

Investigation of Status Number Following Selection from Populations Under Different Mating Designs

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Abstract

We developed formulas to predict the status number or relatedness in the selection from populations generated under four mating designs. Efficiency in conserving status number was evaluated, relative to single-pair mating, for nested, factorial and half-diallel mating designs. Mating designs were investigated in terms of the number of crosses per parent or mating rate, and the full-sib family size. Numerical results were given with assumptions of normal distribution for family means and within-family deviations. Status number increased as the number of parent sets increased and family size decreased. Under balanced factorial mating design, status number was maximized when the numbers of male and female parents were the same. Single-pair mating most favored status number in selection, followed, first, by factorial and, then, by half-diallel mating designs. Nested was the worst mating design in this regard. Nested, partial/disconnected factorial and half-diallel with relatively low mating rate (3–5) would yield high status numbers while providing extra key information for improving the genetic gain.

Key words: Breeding population, family, mating design, selection, relatedness, status number.

Introduction

In a breeding programme, a population for selecting superior individuals as parents of the next generation is often generated under a mating design. Given a mating design, the relatedness (average coancestry) among members of the population is specific. So is the relatedness among selected individuals (ROBERTSON, 1961; BURROWS, 1984a, 1984b; WEI and LINDGREN, 1996). It is well documented that mating pattern also influences progeny test planning, estimates of other genetic parameters, and the genetic gain in selection (e.g. NAMKOONG and ROBERTS, 1974; PEPPER and NAMKOONG, 1978; FALCONER and MACKAY, 1996).

Under certain conditions, the relatedness among parents can be extended to express the relationship among the offspring. When mating among parents is random, the average inbreeding coefficient of the offspring is an estimate of the relatedness and also predicts the corresponding inbreeding effective population size, heterozygosity, etc. (FALCONER and MACKAY, 1996). An expression of effective population size, called status number, was recently suggested to directly describe the relationship among the parents or selected group (LINDGREN *et al.*, 1996; NOITON and ALSPACH, 1996; LINDGREN and MULLIN, 1998). Status number is half the inverse of the relatedness (LINDGREN and MULLIN, 1998), just as inbreeding effective population size is half the inverse of the inbreeding coefficient (FALCONER and MACKAY, 1996).

Relatedness among parents in selection inevitably increases over generations. High relatedness among parents may increase the inbreeding level of the offspring with a possibility of inbreeding depression, and restricts further improvement of genetic gain in later generations. A tough task parallel to improving gain in selection is, therefore, to curtail relatedness at certain level, so that expected gain is realizable and sustainable.

This paper investigates the influences of four mating designs on the relatedness and status number in the selection. We first develop formulas to predict relatedness and status number based on BURROWS (1984a, 1984b) approach to prediction of inbreeding effective population size under random mating without self-mating. Relatedness and status number are related to the predictable inbreeding effective population size. We then generated numerical results for: 1) investigating the interactions in status number with selection and population census structure (parent number and grouping, mating rate, population size, family number and size, etc.), and 2) comparing the relative efficiencies in status number of different mating designs.

Basic Assumptions and Models

Assume that a population is generated with parents mated under certain design schemes. The parents are unrelated, and the population is subject to directional selection of individuals as the parents of the next generation. Mating designs considered in this study are: 1) single-pair (SP); 2) nested (ND); 3) factorial including its variants (FD); and 4) half-diallel, including its variants but excluding selfing (HD). The variants of factorial and half-diallel are those called (a) disconnected and (b) incomplete/partial but balanced, differing in the mating rate of the parents. Unless otherwise stated, we use the same set of symbols (ND, FD and HD) for all of their variants but distinguish amongst the variants by mating rate in the following development. Depending on the mating design, one or two sib types may be identified in the breeding population: half-sib (parental and maternal) and full-sib.

Truncation selection criteria can include an individual's phenotype, BLUP breeding value or family mean, which criteria actually differ in the corresponding fraction of variance explained by the full-sib family component (t) (WEI and LINDGREN, 1996). High t (>0.25 for half-sib and >0.5 for full-sib) is associated with enhanced use of sibs' information in predicting breeding value (e.g. BLUP) and selection, while low t relates to individuals' phenotypic performances.

