

Exact Inbreeding Coefficient and Effective Size of Finite Populations Under Partial Sib Mating

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ABSTRACT

An exact recurrence equation for inbreeding coefficient is derived for a partially sib-mated population of N individuals mated in $N/2$ pairs. From the equation, a formula for effective size (N_e) taking second order terms of $1/N$ into consideration is derived. When the family sizes are Poisson or equally distributed, the formula reduces to $N_e = [(4 - 3\beta)N/(4 - 2\beta)] + 1$ or $N_e = [(4 - 3\beta)N/(2 - 2\beta)] - 8/(4 - 3\beta)$, approximately. For the special case of sib-mating exclusion and Poisson distribution of family size, the formula simplifies to $N_e = N + 1$, which differs from the previous results derived by many authors by a value of one. Stochastic simulations are run to check our results where disagreements with others are involved.

MOST analyses on inbreeding and effective size assume that mating is at random. Nonrandom mating, however, is commonly found in natural populations of plants (JAIN 1976) and animals (MOEHLMAN 1987). In domestic animal or plant breeding programs, nonrandom mating is deliberately utilized by breeders as an important method to change the genetic constitution of the populations; matings between relatives are either purposely carried out or avoided for specific breeding purposes.

Some previous work has considered the effect of nonrandom mating on effective population size (WRIGHT 1951; CROW and MORTON 1955; KIMURA and CROW 1963b; ROBINSON and BRAY 1965; CROW and DENNISTON 1988; POLLAK 1988). Some formulae on effective size derived by the above studies have been shown to be incomplete or incorrect by a recent analysis of CABALLERO and HILL (1992). For stable census number, N (half in each sex), the equation has been expressed as

$$N_e = \frac{N(4 - 3\beta)}{S_k^2 + 2 - 2\beta}, \quad (1)$$

where β is the proportion of full sib matings and S_k^2 is the variance of family size. When $S_k^2 = 2/3$ is included into (1), the result is $N_e = 3N/2$, irrespective of β . Equation 1 gives estimates of N_e accurate enough for large values of N , though it is only a first order approximation. As will be shown, the higher order terms become important for small populations with the variance of family sizes far from the value of $2/3$ and (or) a high proportion of sib matings. In practical domestic animal and captive animal populations, effective sizes are generally small and (1) may result in a large bias.

Furthermore, most previous work has concentrated on the evaluation of effective size. We know, however, in nonrandom mating populations effective size is de-

finied as the limiting value (over time) of the rate of increase of inbreeding. In practice, most populations do not maintain the same characteristics for such a long time, and in breeding programs interest is more likely concentrated on early generations. It has been shown (KIMURA and CROW 1963a; COCKERHAM 1970) that avoiding early inbreeding may have high final rates of inbreeding. For these reasons we concur with WRIGHT (1951) and ROBINSON and BRAY (1965) in deriving the exact recurrence equations for the probability of identity by descent. We differ from them, however, in that we consider both partial sib mating and progeny distribution simultaneously in our model. We also correct their equations for inbreeding and effective size when the number of progeny per family is Poisson distributed.

RECURRENCE FORMULAS FOR INBREEDING COEFFICIENT

Throughout the paper the assumptions are discrete generations, stable census population size with equal numbers of male and female individuals in each generation, and autosomal inheritance involving genes that do not affect viability or reproductive ability so that natural selection is not operating to eliminate them.

In deriving the formula for F_t (*i.e.*, the inbreeding coefficient in generation t), coefficient de parenté (MALÉCOT 1948), translated as coancestry or coefficient of parentage (KEMPTHORNE 1957), is utilized. This coefficient can be defined as the probability that two genes at a given locus, one taken at random from each of two randomly selected individuals from the population, are identical by descent. Generations are measured from a hypothetically infinite base population (generation zero) in which inbreeding coefficients and coancestry of all individuals are zero.

