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Optimal restricted phenotypic selection

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Abstract Phenotypic selection is modified by introducing upper limits on the portion (P_1) of individuals selected from a family as well as on the portion (P_2) of family number that are allowed to contribute. At a preset selection proportion, P and P_1, the maximum genetic gain is obtained by finding an optimum restriction on family number (P_2^*). A numerical procedure for solving the problem of optimization is developed for infinite populations. In small populations, maximum gain and P_2^* can be found by simply comparing all possible P_2. Numerical examples are demonstrated for infinite breeding populations, assuming a normally-distributed family mean and within-family deviation. Selection and its simulation were applied to the field-test results of two tree species. Optimum restriction on family number is very close to P/P_1, especially when heritability is low. In the real world of tree breeding, P_2^* is given, or approximated, by $P/P_1+1/m$ where m is the initial family number. The improvement of gain and the conservation of inbreeding effective population size are easy with high heritability and could be simultaneously obtained by using intense selection with a relatively low P_1.

Key words Breeding population · Phenotypic selection · Genetic gain · Inbreeding · Effective size

Introduction

Many alternatives can be considered when performing selection in populations, especially in those of relatively large family number and size (as found in many tree-breeding programmes). Subjectively, breeders often decline to use those practices that may increase expected genetic gain, such as selection based on the BLP or BLUP of breeding value (Belonsky and Kennedy 1988; White and Hodge 1988) and optimal-index selection (Hazel 1943; Lush 1947; Henderson 1963; Wei and Lindgren 1991). However, high expected genetic gain does not mean high realized gain, the ultimate goal. Selective breeding is a complex system and it is insufficient to consider expected gain as the only criterion in choosing a selection method. Several other elements in addition to expected gain ought to be taken into account as they will, directly or indirectly, more or less, and sooner or later, influence the achievement of the ultimate goal. First, the distribution of selections is highly related to both immediate and continuous gain in a programme. High gain may lead to the convergence of selections among a few families. The consequences are high level of inbreeding in offspring from mating among relatives with a possibility of inbreeding depression, restriction of genetic diversity for further selection, and increasing sensitivities of offspring (plantations) to environmental stresses as well as biotic damage due to low genetic variation. A wise method should be able to balance the cost of these disadvantages against the increased gain it would give. Second, whilst there is an economic constraint in any breeding program, progeny testing becomes restricted. This constraint results in weaker selection intensity (or low genetic gain) in operation. A cost-efficient alternative will increase genetic gain relatively. Finally, in practice a simple and easy-to-operate method is still preferable, although complicated computer calculation is now no longer a problem. Lindgren et al. (1993) derived a method towards maximum gain under constant selection intensity and effective population size. It turned out, however, that time-consuming and complex iterative calculations constrain its practical application (Wei and Lindgren 1995). In addition, it may be costly for large organisms like forest trees since selection is often intensive and breeders have to wait until the test trees are old enough for selection. A method that could be operated in different steps may be helpful in reducing the cost of testing.

Phenotypic selection is a classical means by which superior individuals are selected solely in accordance with their own phenotypic values. It is characterized as a method

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of simplicity and cost-efficiency, and also provides quick returns (Cotterill 1986; Falconer 1989). Recent investigations further suggest that phenotypic selection is an efficient method with regard to the improvement of gain and the conservation of genetic diversity (Cotterill 1986; Wei and Lindgren 1991; Quinton et al. 1992; Wei and Lindgren 1993). Wei (1995) developed a restricted phenotypic selection by considering a restriction on the selected individuals in families or on the family number selected. This method is flexible in balancing gain and inbreeding. Another advantage may be that the method can be extended to two-stage manipulations in order to reduce the cost of progeny testing (Namkoong 1976; Cotterill and James 1981). In the present paper, the method is generalized by introducing restrictions on the selected number of individuals in families as well as on the number of families. Phenotypic selection without restriction, and with restriction only on the family number selected or on the contributions of families, will be treated as special cases. We will, however, focus attention on maximizing the expected gain by finding an optimum restriction on the family number selected, while keeping selection proportion and the restriction on the contributions of families constant.