The relatedness (θ) in the selected group is composed of two sources: sib relationship (θ_{sib}) among and self-pairing (θ_{self}) of selections, that is,

$$\theta = \theta_{self} + \theta_{sib} \quad (1)$$

The contribution of self-pairing is straightforward, depending on the size (n) of selected group. Among n^2 combinations of

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n selected individuals, there are n self-pairings or combinations with two gametes originating from a single parent, thus:

$$\theta_{self} = \frac{0.5}{n} \quad (2)$$

Under certain mating design, there may be half-sib, full-sib or both at the same time among selections. Assuming random mating, sib relationship (θ_{sib}) can be related to the inbreeding effective population size (N_{ei}) without considering self-mating of the next generation population (BURROWS, 1984a) in the form

$$\theta_{sib} = \frac{0.5(n-1)}{nN_{ei}} \quad (3)$$

Therefore, (1) becomes

$$\theta = \frac{0.5}{n} + \frac{0.5(n-1)}{nN_{ei}} \quad (4)$$

and the status number (N_s) that is half the reverse of θ (LINDGREN *et al.*, 1996; NOITON and ALSPACH, 1996; WEI *et al.*, 1997; LINDGREN and MULLIN, 1998) is

$$\frac{1}{N_s} = \frac{1}{n} + \frac{(n-1)}{nN_{ei}} \quad (5)$$

The key is to obtain θ_{sib} or $1/N_{ei}$.

BURROWS (1984a, 1984b) developed mathematical models for approximating that inbreeding effective population size (N_{ei}) which is composed of either a half-sib or a full-sib contribution or both. N_{ei} may be estimated from selection proportion (P) and the fraction (t) of variance contributed by the full-sib family component through its limiting-case, the effective family number [$R(P,t)$] for the corresponding infinite populations (WEI and LINDGREN, 1996):

$$R(P,t) = \frac{P^2}{\int_{-\infty}^{\infty} p^2(x,t)f(x,t)dx} \quad (6)$$

where x is the family mean value distributed with zero mean and the t variance calculated with unit total variance; $f(x,t)$ is the density function of x ; and $p(x,t)$ is the selected proportion of individuals from a family with value x . Eqn (6) is used to predict N_{ei} that is contributed by half-sib and/or full-sib under different mating schemes (BURROWS, 1984a, 1984b):

Single-pair

$$\frac{1}{N_{ei}} = \frac{r_F(s-1)}{(N-1)R(P,t)} \quad (7)$$

where N = the initial population size before selection,
 $r_F = 0.5$, the coefficient of relatedness among full-sibs
and
 s = full-sib family size.

Nested (Male and Female within Male)

$$\frac{1}{N_{ei}} = \frac{r_F(s-1)}{(N-1)R(P,t)} + \frac{r_H s(q_f-1)}{(N-1)R(P,t_m)} \quad (8)$$

where $r_H = 0.25$, the coefficient of relatedness among half-sibs,
 q_f = the mating rate for each male parent,
 t_m = the fraction of variance contributed by the male parent half-sib family component, and
the term r_F having the same meaning as that for the single-pair model.

Factorial

$$\frac{1}{N_{ei}} = \frac{r_F(s-1)}{(N-1)R(P,t)} + \frac{r_H s(q_m-1)}{(N-1)R(P,t_f)} + \frac{r_H s(q_f-1)}{(N-1)R(P,t_m)} \quad (9)$$

where q_m = the mating rate for each female parent,
 t_f = the fraction of variance contributed by the female parent half-sib family component, and
the terms r_F , r_H , q_f and t_m having the same meaning as those for the single-pair and nested models.

Half-diallel

$$\frac{1}{N_{ei}} = \frac{r_F(s-1)}{(N-1)R(P,t)} + \frac{2r_H s(q-1)}{(N-1)R(P,t_g)} \quad (10)$$

where q = the mating rate for one as both male and female parent and
 $t_g = t_m = t_f$, the fraction of variance contributed by the half-sib family component.

It is shown from (9) and (10) that a FD or HD depends on the mating rate (q_m and q_f for FD and q for HD). If the mating rate and other conditions (t , N , s , P) are constant, then the relatedness or status number is the same, regardless of use of partial or disconnected FD and HD. Eqns (7) to (10) were derived with the assumption that family number is infinitely large (BURROWS, 1984a; WEI and LINDGREN, 1996). A modification of (6) to finite family number but infinite family size is suggested to obtain a better approximation (WEI *et al.*, 1997):

$$R(P,t) = \frac{n_f P^2}{\sum_{i=1}^{n_f} p^2(x_i,t)} \quad (11)$$

where $p(x_i,t)$ is the selected proportion of individuals from the i th family with value x_i , and n_f is the countable number of the corresponding half-sib or full-sib families. The $p(x_i,t)$ in selection depends on the selected proportion (P) and the fraction of variance contributed by the corresponding family component (t).