If we assume that, of the $N/2$ mating pairs formed

TABLE 1
Probability of a full sib or non-sib pair of two individuals from each or both sexes

Kind of pairs	Total no. of pairs	No. of full-sibs	No. of non-sibs	Frequency of full-sibs	Frequency of non-sibs
Male with female: mated	$\frac{N}{2}$	X	$\frac{N - 2X}{2}$	$\beta = \frac{2X}{N}$	$1 - \beta = \frac{N - 2X}{N}$
Male with female: unmated	$\frac{N(N - 2)}{4}$	$\frac{(1 - \beta + \theta)N - 2\theta}{2}$	$\frac{N^2 - 2(2 - \beta + \theta)N + 4\theta}{4}$	$\frac{2(1 - \beta + \theta)N - 4\theta}{N(N - 2)}$	$\frac{N^2 - 2(2 - \beta + \theta)N + 4\theta}{N(N - 2)}$
Male with male	$\frac{N(N - 2)}{8}$	$\frac{(N - 2)V_m}{4}$	$\frac{(N - 2)(N - 2V_m)}{8}$	$\frac{2V_m}{N}$	$\frac{N - 2V_m}{N}$
Female with female	$\frac{N(N - 2)}{8}$	$\frac{(N - 2)V_f}{4}$	$\frac{(N - 2)(N - 2V_f)}{8}$	$\frac{2V_f}{N}$	$\frac{N - 2V_f}{N}$

from the N individuals in each generation, X are full sib pairs chosen at random from the total possible full sib matings, then the proportions of full sib mating and non-sib mating will be $\beta = 2X/N$ and $1 - \beta = 1 - 2X/N$, respectively.

In the population with $N/2$ families and m_i male and f_i female progeny per family, the number of total possible full sib mating pairs is $\sum_{i=1}^{N/2} m_i f_i$, which, for stable population size with $\bar{m} = \bar{f} = 1$, gives $[(1 + \theta)N - 2\theta]/2$, where θ is the covariance of numbers of male and female progeny per family. Of the total possible full sib mating pairs, $X = \beta N/2$ are pairs of full sibs actually mated, thus $[(1 - \beta + \theta)N - 2\theta]/2$ are full sib pairs not mated. Analogously, the total number of possible mating pairs is $N^2/4$, of which $N/2$ are pairs actually mated and $N(N - 2)/4$ are not mated. So the probability that a pair of male and female individuals are full sibs given that they are not mated is $[2(1 - \beta + \theta)N - 4\theta]/[N(N - 2)]$. Similarly, the probability that a pair of two male or female individuals are full sibs can also be derived, in which the variances of the numbers of male progeny (V_m) and of female progeny (V_f) per family are involved. All these probabilities are listed in Table 1.

Let $G_{FS,t}$ and $G_{NS,t}$ be the coancestry of full sib and non-sib pairs respectively in generation t . The average inbreeding coefficient in generation t is

$$F_t = G_{t-1} = \beta G_{FS,t-1} + (1 - \beta) G_{NS,t-1}. \quad (2)$$

The corresponding pedigrees for full sib and non-sib

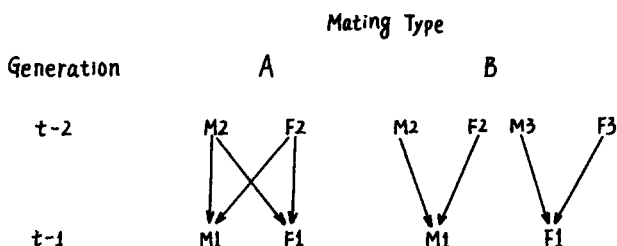


FIGURE 1.—Pedigrees for full sib (A) and non-sib (B) matings.

