

GAIN AND EFFECTIVE POPULATION SIZE FOLLOWING INDEX SELECTION WITH VARIABLE WEIGHTS

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ABSTRACT

The outcome of index selection from a population of families was studied. The selection criteria was a linear index that weighted family value and within-family deviation. The balance between genetic gain and effective population size was controlled by choosing a family weight. Index selection was found to be only slightly inferior to optimal selection. The difference was greater for more closely related families, for lower heritability and for more intense selection. Expected gain and effective population size was described as a function of family type, family number, family size, genetic variance, selected proportion and family weight in the index. Implications to breeding operations were discussed.

Key words: breeding population, index selection, gain, inbreeding, effective number, genetic diversity, family size

INTRODUCTION

Different methods can be used to direct genetic improvement by selection from a population having a known family structure. Traditionally breeders prefer methods that maximize genetic gain at a given level of selection intensity, like selection based on either BLP or BLUP of breeding values (BELONSKY & KENNEDY 1988; WHITE & HODGE 1988; QUINTON *et al.* 1992) or on optimal-index or combined selection (LUSH 1947; OSBORNE 1957; COTTERILL 1986; FALCONER 1989; WEI & LINDGREN 1991). However, maximum gain is produced at the expense of loss in effective population size, which can be great (ROBERTSON 1961; BURROWS 1984; WEI & LINDGREN 1991). A reasonably large effective population size is required to avoid inbreeding and enable continued progress through to later breeding generations (ROBERTSON 1961; TORO & NIETO 1984; QUINTON *et al.* 1992) so as to avoid possible production losses in the production population (LIBBY 1982; LINDGREN 1993).

A selection method considering both gain and effective population size is desirable. To maximize genetic gain at given selection intensity and effective population size, or to maximize effective population size at given selection intensity and gain, optimal procedures allowing unequal distribution of selections among families have been developed (TORO & NIETO 1984; LINDGREN *et al.* 1993; WEI & LINDGREN 1995). These procedures provide the best tradeoff between

gain and effective population size. However, as complex iterative calculations and time consuming programming are needed for a general case, applications usually circumvent this by assuming that families are very large (LINDGREN *et al.* 1993; WEI & LINDGREN 1995).

A technically simple way of compromising between genetic gain and effective population size is to use a linear index that weights family averages and deviations of individuals from family averages. Using this tool, TORO and PEREZ-ENCISO (1990) investigated the effect of the conservation of effective population size on long-term response to selection. They concluded that inbreeding could often be greatly reduced before incurring a significant loss of response. This contrasts with classical strategy, which does not monitor effective population size.

The objectives of this study are the following:

- * develop methods for predicting gain and effective population size when using a family-individual index as the selection criterion,
- * investigate the properties of index selection, and
- * estimate the loss in genetic gain by using a simple index instead of an optimal selection procedure.

THEORY

Consider selection in a population containing m unrelated families, each with s members, and a genetic correlation r . The phenotypic value (x_{jk}) of the k th

individual in the j th family of the trait considered can be split into two independent components – the family mean, x_j , distributed with zero mean and variance σ_{FP}^2 , and the within-family deviation, d_{jk} , distributed with zero mean and variance σ_{WP}^2 . The total phenotypic variance will be $\sigma_p^2 = \sigma_{FP}^2 + \sigma_{WP}^2$. All gene effects are assumed to be additive. The ratio of the phenotypic variance of family mean to the total phenotypic variance is

$$K = [1+(s-1)t]/s,$$

where t is the intraclass correlation. Letting σ_A^2 denote the total genetic variance and k denote the fraction that depends on the family size and the genetic correlation between sibs,

$$k = [1+(s-1)r]/s \quad [1]$$

We will develop the consequences of using the index

$$I_{jk} = (1-\beta)d_{jk} + \beta x_j \quad [2]$$

as the selection criterion. The factor β expresses the weight given to family performance, where $0 \leq \beta \leq 1$. The choice of β (and selection intensity) will determine the outcome of the selection, including gain and effective population size. The variance of the index is σ_I^2 . The fraction of the variance which can be "explained" by the variance of family means is