Theory

Consider a breeding population of family structure that is at its first generation and is ready to be selected to obtain superior individuals. Families are unrelated, originating either from single-pair mating (full-sib) or open-pollination (half-sib). There are m families, each with s members which are genetically related by the coefficient of relatedness, r (0.5 full-sib; 0.25 half-sib). Only an additive gene effect is assumed. The observed performances of all individuals are recorded. The performance of the kth individual of the jth family could be considered as the sum of two independent random variables:

$$x_{jk}=x_j+d_{jk}, \tag{1}$$

where x_j are family means, distributed with mean u (the population mean), and variance σ_b^2, and d_{jk} are within-family deviations, distributed with zero mean and variance σ_w^2. Total observed variance, σ_t^2, and the ratio of the observed variance of family mean to the total observed variance, K, are therefore

$$\sigma_t^2=\sigma_b^2+\sigma_w^2 \quad \text{and} \quad K=\sigma_b^2/\sigma_t^2.$$

From decomposition of the observed performance and variance, the genetic and environmental effect can be estimated. Let t denote the intra-family correlation, measuring the degree of resemblance between members of families. This is a function of K and s

$$t=(sK-1)/(s-1).$$

Genetic variance, σ_g^2, and the ratio of the between-family component to it, k, are given by

$$\sigma_g^2=t\sigma_t^2/r \quad \text{and} \quad k=[1+(s-1)r]/s.$$

The best prediction of an individual's breeding value (A_{jk}, equal to the genetic value in the present case) is given by the multiple regression equation

$$A_{jk}=\alpha(x_j-u)+\beta d_{jk}, \tag{2}$$
$$\text{with} \quad \alpha=tk/(rK) \quad \text{and} \quad \beta=t(1-k)/[r(1-K)]$$

where α and β are the weighting factors that make the most efficient use of the two sources of information (Falconer 1989; Wei and Lindgren 1993). In practice, breeders often have varying sizes of families (denoted by s_j) at the time when selection is conducted. All parameters and breeding values of individuals can be estimated in the same way as above except that the family size (s) has to be adjusted by using the following formula (Becker 1984)

$$\bar{s}=(\sum s_j-\sum s_j^2/\sum s_j)/(m-1).$$

A number (n) of individuals will be selected and, thus, the selected proportion $P=n/(ms)$ or $n/\sum s_j$. Two types of restrictions are introduced. These restrictions are expressed as the proportion of either family number or family members. First, an upper limit (P_1) is intentionally imposed on the contributions of families to the selected group. The possible value of P_1 falls between P and 1. Second, an upper limit (P_2) is arbitrarily chosen in the interval $[P/P_1, 1]$ for the number of families that are eligible to contribute. In other words, the s–sP_1 bottom-ranking individuals in all families and the m–mP_2 bottom-ranking families are first successively excluded from the population. A portion, $P/(P_1P_2)$, of superior individuals is finally phenotypically truncated from the remainder. Taking the restricted conditions into account, the contribution of the jth family to the selected group can be expressed as the selected proportion, p_j, from the family or the fraction of the selected group, w_j with the interval $[0, P_1]$ or $[0, P_1/mP]$, respectively.

Selection diverges to different extreme cases when specified values are given to P_1 or P_2. This is phenotypic selection (unrestricted), as both P_1 and P_2 are equal to one, it is also within-family selection as $P_1=P$ ($P_2=1$), and it is between-family selection as $P_2=P$ ($P_1=1$). These methods are classified as conventional selection methods. Whilst selection with $P_1P_2=P$ represents the combination of between-family and within-family truncation, the case with $P_1=1$ or $P_2=1$ is identified as one-step restricted selection (Wei 1995). In addition, restricted phenotypic selection can be extended to multiple-stage selection (Namkoong 1970; Cotterill and James 1981). Types of restrictions serve as early stage selections, performing in early stages. In this situation, we assume that the genetic structure of the breeding population does not change with age.

Expected genetic gain following selection is measured by the average breeding value of the selected individuals (Wei and Lindgren 1993)

$$\Delta G=\sum w_j(x_j\alpha+i_j\beta\sigma_w), \tag{3}$$

where i_j is the standard selection differential corresponding to p_j or w_j.