matings are diagrammed in Figure 1. Given full sib mating, the coancestry of M1 and F1 in generation $t - 1$ is

$$G_{FS,t-1} = \frac{1}{4} \left[\frac{1 + F_{M2}}{2} + 2G_{M2F2,t-2} + \frac{1 + F_{F2}}{2} \right] = \frac{1}{4} [2F_{t-1} + F_{t-2} + 1]. \quad (3)$$

For non-sib mating, using the probabilities listed in Table 1, we get

$$G_{NS,t-1} = \frac{1}{4} [G_{M2M3,t-2} + G_{M2F3,t-2} + G_{M3F2,t-2} + G_{F2F3,t-2}] = \frac{1}{4} \left[\frac{2V_m}{N} G_{FS,t-2} + \frac{N - 2V_m}{N} G_{NS,t-2} \right] + \frac{1}{2} \left[\frac{2(1 - \beta + \theta)N - 4\theta}{N(N - 2)} G_{FS,t-2} + \frac{N^2 - 2(2 - \beta + \theta)N + 4\theta}{N(N - 2)} G_{NS,t-2} \right] + \frac{1}{4} \left[\frac{2V_f}{N} G_{FS,t-2} + \frac{N - 2V_f}{N} G_{NS,t-2} \right] = \frac{N + V_m + V_f + 2\theta}{2N} G_{FS,t-2} + \frac{2N - V_m - V_f - 2\theta}{2N} G_{NS,t-2} - \frac{1}{N - 2} F_{t-1}. \quad (4)$$

When (3) and (4) are substituted into (2), we therefore find, after some algebra, that

$$F_t = \{4[(2 + \beta)N^2 - (6 + S_k^2)N + 2S_k^2]F_{t-1} - 2[\beta N^2 - (2 + S_k^2)N + 2S_k^2]F_{t-2} - [2\beta N^2 - (2 + 2\beta + S_k^2)N + 2S_k^2]F_{t-3} + (2 - 2\beta + S_k^2)N - 2S_k^2\} / [8N(N - 2)], \quad (5)$$

where the variance of family size is $S_k^2 = V_m + 2\theta + V_f$.

It is evident that $F_0 = F_1 = 0$ and $F_2 = \beta/4$, and $F_t (t \geq 3)$ can be calculated using (5).

Equation 5 is a general form of the exact recurrence equation for the inbreeding coefficient of a population with partial sib mating. Several simple equations can be derived from it.

Case a: If the numbers of male and female progeny per family are Poisson distributed, $V_m = V_f = 1$ and $\theta = 0$, thus $S_k^2 = 2$. Then we get

$$F_t = \{2[(2 + \beta)N^2 - 8N + 4]F_{t-1} - [\beta N^2 - 4N + 4]F_{t-2} - [\beta N^2 - (2 + \beta)N + 2]F_{t-3} + (2 - \beta)N - 2\} / [4N(N - 2)]. \quad (6)$$

For the cases of random mating ($\beta = 2/N$) and non-sib mating ($\beta = 0$), (6) reduces to

$$F_t = F_{t-1} - (2F_{t-1} - F_{t-2} - 1) / 2N \quad (7)$$

and

$$F_t = F_{t-1} - \frac{N - 1}{2N(N - 2)} \times (4F_{t-1} - 2F_{t-2} - F_{t-3} - 1), \quad (8)$$

respectively.

Equation 6 is different from the recurrence equation derived by WRIGHT (1951) and POLLAK (1988) that can be expressed as (in our notation)

$$F_t = [2(2N + \beta N - 4)F_{t-1} - (\beta N - 4)F_{t-2} - (\beta N - 2)F_{t-3} + 2] / 4N. \quad (9)$$

For the cases of random mating and non-sib mating, (9) reduces to (7) and

$$F_t = F_{t-1} - (4F_{t-1} - 2F_{t-2} - F_{t-3} - 1) / 2N, \quad (10)$$

respectively. Equations 7 and 10 are also derived by ROBINSON and BRAY (1965) separately for the two cases. As will be explained, (9) and (10) are incorrect because of an incorrect probability used in their derivation.