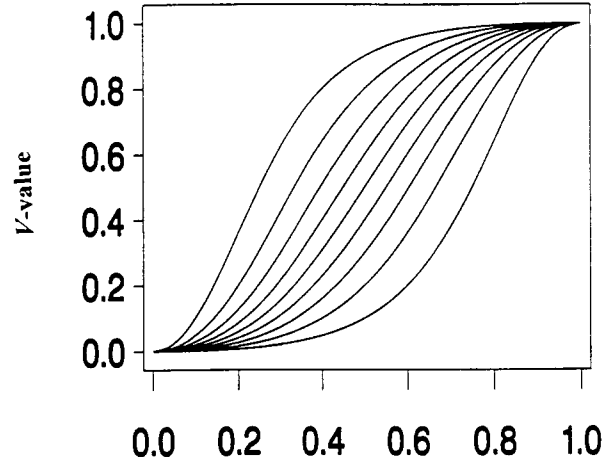
$$V = \beta^2 \sigma_{FP}^2 / [\beta^2 \sigma_{FP}^2 + (1-\beta)^2 \sigma_{WP}^2] = \beta^2 K / [\beta^2 K + (1-\beta)^2 (1-K)] \text{ where } 0 \leq V \leq 1.$$

Although equivalent indices may be constructed (e.g. FALCONER 1989, p. 229–247; TORO & PEREZ-ENCISO 1990; WEI & LINDGREN 1991), we have chosen form [2] because the absolute and relative contributions of family performance to selection are described by a single parameter, which seems straight and simple.

Conventional selection methods appear as special cases of [2], (cf. FALCONER 1989):

- * Between family selection, $\beta = 1$;
- * Individual (or phenotypic) selection, $\beta = 0.5$;
- * Combined (or optimal index) selection, $\beta = k(1-K)/[k(1-K)+K(1-k)]$;
- * Within-family deviation selection, $\beta = 0$.

Note, that the last case will differ from conventional within-family unless family size is infinitely large or within-family deviations are expressed by order statistics (no sampling error). Note also that the term index selection sometimes is used as a synonyme to what we call combined selection; thus the particular index that maximizes the correlation between index values and



The weight given to family performance (β)

Figure 1 V-value (the fraction of variance in selection index explained by family variation) plotted against the weight (β) given to family information. Graphs are drawn for $K = 0.9, 0.8, \dots, 0.1$ (K is the fraction of the phenotypic variance of family mean, the leftmost graph corresponds to the highest K -value).

breeding values. Conventional selection methods produce specific solutions (WEI & LINDGREN 1991), while index selection provides a continuous range of options by choice of β in [2], that will include the conventional.

According to regression theory, we derive the regression of breeding values (A_{jk}) on index values (I_{jk}) in the form

$$B_{AI} = COV(I_{jk}, A_{jk}) / \sigma_I^2 = \sigma_A^2 [(1-\beta)(1-k) + \beta k] / \{ \sigma_I \sigma_p \sqrt{[\beta^2 K + (1-\beta)^2 (1-K)]} \}.$$

Genetic gain following truncation selection is predicted as

$$\Delta G = S_I B_{AI} = i \sigma_A^2 [(1-\beta)(1-k) + \beta k] / \{ \sigma_I \sigma_p \sqrt{[\beta^2 K + (1-\beta)^2 (1-K)]} \}, \quad [3]$$

where S_I and i are the selection differential and the standardized selection differential, respectively. For prediction, i can be approximated using the corresponding value, i_* , or for an infinite population with the same selected proportion, P (HILL 1976),

$$i \approx i_* - (1-P) / \{ 2i_* P [ms(1-V) + mV + 1] \}.$$

For effective population size, the definitions by ROBERTSON (1961) and BURROWS (1984) were used in this study. They will be denoted by N_{eR} and N_{eB} , respectively,

$$N_{eR} = n^2 / \sum n_j^2 \text{ and } N_{eB} = n(n-1) / [r \sum n_j(n_j-1)], \quad [4]$$

where n_j is individuals selected from family j and $n = \sum n_j$. With random selection (or $V = 0$) as a reference point, approximate predictions of the effective population size following selection were given by WEI (1995) and BURROWS (1984),

$$N_{eR} = \frac{mPN_{r\infty}(P,V)(ms-1)(sP-P+1)}{(m+msP-mP-1)} \{ [sP-P+N_{r\infty}(P,V)] \} \quad [5]$$