As the restriction on the family number may be arbitrarily chosen over a range of values, it is interesting to find a P_2 that gives higher expected gain. Studies by Cotterill and James (1981) and Wei (1995) imply that, under constant P and P_1, there is a peak in expected gain at a given restriction to P_2. We define

$$\Delta G = g(P, P_1, P_2). \tag{4}$$

Therefore, the problem of optimization is formulated so as to maximize expected gain, denoted by ΔG^*, by solving for an optimal value, say P_2^*, for P_2 under preset P and P_1

$$\Delta G/\delta P_2 = 0, \quad \text{for} \quad P < P_1 \leq 1. \tag{5}$$

No implicit analytical solution is directed at (4) and (5). However, in a real application, ΔG^* and P_2^* can be easily found by comparing $m(1-P/P_1)+1$ probabilities.

One of the important reasons to constrain the contributions of families is to reduce the probability of selected individuals being sibs in the selected group, or the level of inbreeding in the offspring of selected individuals, which is often summarized as inbreeding effective population size (Robertson 1961; Burrows 1984). Consequently, it is worth having a look at the effect of optimal restricted phenotypic selection on inbreeding effective population size that can be calculated by using Burrows' (1984) formula

$$N_e = (n-1)/[r\sum w_j(nw_j-1)]. \tag{6}$$

Numerical procedure

The main interest here is directed at a general discussion. Thus, assume that both family number and size are infinitely large. For a pair of P_1 and P_2, there are two corresponding truncation points, denoted by d_T and x_T, respectively. A phenotypic threshold value (T) associated with P, P_1 and P_2 determines the acceptance or rejection of the candidate individuals. In addition, also associated with P, P_1 and P_2, there may be a break-point, say B, from where families with higher values start to have equally maximum contributions (P_1). In numerical calculations, these parameters and the contributions of all families to the selected group are needed before the outcome of selection is predicted. Let $f(x)$ and $F(x)$ denote the unit probability and distribution function of the family mean. The truncation point for a family with value x is expressed in a standardized scale, $y=(T-x)/\sigma_w$. Therefore a family's contribution, $p(x)$, is a function of its mean value

$$p(x) = \begin{cases} P_1 & \text{if} \quad x \geq B \\ F(-y) & \text{if} \quad x_T \leq x \leq B \\ 0 & \text{if} \quad x < x_T \end{cases} \tag{7}$$

Expected gain and inbreeding effective population size are rewritten as follows

$$G = \int P^{-1}\{x + i[p(x)]\beta\sigma_w\}\, p(x) f(x)\, dx, \tag{8}$$

and

$$N_e = P^2 / \int [p(x)]^2 f(x)\, dx. \tag{9}$$

Equation (9) is a measure of the inbreeding effective population size relative to the initial inbreeding effective population size (Wei and Lindgren 1991). The value is confined to [0, 1]. Evidently there is no analytical solution to (5) and, even though P_2^* is known, (4) is still an implicit function under the assumption of an infinite population. Iterative computations have been used to search for d_T, x_T, T and B for any set of P, P_1 and P_2, and to solve for P_2^* and ΔG^* for a given P_1. The quadratic method was employed in the iterative "trial and error" calculations. Values for ΔG and N_e were computed by quadrature using the 96-point Gaussian formula (Davis and Polonsky 1964) in equal intervals over the range (–8, 8).

Examples are provided, using the assumption of a normal distribution for family mean and within-family deviation. The population mean and total phenotypic variance were scaled to zero (u=0) and one (σ_t^2=1), respectively. We assumed full-sib families and a selection proportion (P)=0.01. Heritabilities, $h^2(=\sigma_g^2/\sigma_t^2)$, were set to 0.5, 0.25 and 0.05, respectively. Optimal restriction on family number, maximum gain, and the corresponding inbreeding effective population size, are plotted against the restriction on the contributions of families (Fig. 1). In addition, maximum gain as a function of inbreeding effective population size is demonstrated in Fig. 2.

Examples from tree breeding and simulation prediction

To examine the applicability of the theory, we studied two sets of real data which were derived from an 8-year-old multiple-species progeny test in North Sweden (for full details see Lindgren and Lindgren 1990). One consists of 31 unrelated full-sib families of *Pinus sylvestris* and the other of 16 unrelated half-sib families of *Pinus contorta*. With unequal family sizes, both of them will perform as breeding populations for the selection of superior trees. Only height growth measurements was considered. Statistical analysis and selection were applied to both species, respectively. The block effect was removed from all measurements by least squares analysis assuming additive effects of families and blocks so that the phenotypes can be explained by (1). In addition, we made the assumption that there are only additive gene effects, thus no dominance. The family structures and estimated parameters of height growth for both species are summarized in Table 1.