Case b: If one male and one female progeny are selected at random from each family, $V_m = V_f = \theta = 0$. Then $S_k^2 = 0$ and

$$F_t = \{2[(2 + \beta)N - 6]F_{t-1} - (\beta N - 2)F_{t-2} - (\beta N - 1 - \beta)F_{t-3} + 1 - \beta\} / (4N - 8). \quad (11)$$

Equation 11 reduces to

$$F_t = F_{t-1} - (F_{t-3} - 1) / 4N \quad (12)$$

and

$$F_t = F_{t-1} - (4F_{t-1} - 2F_{t-2} - F_{t-3} - 1) / (4N - 8), \quad (13)$$

respectively for the cases of random mating and non-sib mating.

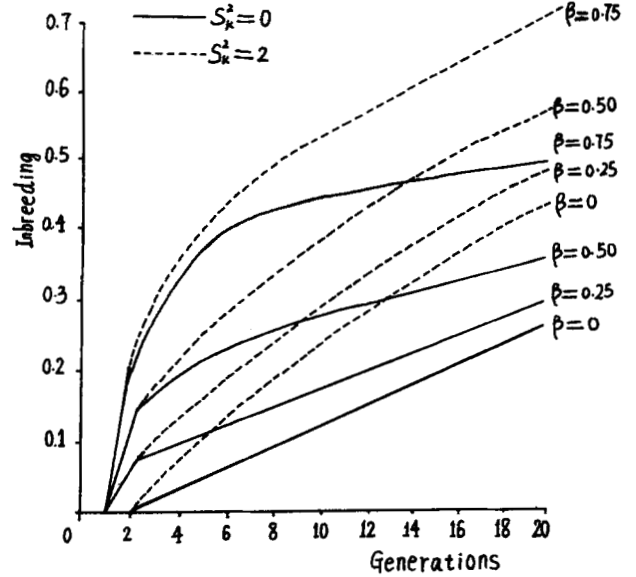


FIGURE 2.—The inbreeding coefficient ($N = 16$). Both male and female progeny are Poisson distributed ($S_k^2 = 2$), plotting (6) (—). One male and one female progeny are selected from each family ($S_k^2 = 0$), plotting (11) (---).

The effect of partial sib mating on the inbreeding coefficient over the first 20 generations for $N = 16$ is shown in Figure 2. In any case, the inbreeding coefficients for any generation increase as the value of β increases. However, differences among the two sets of lines are evident. With male and female progeny Poisson distributed (case a), the lines diverge slightly as the generation number increases, while, with one male and one female progeny from each family (case b), the lines converge slightly and eventually cross; smaller values of β give lower inbreeding coefficients in the first few generations than larger values, but in later generations the order is reversed. These results are generally in accordance with those of ROBERTSON (1964). For case b, the generation at which a reversal takes place for different values of β can be calculated from (11). For example, the line for $\beta = 0.75$ will cross the lines for $\beta = 0.5, 0.25$ and 0 in generations 89, 83 and 80, respectively.

Figure 2 also shows that in the first few generations the inbreeding coefficient for $S_k^2 = 2$ with a smaller value of β is lower than that for $S_k^2 = 0$ with a larger value of β , but in later generations the order is reversed. The generation in which the reversal takes place is dependent on the values of β and the value of N and can be determined by (6) and (11). For example, the line for $S_k^2 = 2$ with $\beta = 0$ will cross the lines for $S_k^2 = 0$ with $\beta = 0.25, 0.5$ and 0.75 in generations 7, 15 and 29, respectively.

Results for other values of N are similar to those shown. When the value of S_k^2 is larger and smaller than $2/3$, the results are similar to those of cases a and b, respectively.