Numerical Examples

To investigate and compare the effects of mating designs, both (6) and (11) are employed to obtain $R(P,t)$ for predicting status number. Eqn (6) is used when half-sib or full-sib family numbers are larger than 100, and (11) is used otherwise. Assume half-sib/full-sib family means and within-family deviations are normally distributed. Family means are mimicked by order statistics with zero mean and variance t , t_m or t_f (the total variance is one). Numerical calculation procedures follow BURROWS (1984a), WEI and LINDGREN (1996) and WEI *et al.* (1997).

In complete and partial/disconnected factorials, the mating rate for a male parent (q_f) can differ from that for a female parent (q_m). We take full factorial ($q_m + q_f = n_p$) as an example to investigate how the ratio of q_m to q_f influences the status number in selection. The conclusions could be extended to partial/disconnected factorials ($q_m + q_f < n_p$). Let $n_p = n = 100$, q_f thus varies from 1 to 99 and $q_m = n_p - q_f$ i.e. $q_m = 99, 98, \dots, 1$. Full-sib family size (s) is allowed to vary from 2 to 50. *Figure 1* plots status number against q_m and s for two values of t . Obviously, maximum status number is obtained at $q_m = q_f$. In the follo-

wing calculations, we focus just on situations with $q_m = q_f$ for factorial.

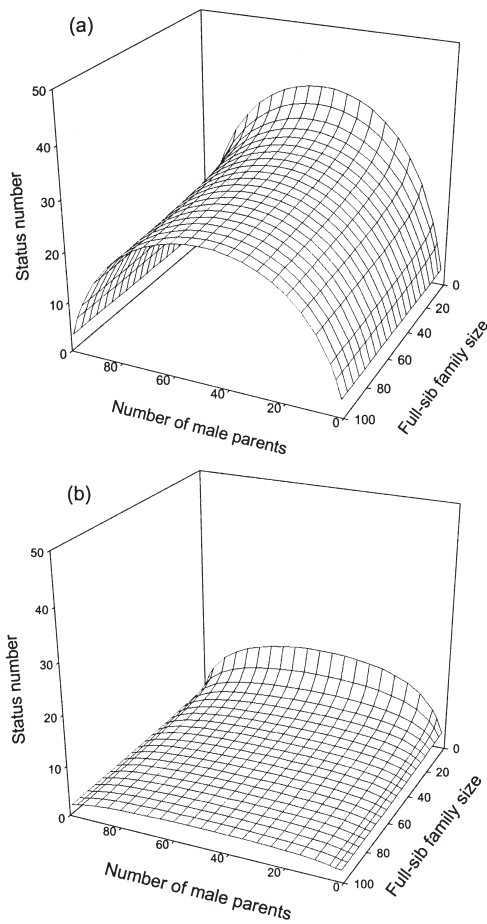


Fig. 1. – Status number against full-sib family size and number of male parents in selection from the population produced using factorial mating design. $n_p = n = 100$. (a) $t = 0.2$, $t_m = t_f = 0.1$ and (b) $t = 0.8$, $t_m = t_f = 0.4$.

Let us consider populations generated with 100 parents (n_p) by using nested (ND), disconnected factorial (FD, $q_m = q_f$) and half-diallel (HD). For FD and HD, each parent has the same mating rate, regardless of its being a male or female parent (FD) or both (HD). The same amount (n) of selections will be screened from these populations as the next generation's parents. The number of male parent for ND ranges from 2 to 50, while the mating rate per parent for FD and HD varies according to the disconnected sets of parents. Single-pair mating is the limiting case for all other three mating designs, i.e. $q_m = q_f = 1$. Full-sib family size (s) is allowed to vary from 2 to 50. As regards ND, Figure 2 plots status number against the number of parent sets (male parents) and full-sib family size for two values of t . Figures 3 and 4 present status number against the number of the disconnected sets and full-sib family size for two values of t , for FD and HD, respectively.

