidence. First, no quantitative trait of economic importance shows negative heterosis as would be the case if dominance variance were due to loci at which the recessive alleles are favoured. Second, lowly heritable and heterotic traits are usually those connected with fitness such as fertility, prolificacy or longevity and there exists evidence, at least in *Drosophila melanogaster*, that genetic variation for fitness is essentially caused by segregation of rare deleterious recessive alleles (Mackay, 1985). As shown in table II, the new method is especially useful in this situation with a relative efficiency over the classical progeny test scheme of up to 68%, after 5 generations of selection for $f(b) = 0.20$ and $d = 1$.

In the short term (5 generations) the superiority of the new method is clear for all situations considered except for complete additivity, where the performances of the 2 methods equal. In the medium term (10 generations), however, the advantage is maintained only for complete or quasi-complete recessivity of unfavourable alleles. The reason seems to be that the system of maximum coancestry mating induced an increased genetic drift and, therefore, a more rapid reduction of additive genetic variance (Caballero and Hill, 1991). Furthermore, simulation results not presented here indicate that with complete additivity a reversal of the types of matings (maximum coancestry matings for testing and minimum coancestry matings for breeding) will be a better solution.

Recently, several authors have indicated the value of a reappraisal of the use of inbreeding in selection programmes. López-Fanjul and Villaverbe (1989) have shown that one generation of full-sib mating increased 4 times the realized heritability of egg-to-pupa viability in *Drosophila melanogaster*. The authors suggested that in this trait selection schemes involving subdivision and selection between and within lines could be more efficient than mass selection. Dickerson (1973) and Sirkkomaa (1986) have argued theoretically and shown by simulation that the response to selection is 10–20% faster with full-sib mating and random mating in alternate generations than with random mating exclusively.

Usefulness of inbreeding in the above proposals rely on the fact that inbreeding increases homozygosity and hence the effectiveness of selection against recessive detrimental alleles. However, the behaviour of the new method suggested here is different. The increased selection response is due to a quicker reduction in the frequency of unfavourable homozygotes while at the same time a higher frequency of heterozygotes is maintained. The overall balance is not a higher reduction of the frequency of unfavourable genes (table III).

Although the idea of using mating among relatives is against normal practice in animal breeding, it must be emphasized that in the new method the inbreeding coefficient is high in the candidates for selection but not in the progenies of the minimum coancestry matings that we have assumed constitute the commercial population. Nevertheless, there will be a cost associated with the inbreeding

Table IV. Response and inbreeding coefficient of the candidates for selection after 5 and 10 generations of selection using the classical progeny test ($R'_P F'_P$) and the new method ($R'_N F'_N$).

	<i>Progeny test</i>		<i>New method</i>	
	R'_P	$F_{P'}$	R'_N	$F_{N'}$
5 generations				
$f(b) = 0.80$				
$d = 0$	11.75	0.08	11.87	0.32
$d = 0.25$	12.58	0.08	11.29	0.32
$d = 0.50$	13.55	0.08	10.54	0.33
$d = 0.75$	14.33	0.08	9.78	0.32
$d = 1$	14.71	0.08	9.21	0.32
$d = 1.125$	15.77	0.09	8.70	0.33
$f(b) = 0.50$				
$d = 0$	13.61	0.09	13.53	0.31
$d = 0.25$	12.52	0.09	11.18	0.31
$d = 0.50$	11.12	0.08	8.02	0.32
$d = 0.75$	10.24	0.08	5.35	0.31
$d = 1$	9.40	0.08	2.88	0.31
$d = 1.125$	8.60	0.08	1.15	0.32
$f(b) = 0.20$				
$d = 0$	9.61	0.09	9.89	0.30
$d = 0.25$	7.80	0.08	7.16	0.32
$d = 0.50$	5.87	0.08	4.28	0.31
$d = 0.75$	3.80	0.08	1.80	0.32
$d = 1$	2.10	0.08	-1.40	0.31
$d = 1.125$	1.22	0.08	-3.14	0.33
10 generations				
$f(b) = 0.80$				
$d = 0$	23.98	0.17	22.05	0.43
$d = 0.25$	24.46	0.16	20.49	0.44
$d = 0.50$	25.13	0.16	18.86	0.46
$d = 0.75$	26.03	0.16	16.88	0.49
$d = 1$	26.54	0.15	15.49	0.48
$d = 1.125$	27.32	0.16	13.68	0.50
$f(b) = 0.50$				
$d = 0$	24.74	0.17	23.70	0.43
$d = 0.25$	22.31	0.16	19.16	0.45
$d = 0.50$	19.49	0.15	14.17	0.46
$d = 0.75$	17.39	0.15	8.94	0.48
$d = 1$	15.10	0.15	3.27	0.52
$d = 1.125$	13.97	0.14	0.19	0.53
$f(b) = 0.20$				
$d = 0$	15.91	0.16	15.44	0.42
$d = 0.25$	12.60	0.16	11.81	0.42
$d = 0.50$	9.59	0.15	7.64	0.43
$d = 0.75$	6.21	0.15	3.59	0.47
$d = 1$	3.28	0.15	-2.89	0.53
$d = 1.125$	1.83	0.15	-10.42	0.59