EFFECTIVE POPULATION SIZE

An estimate of effective size may be obtained by a consideration of the panmictic index ($P = 1 - F$). WRIGHT (1931) has shown that, after some generations under a particular system, the relative rate of change of P (*i.e.*, $\Delta P/P$) becomes approximately constant. Letting x be the asymptotic rate of change of P , the value of P in generation t will be $P_t = xP_{t-1} = x^2P_{t-2} = x^3P_{t-3}$. Substituting the relation into (5), we get

$$8N(N - 2)x^3 - 4[(2 + \beta)N^2 - (6 + S_k^2)N + 2S_k^2]x^2 + 2[\beta N^2 - (2 + S_k^2)N + 2S_k^2]x + 2\beta N^2 - (2 + 2\beta + S_k^2)N + 2S_k^2 = 0. \quad (14)$$

The Equation has three solutions; it is the largest one of the solutions lying between zero and one that is required. By definition, $\Delta F = 1 - x = 1/2N_e$, so the general formula for effective size is obtained, to the second order of $1/N$, as the following

$$\frac{1}{N_e} = \frac{2 - 2\beta + S_k^2}{(4 - 3\beta)N} - \frac{2S_k^2}{(4 - 3\beta)N^2} + \frac{(2 - 3S_k^2)(2 - 2\beta + S_k^2)}{(4 - 3\beta)^2N^2} + \frac{(4 - \beta)(2 - 2\beta + S_k^2)^2}{(4 - 3\beta)^3N^2}. \quad (15)$$

Several simple forms can be derived from (15).

1. When N is large, ignoring second order terms of $1/N$, (15) reduces to (1).

2. When N is small or a more accurate estimate of N_e is required, second order terms of $1/N$ should be considered. With family size Poisson distributed, (15) reduces to

$$N_e = \frac{(4 - 3\beta)N}{4 - 2\beta} + \frac{8 - 5\beta}{(2 - \beta)^2} - \frac{4 - \beta}{4 - 3\beta} \approx \frac{(4 - 3\beta)N}{4 - 2\beta} + 1. \quad (16)$$

It is clear that, in this case, N_e is a monotone decreasing function of β .

For the cases of random mating and non-sib mating, (16) reduces to

$$N_e = N + \frac{1}{2} \quad (17)$$

and

$$N_e = N + 1, \quad (18)$$

respectively.

From WRIGHT-POLLAK's Equation 9, the effective size can be derived (to the second order of $1/N$) as

$$N_e = (4 - 3\beta)N/4 + 2, \quad (19)$$

which reduces to (17) and

$$N_e = N + 2, \quad (20)$$

respectively for random mating and non-sib mating. Equation 20 was also derived by ROBINSON and BRAY (1965) and JACQUARD (1971), which always differs from (18) by a value of approximately one irrespective of the census population size. The reason for the difference between the equations is explained and our results are verified by a simulation study in the next part of the paper.

3. As in 2 but with equal family sizes for each sex, (15) reduces to

$$N_e = \frac{(4 - 3\beta)N}{2 - 2\beta} - \frac{8}{4 - 3\beta}, \quad (21)$$

and N_e is a monotone increasing function of β . Equation 21 can be simplified approximately to

$$N_e = 2N - 1 \quad (22)$$

and

$$N_e = 2N - 2, \quad (23)$$

respectively for random mating and non-sib mating.

Equation 22 is in agreement with previous work. If family sizes are equal, JACQUARD (1971) concluded that there was no reduction in effective size if full sib matings were avoided, whereas ROBINSON and BRAY (1965) found the effective size to be reduced by one, in agreement with our (23).

SIMULATION

Stochastic simulations have been carried out to check the equations of the present study that are in discrepancy with those of the previous studies. Two distinct operations are involved in the simulation. First, the N individuals (half of each sex) that are to be parents must be selected, and second, having been chosen, they must be mated in $N/2$ pairs. Selection schemes are random selection for both sexes (family size of male or female progeny following a multinomial distribution with an average number of one) and equal family sizes for both sexes. Selected individuals are either mated at random (random mating) or by crossing a given number of full sibs whenever possible, otherwise at random (partial sib mating).