Using single-pair (SP) as reference case, we can study the relative efficiencies in conserving status number of the three other mating designs (ND, FD and HD) in several ways. Efficiency is defined as the ratio of status number under a mating design to that under SP at the same parent number. First,

parent number ($n_p = 100$) and full-sib family sizes ($s = 5$ and 25) are constant. Parent sets vary from 1 to 50 but only those parent sets that result in exact n_p are considered. The efficiencies in status number under ND, FD and HD were plotted against parent sets for two values of t and s (Figure 5). Second, N (4000) and s (25) are constant. Parent numbers can range from 2 to 320, but only those parent numbers that result in exact N are considered. The efficiencies under ND, FD and HD were plotted against n_p for two values of t (Figure 6). Finally, N (4000) and n_p (100) are constant. Family size varies from 2 to 80, but only those family sizes that result in exact N are considered. The efficiencies were plotted against s for two values of t (Figure 7).

Given parent number (n_p), a series of full-sib family numbers (n_f) may be obtained for different mating designs. Values for nest (ND), factorial (FD) and half-diallel (HD) designs converge at single-pair with minimum $n_f (= 0.5 n_p)$. Maximum n_f varies over mating designs. Status number has a relationship with n_f , based on which breeders could decide n_f appropriate for their breeding programmes. In principle, high status number should be obtained at possibly low n_f . Considering $n_p = 100$ and $s = 30$ as an example, we list minimum, maximum and suggested n_f with corresponding status numbers for different t values in Table 1. For minimum family number, parent sets (Ps) and mating rates are 50 and 1, respectively, for all mating designs; but for the maximum family number, they are 1 and 99 for ND and HD, and 1 and 50 for FD. Table 1 also includes the number of parent sets (Ps) and mating rates (Mr) for the suggested n_f .

Results and Discussion

Given the total parent number (N) in factorial mating, male parent number (q_m) can be chosen from 1 to $N-1$ and corresponding female parent number (q_f) from $N-1$ to 1. Status number (N_s) following a directional selection is a function of q_m or q_f (Figure 1). Status number is maximized for $q_m = q_f$, and decreases as q_m or q_f decreases and increases (BURROWS, 1984b). However, the deviation from maximum status number is small if the mating rate does not sway far away from $q_m = q_f$.

In all mating designs studied, parents can be grouped into a number of parent sets. Only within a set is a parent allowed to mate with one or several others. Single-pair is a special case as well as the extreme case of nested (ND), factorial (FD) and half-diallel (HD) mating, which has a maximum number ($0.5 n_p$) of parent sets but a minimum numbers of parents in a set (2). Given n_p , status number for ND, FD and HD is highest at the maximum number of parent sets or the smallest number of parents in a set, and starts to decrease as the number of parent sets decreases, as is particularly evident at small full-sib family size and for ND (Figures 2–4). Smaller numbers of parent sets allow an individual parent to mate with more other parents, thus creating more related families and reducing status number. This phenomenon is particularly evident for ND (Figure 2) with a single set of parents because an individual serves as the only male parent and is mated to all others.

Status number decreases rapidly as full-sib family size (s) increases from a very low value but reaches a relatively stable value after a certain s (Figures 1–4). Small family size forces selections to be relatively even-distributed over more families, thus reducing relatedness within families. Large family size allows more selections from relatively few superior families, thus increasing relatedness, particularly at high t (WEI and LINDGREN, 1996). It can be concluded that full-sib family size smaller than 5 could effectively conserve status number while family size larger than 40 would not lead to much further loss in status number.