Two different selection intensities were compared. The selected numbers were set to 25 and 50 for *P. sylvestris*, and 20 and 40 for *P. contorta*, respectively. Results of selection from both populations are compiled at a different restriction on the contributions of families (Table 2). For comparison, selection was predicted by empoying Monte Carlo simulation. Without losing reality, we assumed u=0 for height growth. Populations of the same family structures and variance components (Table 1) were constructed by generating normally-distributed random variables for family means and within-family deviations in each family. In each run of simulation, the expected gain and the inbreeding effective population size were calculated for all

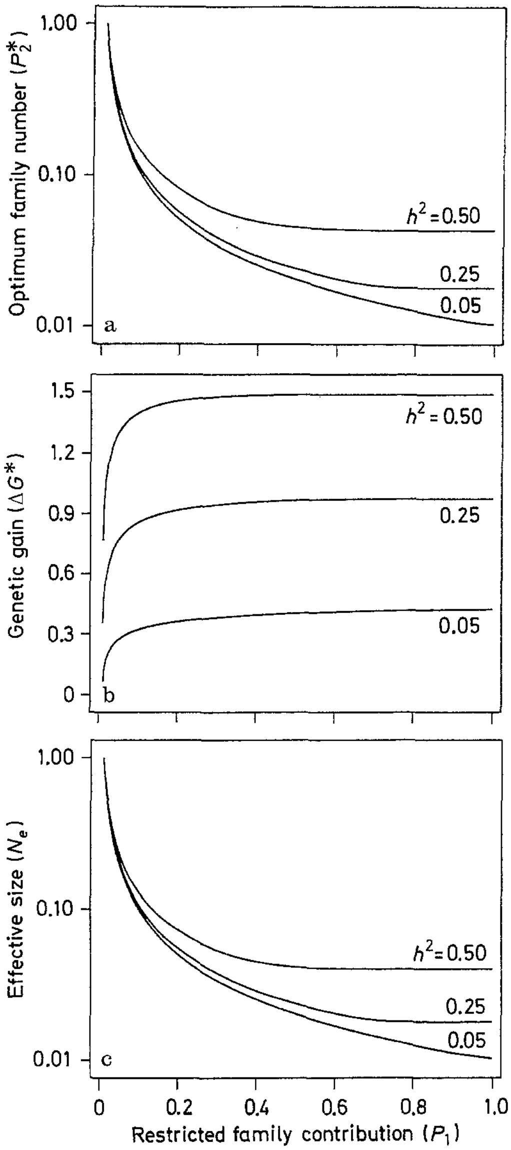

Fig. 1a–c Optimal restricted family number (P_2^*), gain (ΔG^*) and the corresponding effective size (N_e) against the restricted family contribution for P=0.01 and varying genetic variances. The scales for the axes of P_2^* and N_e are logarithmic. Infinite full-sib family number and size were assumed for the breeding populations

possible choices of the restriction on family number (P_2) under the constraint of restriction imposed on the contributions of families. Maximum gain, ΔG^*, and the corresponding optimal restriction on family number (P_2^*) and inbreeding effective population size (N_e) were recorded. Simulations were repeated 50 times. Averaged optimum restricted family number ($\hat{P}_2^*$), expected gain ($\Delta \hat{G}_2^*$), inbreeding effective population size ($\hat{N}_e$), and the their respective variable coefficients (CV), are given in Table 2.

Results and discussion

Imposed on restrictions, phenotypic selection will not lose its simplicity but becomes more flexible, effective, and

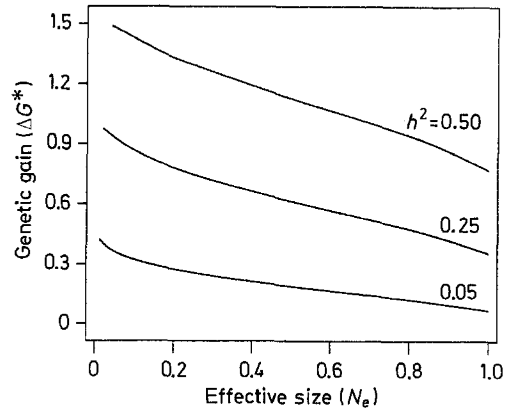

Fig. 2 Gain (ΔG^*) against effective size (N_e) for P=0.01 and varying genetic variances for optimal restricted phenotypic selection. Infinite full-sib family number and size were assumed for the breeding populations

probably cost-efficient. In this paper, however, we will not discuss these features.