N individuals are sampled from a hypothetically infinite base population that is referred to as generation zero. Thus inbreeding coefficients of and coancestry between sampled individuals are zero. In each generation, pedigrees of all the N individuals are recorded and inbreeding coefficients and coancestry calculated. When the asymptotic rate has been reached (the generations required depend on the population size, selection and mating schemes), observed effective sizes are calculated from the rate of inbreeding. Each simu-

TABLE 2

Observed (N_e) and predicted (N_{eCH} , N_{eWP} , N_{eW}) effective size for different mating and selection schemes when $N = 16$

Selection scheme	NFS^a	$N_e \pm SE$	N_{eCH}	N_{eWP}	N_{eW}^b
Random selection for both sexes ($S_k^2 = 2$)	0 (0.00)	16.81 ± 0.32	16.00	18.00	17.00
	1 (1.00)	16.24 ± 0.65	15.47	16.50	16.47
	2 (1.98)	15.89 ± 0.53	14.87	15.03	15.87
	3 (2.88)	15.11 ± 0.52	14.24	13.68	15.24
Equal family sizes for both sexes ($S_k^2 = 0$)	0 (0.00)	30.08 ± 0.10	32.00		30.00
	2 (2.00)	32.45 ± 0.38	34.67		32.21
	4 (4.00)	37.80 ± 1.32	40.00		36.80
	6 (6.00)	51.32 ± 2.21	56.00		51.43

^a NFS , intended and actually performed (in parentheses) number of full sib matings. When $NFS = 1$, mating is at random; otherwise the mating schemes are partial sib mating.

^b N_{eCH} , N_{eWP} and N_{eW} are obtained using (1), (19) and (16), or (21), respectively.

lation is run for 100 generations and 1000 (for random selection) or 3000 (for equal family size selection) replicates.

Table 2 shows the observed values of effective size (N_e), predicted values by CABALLERO and HILL's Equation 1 [denoted as N_{eCH}], WRIGHT-POLLAK's Equation 19 (denoted as N_{eWP}) and our (16) and (21) (denoted as N_{eW}), as well as the number of full sib matings achieved for different mating and selection schemes when $N = 16$. As clearly seen from Table 2, results from (16) and (21) and simulations are in very close agreement. CABALLERO and HILL's equation underestimates effective size for the case of large values of variance of family sizes ($S_k^2 > 2/3$). When the numbers of both male and female progeny are Poisson distributed, the underestimation is approximately one from the exact value irrespective of the values of N and β . When the variance of family size is zero, however, (1) overestimates effective size. The overestimation is independent of population size but increases rapidly with the increment of the value of β . These results are expected by a comparison between (1), (16) and (21). WRIGHT-POLLAK's equation gives correct estimations of effective size only when mating is at random; it overestimates and underestimates effective size when $\beta < 2/N$ and $\beta > 2/N$, respectively. By a comparison between (19) and (16), we can see that the larger the values of β

and N , the more serious is the underestimation of N_e by (19).

Another formula for effective size derived by CABALLERO and HILL (1992) is

$$N_e = \frac{4N}{2(1 - \alpha) + S_k^2(1 + 3\alpha)}, \quad (24)$$

where α is the departure from Hardy-Weinberg proportions. Though it is also a first order approximation, it generally gives a more satisfactory estimation of N_e than (1). It is well known that $\alpha = F_{IS} - \alpha_R$, where $\alpha_R = -1/2N - 1/2T$ is the value of α for the random mating case with multinomial distribution of family size and T scored individuals (ROBERTSON 1965); F_{IS} is the correlation of uniting gametes relative to gametes drawn at random from the population. When N is large, $\alpha \approx F_{IS} = \beta/(4 - 3\beta)$ (GHAI 1969). Substituting the relation into (24), we therefore get (1).