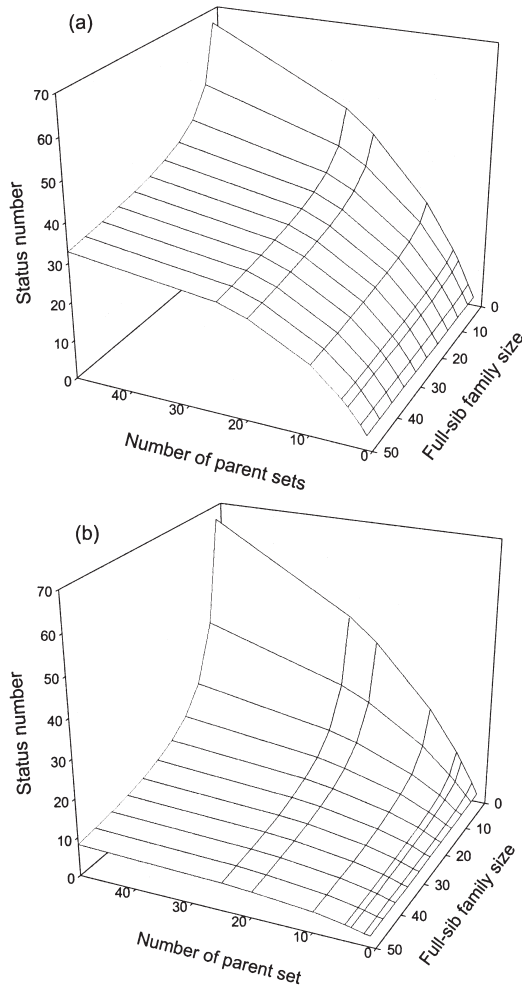


Fig. 2. – Status number against full-sib family size and number of male parents in selection from a population produced using nested mating design. $n_p = n = 100$. (a) $t = 0.2$, $t_m = 0.1$ and (b) $t = 0.8$, $t_m = 0.4$.

At a constant parent number (n_p), number (p_s) of parent sets can range from 1 to $0.5 n_p$, and the full-sib family number varies accordingly. Single-pairing (SP) is most efficient in conserving status number, followed by factorial (FD) and half-diallel (HD) mating. In general, nested (ND) is the worst (Figure 5). Although large family size trivially improves the relative efficiencies of ND, FD and HD, this improvement evidently does not compensate for the absolute loss in status number compared to small family size. A small number of parent sets increases a parent's mating rate, creates large number of related families and, thus, reduces status number compared to SP. At low t , those reductions in status number associated with the use of FD and HD are small over all possible numbers of parent sets, but the reduction associated with the use of ND significantly increases as the number of parent sets decreases. At high t , all reductions in status number by ND, FD and HD are significant, and rapidly decrease as the numbers of parent sets decrease. Yet, the differences between ND and FD and HD become small. Meanwhile, the superiority of FD over HD and ND becomes visible, and ND can be slightly more efficient than HD at some intermediate numbers of parent sets.

Different parent numbers (n_p) are available to keep constant the initial population size (N), full-sib family number (n_f) and full-sib family size (s). Mating rate and parent sets then vary with n_p . While the mating rate for each male parent in ND is

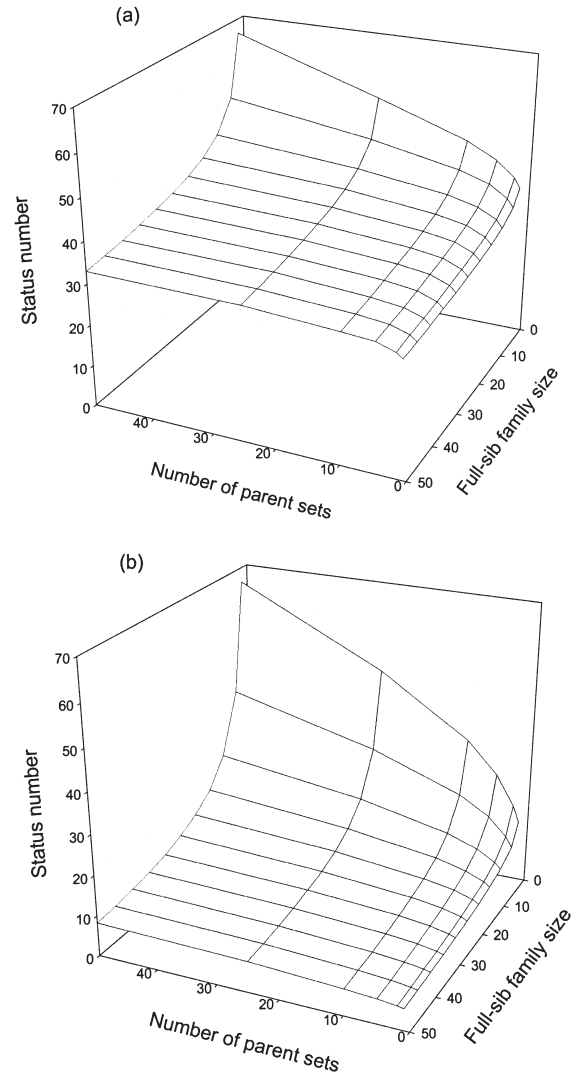


Fig. 3. – Status number against full-sib family size and disconnected set in selection from the population produced using factorial mating design. $n_p = n = 100$. (a) $t = 0.2$, $t_m = t_f = 0.1$ and (b) $t = 0.8$, $t_m = t_f = 0.4$.