There are many combinations for the two restrictions, P_1 and P_2, given that P is constant. If P_1 is restricted, then expected gain increases as P_2 becomes small. The maximum gain takes place when P_2 is close to P/P_1, especially when heritability is low (Wei 1995). The maximum was also obtained when two-stage selection aiming at different traits was optimized (Cotterill and James 1981). A restriction on family contributions leads to a diverse distribution of selections among families with a higher inbreeding effective population size but low expected gain. It seems, however, that a little gain sacrifice could buy a much more effective size if P_1 is not so low so that the selection is forced to be close to the within-family selection (Wei 1995; Wei and Lindgren 1995). Wei (1995) concluded that phenotypic selection with restriction solely on the family's contributions (or P_2=1, one of the extreme cases in the present situation) is superior to other restricted selections when the conservation of effective size is considered. Excluding the cases with $P_2 < P_2^*$, this conclusion could be extended to the present study.

The most interesting case is optimally restricted phenotypic selection that maximizes expected gain (ΔG^*) at given P and P_1, by finding an optimum value (P_2^*) for P_2. There is no analytical solution to P_2^* and ΔG^*. While numerical methods are needed for infinite cases, ΔG^* and P_2^* could be easily obtained by simply comparing $m(1-P/P_1)+1$ possible solutions for finite cases. It is apparent from Fig. 1a that P_2^* decreases exponentially as P_1 is increased from P to between 0.2 to 0.4. Little further reduction is achieved by allowing higher contributions of families, particularly when heritability is low. A similar trend was also found for the corresponding effective size that is slightly lower than P_2^* (Fig. 1c). Inversely, ΔG^* increases exponentially as P_1 is increased from P to about 0.2. Little further increase is obtained with a large P_1 (Fig. 1b). It seems reasonable to recommend that the restriction on the family's contributions should be around 0.2

Table 1 Family structures and estimated parameters of height growth for *P. sylvestris* and *P. contorta* breeding populations derived from an 8-year-old multiple-species test in North Sweden

Item	*P. sylvestris*	*P. contorta*
Sib type (r)	Full-sib(0.5)	Half-sib(0.25)
Family number (m)	31	16
Family size (s_j)	22–36	30–39
Adjusted family size ($\bar{s}$)	28.89	34.99
Total number ($\sum s_j$)	896	560
Population mean (u)	205.54	225.67
Total variance (σ_t^2)	3180.9793	4154.4098
Variance of family means (σ_b^2)	348.8736	3919.3445
Variance of within-family deviations (σ_w^2)	2832.1057	235.0653
Heritability (σ_g^2/σ_t^2)	0.1555±0.0508	0.1153±0.0813

Table 2 Optimum restricted family numbers (P_2^*), gains (ΔG^*), inbreeding effective population sizes (N_e) and simulated values ($\hat{P}_2^*$, $\Delta\hat{G}^*$ and $\hat{N}_e$) for selection from one breeding population of 31 *P. sylvestris* full-sib families and another of 16 *P. contorta* half-sib families