The results of a simulation study by CABALLERO and HILL (1992) are listed in Table 3, in which $N_{e\alpha}$ and N_{eW} are the predicted values of N_e from (24) and (16), and other symbols are explained in Table 2. It can be seen that in any case our (16) gives a slightly better estimation than either (24) or (1). For smaller population sizes and larger proportions of sib matings, the difference may be more evident.

Equation 20 derived by WRIGHT (1951), ROBINSON and BRAY (1965), JACQUARD (1971) and POLLAK

TABLE 3

Observed (N_e) and predicted (N_{eWP} , N_{eCH} , $N_{e\alpha}$, N_{eW}) effective size for populations with size N and the number of full sib matings NFS

N	NFS	α	$N_e \pm SE$	N_{eWP}	$N_{e\alpha}$	N_{eCH}	N_{eW}
64	1.0	-0.011	64.0 ± 0.07	66.2	64.7	63.5	64.5
64	15.5	0.159	54.5 ± 0.05	43.3	55.2	53.8	54.8
200	1.0	-0.005	200.4 ± 0.22	202.8	200.9	199.5	200.5
200	47.8	0.182	170.0 ± 0.46	129.4	169.2	168.6	169.6

Figures in the first six columns are cited from CABALLERO and HILL (1992). NFS , number of full sib matings achieved; α , observed departure from the Hardy-Weinberg proportions.

TABLE 4

Observed and predicted values of effective size and the probability that two individuals from each sex are full sibs given that they are not mated for the case of random selection and full sib matings excluded

N	Probability			Effective size		
	Observed	$Y = 2/N$	$Y = 2/(N - 2)$	$N_e \pm SE$	$N_e = N + 2$	$N_e = N + 1$
8	0.3210	0.2500	0.3333	8.93 ± 0.09	10	9
16	0.1407	0.1250	0.1429	16.81 ± 0.32	18	17
32	0.0696	0.0625	0.0667	33.04 ± 0.18	34	33

(1988) for the case of random selection and full sib mating exclusion has been widely cited (HILL 1972; FALCONER 1981, p. 64; ROCHAMBEAU and CHEVALET 1990). The equation is, however, incorrect. In the derivation of (9) or (10), they assumed that the probability that two individuals, one from each sex, are full sibs, given that they are not mated, was $2/N$, a result that is true for random mating but not for nonrandom mating. As shown in Table 1, the correct corresponding probability is $Y = [2(1 - \beta + \theta)N - 4\theta] / [N(N - 2)]$, which reduces to $Y = 2/(N - 2)$ when selection is at random ($\theta = 0$) and full sib matings are excluded ($\beta = 0$). In Table 4 values for Y and effective sizes calculated as stated above from (18) and (19) or (20) are compared with their simulated results for various values of N . It is clear that, because of the incorrect probability used, (19) or (20) always overestimate effective size by approximately one, regardless of the value of N .

DISCUSSION

We have given a general and exact recurrence equation for the inbreeding coefficient in populations with partial sib mating. The equation is particularly important for cases where inbreeding coefficients in early generations are more relevant. A uniform rate of inbreeding of $1/2N_e$ per generation is attained only in the later stages of the early phase of an erratic increase of inbreeding in partially sib-mated populations. The higher the proportion of full sib matings, the more generations are required before the asymptotic rate of inbreeding is attained. Assuming a uniform rate of inbreeding from the outset may result in a large bias, especially with large values of β . When the variance of family sizes is small enough, avoiding sib matings results in a higher final rate of inbreeding and vice versa. ROBERTSON (1964) explained why with $S_k^2 = 0$, the smaller the proportion of inbred matings, the higher the final rate of inbreeding. Thus the ranking of populations on the basis of effective size may be opposite to the ranking based on inbreeding coefficients over early generations.