and

$$N_{eB} = N_{r\infty}(P,V)(ms-1)/[r(s-1)], \quad [6]$$

where $N_{r\infty}(P,V)$ is the relative effective population size after selection from an infinite population with the same P and V (WEI & LINDGREN 1991). The inverse of $2N_{eB}$ equates the average coancestry in the selected group and the average inbreeding coefficient in the offspring obtained following random mating among selected individuals (excluding selfing). Letting $f(x)$ denote the continuous density function of family mean, and x , and $p(x)$ the expected contribution of families,

$$N_{r\infty}(P,V) = P^2 / \int [p(x)]^2 f(x) dx,$$

which is identical to Burrows' $R(\alpha, \rho)$ if the distribution is normal. Both [5] and [6] were derived assuming many families. For small m , a modified formula can be used,

$$N_{r\infty}(P,V) = mN_{r\infty}(P,V)/[m-1+N_{r\infty}(P,V)].$$

Normal distributions were assumed for individual phenotypes, family means and within-family deviations. The total variance, σ_p^2 , was set to one. Thus $h^2 = \sigma_A^2/\sigma_p^2 = \sigma_A^2$ below (h^2 is heritability in narrow sense). Since N_{eB} and N_{eR} are functions of each other (WEI & LINDGREN 1995), only N_{eB} will be considered below. Note that N_{eB} can be higher than the census number (it may approach infinity).

RESULTS

The quantitative relationship between the family weight, β , and its influence on the selection index, V , is illustrated in Fig. 1. Knowledge of V was used to calculate $N_{r\infty}(P,V)$ for an infinite population, which was used in a small population calculating effective population size N_{eB} , in a small population (formula [6]). Required values for $N_{r\infty}(P,V)$ can be interpolated using the table of BURROWS (1984) or computed using WEI and LINDGREN'S (1991) procedure.

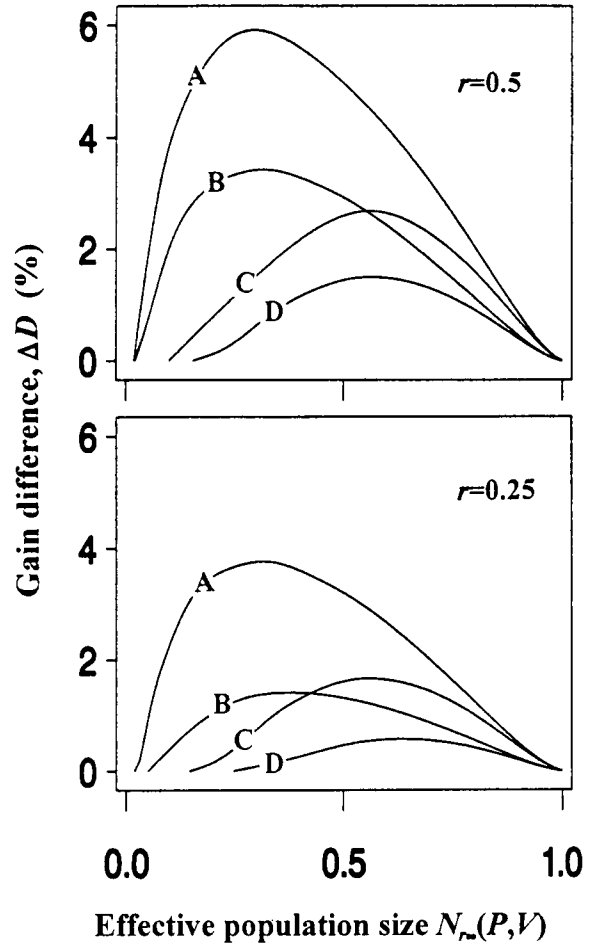


Figure 2 Relative gain differences (D) between index and optimal selection as a function of the relative effective population size $Nr8(P,V)$. Graphs are shown for full sibs ($r = 0.5$) and half-sibs ($r = 0.25$) for two values of heritabilities and selected proportions. Legends: A - $h^2 = 0.05, P = 0.01$; B - $h^2 = 0.25, P = 0.01$; C - $h^2 = 0.05, P = 0.1$; D - $h^2 = 0.25, P = 0.1$.

Index selection was compared with optimal selection for infinite populations (LINDGREN *et al.*, 1993 and WEI & LINDGREN 1995) at the same effective population size. Selections resulting in lower effective population size than achieved by "combined selection" are sub-optimal and were not considered in this comparison (WEI & LINDGREN 1995).