Breeding pop.	sP_1	mP_2^*	ΔG^*	N_e	$m\hat{P}_2^*$	$\hat{P}_2^*$ (CV)	$\Delta\hat{G}^*$ (CV)	$\hat{N}_e$ (CV)
	2	14	18.11	50.00	14.28	0.461(.232)	22.50(.186)	53.91(.235)
	4	7	23.38	18.18	7.94	0.256(.210)	27.05(.188)	19.53(.214)
P. sylvestris	6	5	26.67	11.11	5.32	0.172(.127)	27.12(.163)	11.78(.124)
n=25	10	4	28.94	7.69	3.42	0.110(.287)	28.92(.184)	7.13(.287)
	15	2	30.49	4.17	2.74	0.088(.478)	29.85(.201)	5.67(.499)
	36	2	30.49	4.17	2.32	0.075(.670)	30.91(.235)	4.78(.696)
	–[a]	–	17.22	46.15	–	–	19.31(.234)	48.40(.390)
	2	25	11.25	98.00	28.00	0.903(.301)	13.90(.246)	108.62(.301)
	4	13	16.75	33.56	13.56	0.437(.132)	19.98(.026)	35.02(.137)
P. sylvestris	6	9	19.74	20.94	9.28	0.299(.053)	22.14(.143)	21.25(.033)
n=50	10	5	23.84	10.89	5.28	0.170(.107)	24.50(.155)	11.36(.085)
	15	4	26.62	8.11	4.28	0.138(.162)	25.37(.164)	8.79(.168)
	36	2	27.62	4.08	3.46	0.112(.348)	25.84(.176)	7.03(.357)
	–	–	15.62	45.37	–	–	16.64(.208)	46.93(.175)
	2	11	13.38	76.00	13.18	0.824(.375)	18.88(.360)	92.00(.387)
	4	6	17.35	28.15	6.32	0.395(.103)	19.82(.098)	29.01(.157)
P. contorta	6	4	18.60	18.54	4.60	0.288(.184)	19.88(.177)	18.86(.135)
n=20	10	2	21.39	8.44	3.34	0.209(.404)	20.57(.179)	13.18(.375)
	15	2	21.48	7.68	3.22	0.201(.418)	20.64(.179)	12.83(.407)
	39	2	21.48	7.68	2.94	0.184(.533)	20.80(.183)	11.77(.517)
	–	–	18.10	24.52	–	–	16.56(.198)	54.54(.342)
	3	14	10.37	82.11	15.68	0.980(.300)	13.71(.247)	86.92(.301)
	4	12	12.62	56.73	11.32	0.708(.227)	15.42(.172)	55.62(.231)
P. contorta	6	8	14.54	36.71	7.98	0.499(.141)	16.29(.164)	34.18(.104)
n=40	10	4	16.29	17.33	5.18	0.324(.203)	17.65(.164)	20.59(.172)
	15	3	17.91	12.43	4.56	0.285(.311)	18.07(.169)	17.68(.293)
	39	2	19.10	8.13	4.24	0.265(.376)	18.27(.176)	16.46(.372)
	–	–	13.84	46.57	–	–	14.20(.184)	55.59(.171)

[a] Unrestricted phenotypic selection

in order to obtain a high gain and to keep the loss of effective size acceptable. These findings and conclusions were verified in two practical cases of *P. sylvestris* and *P. contorta* where the real results of selection and simulation predictions are in close agreement with each other (Table 2). Moreover, it could be concluded from both infinite and finite cases that, at a given selection proportion and limited maximum contribution for families, optimum restriction on family number is always close to P/P_1, especially when heritability is low. In practice, P_2^* is given or approximated by $P/P_1+1/m$.

Selection is influenced by genetic variance (equivalent to heritability in the present situation) and selection proportion. Maximum gain and effective size increase with high genetic variance (Fig. 1), indicating that a powerful method to improve genetic gain and effective size is to increase genetic variance (Grundy and Hill 1993; Grundy et al. 1994; Wei and Lindgren 1995). Genetic variance is higher under environmentally uniform conditions and by testing clones instead of individuals. Therefore, breeders may improve selection accuracy efficiently by identifying and using such test environments or by employing clonal testing if genetic variance is low. High selection proportion leads to lower genetic gain but a much higher effective size at a given P_1. However, with a lower P_1, a small selection proportion could give both a higher gain and a higher effective size (Table 2). Both selection proportion and restriction on the family's contributions may play a role in the artificial evolution of a long-term breeding program through influencing effective size (Robertson 1960;

Toro and Perez-Enciso 1990; Quinton et al. 1992). This problem deserves to be studied further.

One of the purposes of restricting the contribution of a family is to conserve effective population size. Thus, the outcome of optimal restriction phenotypic selection could be re-formulated as the gain under restricted effective size (Fig. 2). This is a common way of combining the improvement of genetic gain and the conservation of effective size in selective breeding. Optimal selection is the best way of dealing with such problems (Lindgren et al. 1993; Wei and Lindgren 1995). However, the lack of refinement for finite populations, and the complicated computation, poses hurdles to its use in practice. Technically, the method derived in this study is exceedingly simple. The selection efficiency is probably close to that of the optimal selection.

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