If the long-term behavior of inbred populations is required, then effective size may be convenient and also sufficient. Most previous work centers on this

simple parameter. However, the equations for effective size of partial inbreeding populations derived in various studies (*e.g.*, CROW and DENNISTON 1988; POL-LAK 1988) have been shown to be incomplete or incorrect by a recent study of CABALLERO and HILL (1992). It is shown that, regardless of population census number and the value of β , CABALLERO and HILL's equation always underestimates effective size by a value of about one when family sizes are Poisson distributed. On the contrary, when the variance of family sizes is zero, their equation gives an overestimation. In this case the absolute value of bias from the exact value is also independent of population census number but is sensitive to the changes of the value of β . It is clear from the present study that, when breeding schemes are run for short periods, recurrence equations should be utilized for predicting inbreeding coefficients; when population sizes are small, accurate formulae for N_e taking second order terms of $1/N$ into consideration should be used, especially when S_k^2 is small and β is large.

LITERATURE CITED

- CABALLERO, A., and W. G. HILL, 1992 Effective size of nonrandom mating populations. *Genetics* **130**: 909-916.
- COCKERHAM, C. C., 1970 Avoidance and rate of inbreeding, pp. 104-127 in *Mathematical Topics in Population Genetics*, edited by K. KOJIMA. Springer-Verlag, New York.
- CROW, J. F., and N. E. MORTON, 1955 Measurement of gene frequency drift in small populations. *Evolution* **9**: 202-214.
- CROW, J. F., and C. DENNISTON, 1988 Inbreeding and variance effective population numbers. *Evolution* **42**: 482-495.
- FALCONER, D. S., 1981 *Introduction to Quantitative Genetics*, Ed. 2, Longman, New York.
- GHAJ, G. L., 1969 Structure of populations under mixed random and sib mating. *Theor. Appl. Genet.* **39**: 179-182.
- HILL, W. G., 1972 Estimation of genetic change. I. General theory and design of control populations. *Anim. Breed. Abst.* **40**: 1-15.
- JACQUARD, A., 1971 Effect of exclusion of sib-mating on genetic drift. *Theor. Popul. Biol.* **2**: 91-99.
- JAIN, S. K., 1976 The evolution of inbreeding in plants. *Annu. Rev. Ecol. Syst.* **7**: 469-495.
- KEMPTHORNE, O., 1957 *An Introduction to Genetic Statistics*. John Wiley and Sons, New York.
- KIMURA, M., and J. F. CROW, 1963a On the maximum avoidance of inbreeding. *Genet. Res.* **4**: 399-415.
- KIMURA, M., and J. F. CROW, 1963b The measurement of effective population number. *Evolution* **17**: 279-288.
- MALÉCOT, G., 1948 *Les Mathématiques de l'hérédité*. Masson et Cie., Paris.
- MOEHLMAN, P. D., 1987 Social organization in jackals. *Am. Sci.* **75**: 366-375.

- POLLAK, E., 1988 On the theory of partially inbreeding finite populations. II. Partial sib mating. *Genetics* **120**: 303–311.
- ROBERTSON, A., 1964 The effect of non-random mating within inbred lines on the rate of inbreeding. *Genet. Res.* **5**: 164–167.
- ROBERTSON, A., 1965 The interpretation of genotypic ratios in domestic animal populations. *Anim. Prod.* **7**: 319–324.
- ROBINSON, P., and D. F. BRAY, 1965 Expected effects on the inbreeding and rate of gene loss of four methods of reproducing finite diploid populations. *Biometrics* **21**: 447–458.
- ROCHAMBEAU, H. DE, and C. CHEVALET, 1990 Genetic principles of conservation. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production*, **XIV**: 434–442.
- WRIGHT, S., 1931 Evolution in Mendelian populations. *Genetics* **16**: 97–159.
- WRIGHT, S., 1951 The genetical structure of populations. *Ann. Eugen.* **15**: 323–354.

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