Figure 2 demonstrates the percentage difference in gain ($\Delta D = 100(\Delta G_{opt} - \Delta G)/\Delta G$) between the two algorithms as a function of effective population size for two family types ($r = 0.5$ and 0.25), two heritabilities ($h^2 = 0.25$ and 0.05) and two selected proportions ($P = 0.01$ and 0.1). The left ends of the curves represent "combined selection" while the right ends represent "within-family selection" ($N_{r\infty}(P,V) = 1$). For these two

Table 1 Predicted genetic gain (ΔG^*) and effective population size (N_{eB}) as influenced by the sib type (r), heritability (h^2), initial family number (m), family size (s), selected proportion (P) and the weight given to family information (β)

			$m = 10$											
			$s = 20$				$s = 40$				$s \rightarrow \infty$			
			$P = 0.1$		$P = 0.2$		$P = 0.1$		$P = 0.2$		$P = 0.1$		$P = 0.2$	
			r	h^2	β	ΔG	N_{eB}	ΔG	N_{eB}	ΔG	N_{eB}	ΔG	N_{eB}	ΔG
0.25	0.1	1.0	.161	4.19	.134	8.38	.184	4.09	.154	8.18	.234	4.00	.201	8.00
		*	.222	10.22	.178	16.44	.247	9.13	.198	15.07	.275	7.57	.225	13.10
		2/3	.203	23.19	.162	28.62	.207	26.48	.165	30.95	.209	31.31	.167	34.20
		0.5	.174	34.43	.139	36.96	.175	35.82	.140	37.59	.175	37.36	.140	38.30
		1/3	.153	39.71	.123	40.49	.154	39.50	.123	40.01	.155	39.30	.124	39.55
		0.0	.129	41.89	.103	41.89	.131	40.92	.105	40.92	.133	40.00	.106	40.00
0.25	0.25	1.0	.331	4.19	.276	8.38	.349	4.09	.291	8.18	.385	4.00	.318	8.00
		*	.497	12.24	.398	18.64	.519	11.54	.415	17.77	.512	10.60	.443	16.63
		2/3	.485	19.28	.388	25.34	.494	21.16	.395	26.73	.492	23.71	.401	28.58
		0.5	.435	31.48	.348	34.90	.437	32.60	.349	35.39	.436	33.84	.350	35.95
		1/3	.389	38.63	.311	39.78	.391	38.43	.312	39.32	.393	38.24	.314	38.87
		0.0	.329	41.89	.263	41.89	.334	40.92	.267	40.92	.340	40.00	.271	40.00
0.5	0.1	1.0	.256	2.09	.214	4.19	.287	2.05	.240	4.09	.344	2.00	.284	4.00
		*	.291	3.19	.236	5.84	.329	3.01	.266	5.56	.350	2.81	.291	5.26
		2/3	.233	10.20	.186	13.16	.239	11.33	.191	13.98	.241	12.88	.192	15.08
		0.5	.174	16.21	.139	17.78	.175	16.81	.140	18.05	.175	17.48	.139	18.35
		1/3	.133	19.50	.107	20.01	.134	19.40	.107	19.78	.134	19.30	.107	19.55
		0.0	.087	20.95	.070	20.95	.089	20.16	.071	20.46	.090	20.00	.072	20.00
0.5	0.25	1.0	.486	2.09	.406	4.19	.509	2.05	.425	4.09	.544	2.00	.449	4.00
		*	.582	3.63	.470	6.44	.616	3.50	.495	6.22	.585	3.35	.482	5.99
		2/3	.538	7.65	.431	10.85	.550	8.07	.439	11.16	.538	8.59	.431	11.56
		0.5	.435	13.66	.348	15.92	.437	14.04	.349	16.08	.433	14.47	.345	16.26
		1/3	.344	18.39	.275	19.28	.345	18.30	.275	19.05	.344	18.21	.275	18.84
		0.0	.227	20.95	.181	20.95	.231	20.46	.184	20.46	.235	20.00	.187	20.00

Gain was calculated using order statistics as family means;

* $\beta = k \cdot (1 - K) / [k \cdot (1 - K) + K \cdot (1 - k)]$ combined index, which maximizes the gain.

extreme cases index selection is identical to optimal selection. The difference between the methods reaches a maximum somewhere in between. The difference was strongly influenced by family type (r), heritability (h^2) and selected proportion (P). The difference was much smaller for the lower value of r and for the higher values of h^2 and P , especially when selection was close to "combined selection" or "within-family selection".