$N/(n_p s - N)$ with $n_p > N/s$, the mating rate for each parent in FD and HD is $2N/(n_p s)$. Accordingly, there are $n_p - N/s$ sets of parents in ND and $n_p^2 s / (4N)$ sets of parents in FD and HD. Over the range of n_p , SP is again most efficient, followed by FD and HD. ND mating is the least efficient design (Figure 6). The efficiencies of ND, FD and HD significantly increase as the parent numbers (n_p) become large, for large n_p is associated with low mating rate and large unrelated family number. In general, a low t value results in higher efficiency than a high t value, but the difference is slight, except for FD with small parent number.

Given initial population size (N) and selected number ($n = n_p$), different full-sib family sizes (s) can be chosen to ensure different mating rates (except for SP), parent sets and full-sib family number (n_f). Maximum s (constant) occurs with SP. Over the full range of s , ND, FD and HD are superior to SP except at low t for ND (Figure 7). FD is superior to HD, which is followed by ND. The three designs are more efficient with smaller s , particularly at high t and for FD and HD. At high t , the fact that few family numbers contribute most of selections results in low status number (e.g. Figures 1–4). Small family sizes restrict family contributions, thus greatly improving the

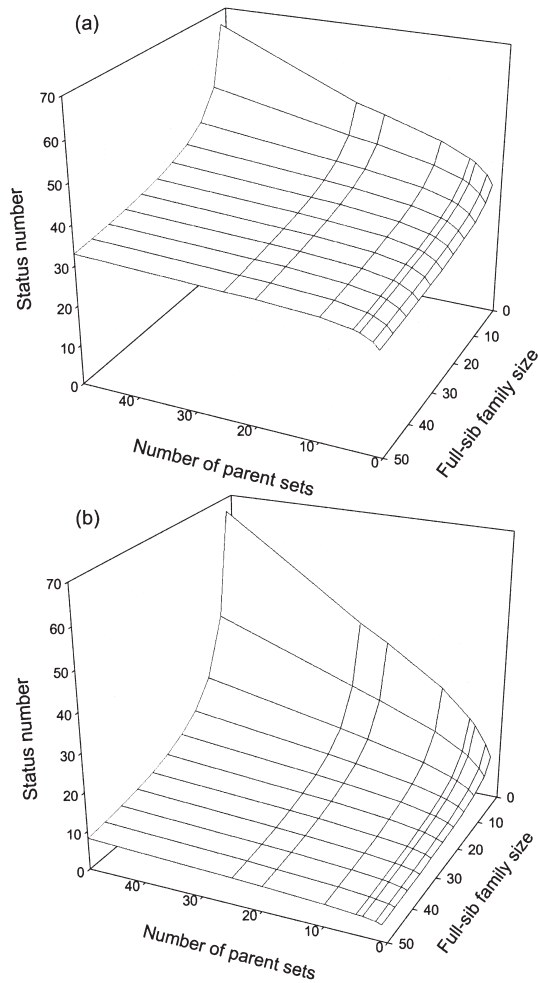


Fig. 4. – Status number against full-sib family size and disconnected set in selection from the population produced using half-diallel mating design. $n_p = n = 100$ (a) $t = 0.2, t_g = 0.1$ and (b) $t = 0.8, t_g = 0.4$.

efficiencies in status number of ND, FD and HD, compared to SP with maximum family size. It is also shown from eqns (2) and (4)–(7) that status number is negatively proportional to family size. Restriction on family's contribution counters loss of effective population size but worsens genetic gain in selection (WEI and LINDGREN, 1996; WEI *et al.*, 1997). A more efficient way is probably to balance s and n_f appropriately in the establishment of a population for selection.

Low t represents the phenotypic variance contributed by the family component. High t is usually associated with intense use of sibs' information in selection or predicting breeding values, indicating the genotypic variance contributed by the family component. This association is in terms of half-sib families, $0 < t \leq [1 + 0.25(s-1)]/s$ for phenotypes but $1 > t \leq [1 + 0.25(s-1)]/s$ for the corresponding BLUP breeding values. In terms of full-sib families, $0 < t \leq [1 + 0.5(s-1)]/s$ for phenotypes but $1 > t \geq [1 + 0.5(s-1)]/s$ for the corresponding BLUP breeding values. Both phenotypes and BLUP are identical at $t = [1 + 0.25(s-1)]/s$ for half-sib and $t = [1 + 0.5(s-1)]/s$ for full-sib, i.e. individual heritability=1 for both half-sib and full-sibs. Evidently, high t dramatically erodes N_s (WEI and LINDGREN, 1996; Figures 1–4), except at very small family sizes. It is well known that inclusion of sibs' information yields high gain. We conclude from this study, therefore, that high gain through the use of BLUP is obtained at the expense of status number.