Standard errors of R'_P and R'_N range from 0.06–0.16. $f(b)$ and d defined in table I.

Table V. Responses and inbreeding coefficient of the commercial population ($R_N F_N$) and of the candidates for selection ($R'_N F'_N$) after 5 and 10 generations of selection using the new method; $d = 1$ and $f(b) = 0.20$.

	R_N	R'_N	F_N	F'_N
5 generations				
$p = 1.00$	3.17	-1.40	0.005	0.31
$p = 0.75$	3.23	-0.83	0.005	0.26
$p = 0.50$	3.16	-0.59	0.005	0.24
$p = 0.25$	3.03	-0.00	0.006	0.18
$p = 0.00$	2.95	1.01	0.010	0.11
10 generations				
$p = 1.00$	4.30	-2.89	0.040	0.53
$p = 0.75$	4.23	-2.57	0.040	0.47
$p = 0.50$	4.29	-1.94	0.040	0.44
$p = 0.25$	4.22	-0.91	0.040	0.35
$p = 0.00$	4.16	0.52	0.040	0.25

p : proportion allowed of all possible brother-sister matings; standard errors of R_N and R'_N range from 0.06-0.16.

depression of candidates for selection even if the tactic of imposing additional restrictions is utilized (table V). This cost will depend on several parameters such as the relative proportion of both types of matings and the magnitude of inbreeding depression, either for the quantitative trait of economic importance or for other fitness-related traits. The first factor, in its turn, depends on the reproductive rate of the species, the generation interval and the structure of dissemination of genetic progress. Therefore the application of this method in practical breeding programmes would require an economics evaluation including this cost.

In the new scheme commercial animals are produced by minimum coancestry matings and part of their better performance is due to avoiding inbreeding and therefore avoiding inbreeding depression. It is not clear how to discount for this effect because it is inherent in the new method to induce a process of sublining in the propagated population that will cause a very low level of inbreeding in the commercial population. Even if we had avoided inbreeding in the standard selection method using minimum coancestry in both types of matings, the values of R_P and F_P , after 10 generations of selection and for $d = 1$ and $f(b) = 0.20$, would be 3.31 and 0.11 and the new method will still show its advantage. Furthermore, the results of the additive \times additive epistatic model, where inbreeding depression is absent, are indirect evidence that avoiding inbreeding is not the only explanation for the better performance of the new method.

The present study has some limitations that warrant further research. First, there has not been a systematic consideration of different heritabilities, gene frequencies, selection intensities or population sizes. Second, no comparison with other methods except a special type of progeny test with one dam per sire has been made and only short-term responses have been considered. Third, the method has not been optimized with respect to family size or the proportion of coancestry matings.

Finally, for the method to be applied in practical breeding schemes, it is necessary to take advantage of mixed model methodology. For example, the limitation of a progeny test scheme could be overcome if estimated values of the expected progenies rather than actual values are used. Recent papers have shown how to estimate dominance effects either in non-inbred or in inbred populations (Smith and Maki-Tanila, 1990; Hoeschele and VanRaden, 1991; De Boer and Van Arendok, 1992).

In conclusion, the use of dominance variance in within population selection programmes is an open question that can be tackled by an adequate planning of evaluation, selection and mating policy. The next step of the research will be to study these ideas in the framework of the standard methodology of genetic evaluation.

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