In small populations, both predicted genetic gain and effective population size are influenced by the family type (r), heritability (h^2), family number (m), family size (s), selected proportion (P) and the weight (β) given to family mean [Eqs (3) and (6)]. Numerical values have been calculated for a range of situations (Table 1). Genetic gain, while a single factor varied, appeared to be a monotonically increasing function of r , h^2 , m and s , and a monotonically decreasing function of P . Effective population size became higher when r

became smaller and m and P larger. The effects of h^2 and s on effective population size depended on β . Effective population size was often well preserved when a small h^2 was combined with a low β but not when β was high. This occurred because, at high β , lower h^2 forced the selection to be more dependent on family mean so that the frequency of individuals selected from better families was high. It seems that larger family size combining an intermediate value of β , can give a higher effective population size. However, if N_{eB} is scaled as the ratio relative to the possible maximal value corresponding to within-family selection, $N_{eB} = (msPw - 1) / [r(sP - 1)]$, the effective population size appeared to be a monotonically increasing function of family size (Fig. 3). For fixed r , h^2 , m , s and P , effective population size strictly increases as β decreases while genetic gain shows a more complicated relation to β . Gain increased when the weight applied to family mean was increased

Table 1 (continued) Predicted genetic gain (ΔG^*) and effective population size ($N_{e\beta}$) as influenced by the sib type (r), heritability (h^2), initial family number (m), family size (s), selected proportion (P) and the weight given to family information (β)

			$m = 20$											
			$s = 20$				$s = 40$				$s \rightarrow \infty$			
			$P = 0.1$		$P = 0.2$		$P = 0.1$		$P = 0.2$		$P = 0.1$		$P = 0.2$	
r	h^2	β	ΔG	$N_{e\beta}$	ΔG	$N_{e\beta}$	ΔG	$N_{e\beta}$	ΔG	$N_{e\beta}$	ΔG	$N_{e\beta}$	ΔG	$N_{e\beta}$
0.25	0.1	1.0	.173	8.40	.141	16.80	.197	8.19	.161	16.39	.259	8.00	.211	16.00
		*	.224	19.67	.180	31.89	.248	17.52	.198	29.16	.290	14.49	.235	25.25
		2/3	.203	45.37	.163	56.39	.207	52.00	.165	61.15	.210	61.86	.168	67.86
		0.5	.175	68.35	.140	73.63	.175	71.24	.140	74.94	.175	74.44	.140	76.41
		1/3	.154	79.39	.123	81.04	.155	78.96	.123	80.03	.155	78.53	.124	79.06
		0.0	.129	84.00	.103	84.00	.131	81.95	.105	81.95	.133	80.00	.106	80.00
0.25	0.25	1.0	.355	8.40	.289	16.80	.374	8.19	.305	16.39	.409	8.00	.333	16.00
		*	.501	23.61	.401	36.25	.522	22.23	.417	34.50	.531	20.36	.427	32.21
		2/3	.488	37.54	.390	49.72	.495	41.26	.395	52.52	.497	46.37	.397	56.26
		0.5	.437	62.26	.349	69.33	.438	64.56	.349	70.35	.437	67.10	.349	71.50
		1/3	.391	77.11	.312	79.54	.392	76.70	.313	78.56	.393	76.29	.313	77.62
		0.0	.330	84.00	.264	84.00	.335	81.95	.267	81.95	.340	80.00	.271	80.00
0.5	0.1	1.0	.275	4.20	.224	8.40	.308	4.10	.251	8.19	.366	4.00	.298	8.00
		*	.299	6.10	.241	11.26	.336	5.75	.270	10.71	.376	5.37	.306	10.10
		2/3	.234	19.89	.187	25.85	.240	22.13	.191	27.51	.243	25.27	.194	29.76
		0.5	.175	32.10	.140	35.36	.175	33.34	.140	35.91	.175	34.71	.140	36.54
		1/3	.134	38.94	.107	40.02	.134	38.73	.107	39.53	.134	38.52	.107	39.05
		0.0	.087	42.00	.070	42.00	.089	40.97	.071	40.97	.090	40.00	.072	40.00
0.5	0.25	1.0	.522	4.20	.426	8.40	.546	4.10	.445	8.19	.579	4.00	.471	8.00
		*	.594	6.97	.476	12.43	.623	6.69	.499	11.99	.622	6.40	.505	11.53
		2/3	.542	14.81	.433	21.19	.551	15.63	.440	21.80	.548	16.66	.438	22.59
		0.5	.437	26.86	.349	31.50	.438	27.64	.349	31.82	.435	28.49	.347	32.18
		1/3	.345	36.62	.275	38.48	.345	36.43	.276	38.01	.345	36.24	.275	37.56
		0.0	.228	42.00	.182	42.00	.231	40.97	.184	40.97	.235	40.00	.187	40.00