A population census structure that is under a mating design rather than single-pair can differ greatly, according to parent number, sets and mating rate. Full-sib family number (n_f), for example, is a function of parent number (n_p), sets and mating rate. Small n_f is associated with large number of parent sets and low mating rate. The same minimum ($=0.5 n_p$) is reached when nested (ND), factorial (FD) and half-diallel (HD) converge at single-pair. Maximum n_f varies over mating designs. Given $n_p = 100$, for instance, the n_f for full FD and HD are 2500 and 4950, respectively, while it is 50 for SP. The maximum n_f for ND is 99 (Table 1). In practice, available resources also restrict family number (n_f) and size (s) or total initial

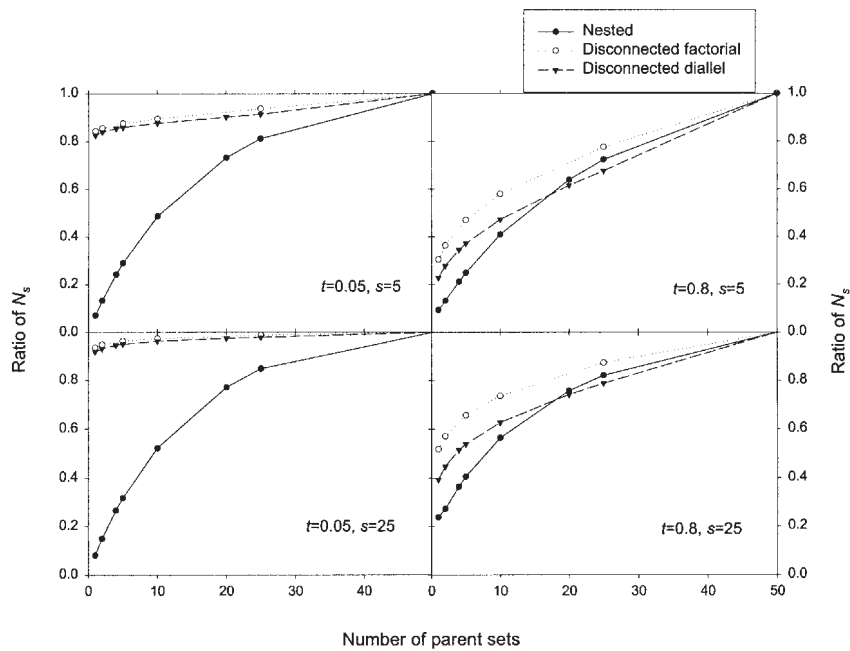


Fig. 5. – Efficiencies of nested, disconnected factorial and half-diallel relative to single pair against the number of parent sets for two t values and two full-sib family sizes. Assume $n_p = n = 100$ and $t_m = t_f = 0.5 t$.

population size ($N = n_f s$) and, therefore, influence the deployment of parents in the mating. Full FD and HD, or their variants with large n_f and s are neither economically affordable nor operationally feasible.

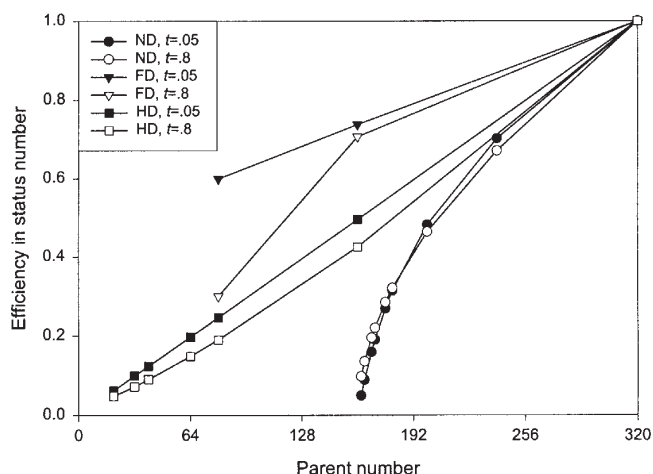


Fig. 6. – Efficiencies of nested (ND), disconnected factorial (FD) and half-diallel design (HD) as a function of parent number (n_p) for two t values given $N = 4000$ and $s = 25$. In ND, mating rate for each male parent is $N/(sn_p - N)$. In FD and HD, mating rate for each parent is $2N/(sn_p)$.