Gain was calculated using order statistics as family means;

* $\beta = k \cdot (1 - K) / [k \cdot (1 - K) + K \cdot (1 - k)]$ combined index, which maximizes the gain.

and reached a maximum where "combined index selection" occurs (LUSH 1947). Thereafter, ΔG decreased with increasing β . Evidently there are better choices of β than above what corresponds to "combined selection".

Although selection based on within-family deviation yielded a maximum in effective population size in the case studied, it was not the best in preserving effective population size. In comparison with the best method, within-family selection (ASKEW & BURROWS 1983; BURROWS 1984; WEI & LINDGREN 1991), selection by using [2] or other types of index function (e.g. TORO & PEREZ-ENCISO 1990) unavoidably lead to a loss in effective population size due to the sampling error caused by small size (ROBERDS *et al.* 1980; BURROWS 1984; WEI & LINDGREN 1995b). Large family size reduced the loss (Fig. 3). When family size approaches infinity or within-family deviations can be

expressed by order statistics, the sampling error disappears and selection based on within-family deviation preserves effective population size in the same way as within-family selection.

DISCUSSION

Methods to compromise between gain and effective population size

A fundamental selection problem is how to combine genetic improvement and conservation of effective population size, as these goals are in conflict with each other. There are a number of approaches to this problem. A single best solution can be identified only if effective population size and genetic gain can be quantified on a compatible scale. In this case a value-function can be constructed, that considers both factors

Table 1 (continued) Predicted genetic gain (ΔG) and effective population size ($N_e = N_{eB}r(1 - 1/Ps) / (m - 1/Ps)$) as influenced by the sib type (r), heritability (h^2), initial family number (m), family size (s), selected proportion (P) and the weight given to family information (β)

			$m = \infty$											
			$s = 20$				$s = 40$				$s \rightarrow \infty$			
			$P = 0.1$		$P = 0.2$		$P = 0.1$		$P = 0.2$		$P = 0.1$		$P = 0.2$	
			r	h^2	β	ΔG	N_e	ΔG	N_e	ΔG	N_e	ΔG	N_e	ΔG
0.25	0.1	1.0	.186	0.1000	.148	0.2000	.212	0.1000	.169	0.2000	.277	0.1000	.221	0.2000
		*	.227	0.2251	.181	0.3676	.250	0.2053	.199	0.3441	.308	0.1736	.246	0.3046
		2/3	.204	0.5274	.163	0.6599	.208	0.6226	.166	0.7364	.212	0.7642	.169	0.8415
		0.5	.175	0.8058	.140	0.8708	.175	0.8634	.140	0.9104	.175	0.9271	.140	0.9529
		1/3	.155	0.9424	.123	0.9229	.155	0.9616	.123	0.9754	.155	0.9807	.124	0.9876
		0.0	.130	1.0000	.104	1.0000	.132	1.0000	.105	1.0000	.133	1.0000	.106	1.0000
0.25	0.25	1.0	.381	0.1000	.304	0.2000	.402	0.1000	.321	0.2000	.439	0.1000	.350	0.2000
		*	.505	0.2708	.403	0.4190	.524	0.2612	.418	0.4085	.555	0.2449	.443	0.3903
		2/3	.490	0.4342	.391	0.5795	.496	0.4907	.396	0.6291	.503	0.5671	.401	0.6924
		0.5	.439	0.7313	.350	0.8179	.439	0.7791	.350	0.8521	.439	0.8316	.350	0.8887
		1/3	.392	0.9141	.313	0.9443	.393	0.9328	.313	0.9566	.393	0.9513	.314	0.9687
		0.0	.331	1.0000	.264	1.0000	.336	1.0000	.298	1.0000	.340	1.0000	.271	1.0000
0.5	0.1	1.0	.295	0.1000	.235	0.2000	.331	0.1000	.264	0.2000	.392	0.1000	.313	0.2000
		*	.308	0.1391	.246	0.2582	.343	0.1344	.274	0.2516	.403	0.1283	.321	0.2430
		2/3	.235	0.4609	.188	0.6032	.240	0.5274	.192	0.6599	.245	0.6197	.196	0.7341
		0.5	.175	0.7550	.140	0.8349	.175	0.8058	.140	0.8708	.175	0.8618	.140	0.9093
		1/3	.134	0.9236	.107	0.9506	.134	0.9424	.107	0.9629	.134	0.9611	.107	0.9751
		0.0	.080	1.0000	.070	1.0000	.089	1.0000	.071	1.0000	.090	1.0000	.042	1.0000
0.5	0.25	1.0	.561	0.1000	.447	0.2000	.587	0.1000	.468	0.2000	.620	0.1000	.495	0.2000
		*	.606	0.1589	.483	0.2854	.631	0.1564	.503	0.2820	.663	0.1533	.529	0.2778
		2/3	.545	0.3410	.435	0.4917	.553	0.3693	.441	0.5193	.561	0.4041	.448	0.5521
		0.5	.439	0.6277	.350	0.7403	.439	0.6632	.350	0.7675	.439	0.7017	.350	0.7962
		1/3	.346	0.8660	.276	0.9122	.346	0.8838	.267	0.9242	.346	0.9015	.276	0.9360
		0.0	.229	1.0000	.182	1.0000	.232	1.0000	.185	1.0000	.235	1.0000	.187	1.0000

Gain was calculated in the same way as $N_{rs(P,V)}$;* $\beta = k \cdot (1 - K) / [k \cdot (1 - K) + K \cdot (1 - k)]$ combined index, which maximizes the gain.

and a selection level that maximizes the value-function can be found (LINDGREN & WEI 1994). Other approaches are to introduce effective population size as a formal constraint, or informally adjust selection so effective population size is increased, or apply a formal constraint on the maximum number of relatives for a selection. It is important to know how efficient such procedures are.

Optimal selection provides maximum gain at a given effective population size (LINDGREN *et al.* 1993). However, the lack of refinement for finite populations and the complex computation poses hurdles to its use in practice. An alternative is to find and use a simple but reliable selection algorithm that manages gain and effective population size close to their optimal combination.

The simplest method is to allocate selection intensity into two consecutive truncation selections, between-

and within-family selection, where selected families contribute equally (BURROWS 1984; WEI 1995). However, the genetic gain obtained by this procedure is often rather low compared to other methods like restricted phenotypic or optimal-index selection at the same effective population size (WEI 1995). Restricted phenotypic selection with a limit on the contributions of families is a more efficient alternative (WEI 1995; WEI & LINDGREN 1995b). Linear deployment based on family performance is a good approximation of optimal selection, particularly when siblings are closely related, genetic variance is low, selection is less intense, and effective population size is large (WEI & LINDGREN 1995a). However, linear deployment is somewhat impractical to use for a practical selection operation.

In this study we have shown that index selection using a linear combination of information from

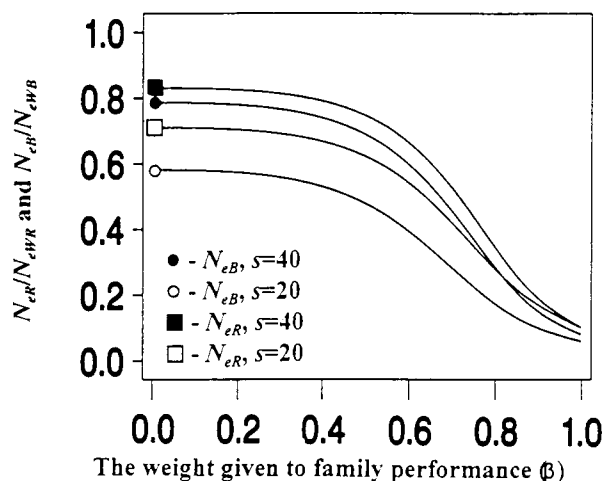


Figure 3 The relative effective population size, thus the quotient between the effective population size (N_{eR} and N_{eB}) and the value (N_{eWR} and N_{eWB} , respectively corresponding to within-family selection) plotted against the weight (β) given to family performance. Graphs are shown for populations of full-sib families ($r = 0.5$) with the same heritability ($h^2 = 0.25$) and family number ($m = 10$) but with different family size ($s = 20$ or 40)

families and individuals can be a useful tool. Only a rather small fraction of the theoretically obtainable gain was lost (Fig. 2). The method seemed most efficient when selection was of limited intensity and additive genetic variance (heritability) was high, and seemed more efficient for half-sibs than full-sibs. Index selection was only compared with optimal selection for the case of large families.