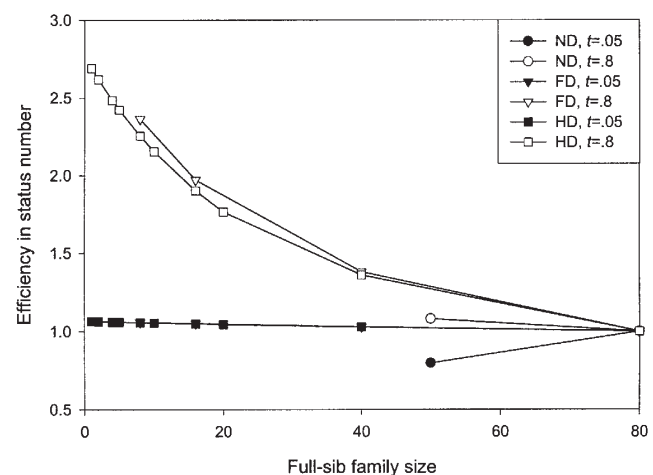


Fig. 7. – Efficiencies of nested (ND), disconnected factorial (FD) and half-diallel design (HD) as a function of full-sib family size (s) for two t values given $N = 4000$ and $n = n_p = 100$. In ND, mating rate for each male parent is $N/(sn_p - N)$. In FD and HD, mating rate for each parent is $2N/(sn_p)$.

Table 1. – Status number following selection from populations with minimum, maximum and suggested full-sib family number (n_f) for different t values and three mating designs – nested (ND), disconnected factorial (FD) and half-diallel (HD). Assume that $n_p = 100$ and $s = 30$.

	Minimum n_f			Maximum n_f			Suggested n_f							
	n_f	t			n_f	t			n_f	p_s	m_r	t		
		0.05	0.2	0.8		0.05	0.2	0.8				0.05	0.2	0.8
ND	50	46.8	36.1	11.9	99	3.8	3.8	3.1	75	25	3	39.8	30.5	9.9
FD	50	46.8	36.1	11.9	2500	44.1	29.7	6.6	100	25	2	46.4	35.3	10.5
HD	50	46.8	36.1	11.9	4950	43.2	27.2	5.0	150	25	3	46.0	34.1	9.5

Ps = number of parent sets; mr = mating rate

Single-pair (SP) is most efficient in status number, while complicated mating designs (ND, FD and HD) provide more sib information than does a simple one (SP) from the offspring populations. Use of sib information gives a close prediction of breeding value and, thus, of a high gain. On the other hand, high status number occurs with small n_f and s , given n_p ; but large n_f and s increase selection intensity and the efficiency of utilizing within-family variation in selection. As SP with minimum n_f is the extreme case of ND, FD and HD, it is probably wise to consider the appropriate variants of ND, FD and HD for a sound balance between status number and gain. A proper consideration of family number and size is also necessary to make breeding operations affordable and ensure high gain and status number. Without considering status number, VAN BUIJTENEN and BURDON (1990) showed that high gain could be obtained at relatively low mating rate (several crosses per parent). NAMKOONG and ROBERDS (1974) concluded that no more than six full-sib families per half-sib in nested and diallel designs could be used to efficiently estimate both dominance and additive genetic variances. From their work, together with the findings in this study, it seems that mating rates with 3-5 crosses per parent could probably provide optimum choices in terms of efficient sib information, census population structure for status number and affordability in breeding programmes.

Conclusions

Status number following selection is influenced by mating designs and their interactions with selection methods and population census structure in terms of parent number and grouping, mating rate, population size, and family number and size. In general, single-pair mating is most efficient as regards status number, followed by factorial and half-diallel mating. Nested mating design is least efficient. The choice of parent number, grouping and mating rate, and family size can effectively improve the efficiency of a mating design. Status number under a mating design can be maintained by deploying large parent numbers and groups, a low mating rate, and small family sizes. Factorial and half-diallel mating designs with low mating rate are recommended for obtaining acceptable status numbers, and information on relatives, for the prediction of breeding values.

Literature

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