The method should be easy to implement as breeders are well accustomed to the idea of weighting information from the phenotypes with information from their relatives, although it may seem unorthodox to choose the weight on more or less subjective opinions of the relative importance of gain versus effective population size rather than to derive the weight from a well established algorithm. A possible approach is to fix a certain effective population number as the selection target and find the weight that results in that value by iterative search. The genetic gain obtained by using that weight will not be far from the maximum achievable resulting in the fixed effective population number.

Selection with more attention paid to phenotype or within-family deviation may yield both higher gain and larger effective population size compared to selections close to the weight maximizing gain, if a smaller selected proportion is accepted in the former case than in the latter (Table 1). This finding agrees with some recent published results concerning single- (WEI & LINDGREN 1991) and multi-generation breeding (-

QUINTON *et al.* 1992). A problem with this operation is the role the demographic size of the breeding population plays in a long-term breeding program, especially in comparison with effective population size. A large selected proportion can often be regarded as desirable (LINDGREN & WEI 1994).

Implications of the heritability

When heritability is low, a reasonable gain is hard to achieve without a high selection intensity (thus a big population) and a large sacrifice in effective population size. One counter-measure is to use testing methods that increase heritability. This can be achieved by identifying and using uniform and genetically discriminative test environments, and by testing clones instead of individuals. Another option is to invest in a larger number of initial families, so that the effective population size remaining after selection will be acceptable.

Utilization of half-sib families

Like the total variance, the additive genetic variance can be decomposed into two components – family mean and within-family deviation. The distribution depends on the genetic relation between siblings (r). From formula (1) for k it is evident that lower values of r result in a larger component of within-family deviation. A requirement for a high effective population size forces selection to be more dependent on within-family information. It is, therefore, possible to simultaneously obtain higher gain and large effective population size using half-sibs instead of full sibs, especially when heritability is high and the selected proportion low (WEI & LINDGREN 1995a). Gain will be favoured by using half-sib families if the heritability is relatively high. It should be emphasised that we have assumed unrelated families. The main reason why half sibs had high effective population size is that each member of a family brings in the genes of a new founder. However, this situation will persist only in the initial generation.

Family number and size

Higher efficiency of breeding population management will result from a better understanding of the respective roles of initial family number and size. The formulae relating gain and effective population size ([3], [4] and [6]) permit a comparison of the effects of family number and size on gain and effective population size. Increasing family number is a potentially powerful way to improve effective population size while the role in

improving gain is probably more trivial (Table 1). Large family size reduces the loss of effective population size caused by sampling error (Fig. 3). However, increasing family size can hardly help in both gain and effective population size unless a strong utilisation of family information is expected. In practice, the efforts in increasing family number and size are often constrained by biological and economical factors. A common approach is to search for the optimal allocation of resources between family number and size under constant size of the test population (ms). A more sophisticated approach would be to formulate the economic constraints as functions of the components of the system (costs of families and individuals). For given cost components and heritability, family number and size which maximize expected genetic gain at a given cost, effective population size and number of selected individuals can be derived. Calculations like those presented in Table 1 would be a component in such optimizations.

Index selection from related families

Index selection used in this study is restricted to populations composed of unrelated families with a single level of uniform intrafamily relationship. Breeders often employ populations or tests with mixtures of family relationships produced by complex mating systems like factorial, hierarchical and diallel mating. Similar to constructing an "optimal index" for these structures (OSBORNE 1957; COTTERILL 1986), an index permitting restriction on effective population size by changing the utilization of family information (full-sib, half-sib and others) could probably be constructed to achieve a balance between gain and effective population size (inbreeding, coancestry). A structure where families are equally related can be handled by an adjustment of r .

Concluding remarks

We propose to use index selection to balance gain and effective population size in situations where the heritability is reasonable high, the selected proportion is reasonably high, and the families are uniformly related. A range of weights may be tested as a basis for decision. The next breeding generation can then be recruited based on index values which balance gain and effective population size in a desirable way. Predictions based on index selection can be used for planning efficient breeding tests (like choosing family number and size).

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