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Inbreeding under a cyclical mating system

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Summary. General recursion formulae for the coefficient of inbreeding under a cyclical mating system were derived in which one male and one female are selected from each of the n families per generation (population size $N = 2n$). Each male is given the family number of his sire in each generation, while his mate comes from another family, varying systematically in different generations. Males of the r-th family in generations $1, 2, 3, \ldots, t' = n - 1$ within each cycle mate with females from families $r + 1$, $r + 2$, $r + 3$, …, $r + t'$ to produce generations $2, 3, 4, \ldots, t' + 1 = 1$, respectively. The change in heterozygosity shows a cyclical pattern of rises and falls, repeating in cycles of $n - 1$ generations. The rate of inbreeding oscillates between $< -3\%$ to $> 6\%$ in different generations within each cycle, irrespective of the population size. The average rate of inbreeding per generation is approximately $1/[4N - (\mathrm{Log}_2 N + 1)]$, which is the rate for the maximum avoidance of inbreeding. The average inbreeding effective population size is approximately $2N - 2$.

Key words: Cyclical mating – Rate of inbreeding – Population size

Introduction

It is often desirable to keep the rate of inbreeding in control populations as low as possible. In addition to equalizing the number of progeny per parents, further reduction in the rate of inbreeding can be achieved by imposing the restriction of avoiding matings between individuals which are related to a specific degree (Wright 1921, 1965; Robinson and Bray 1965; Cockerham 1970).

Splitting populations into several inbred lines, or using mating systems which lead to a lower final rate of approach to homozygosity at the expense of the greater initial rate (Kimura and Crow 1963; Robertson 1964) are not easily applicable to control populations in farm and laboratory animals because it would be rather difficult to overcome inbreeding depression without high selection pressure (Hill 1972).

The cyclical mating systems are easy to follow at the practical level, and have been in use for some time; for example, in the mouse colonies of the Agriculture Canada Research Station at Lacombe, Alberta (since 1961), and the University of Melbourne, Australia (Beilharz 1972, 1982), and in some swine populations in Australia (Beilharz, personal communication). One of the advantages of these systems over the maximum avoidance system (Wright 1921, 1965) is that the former can easily be used with any number of breeding pairs, while the latter is convenient to use only when size of breeding population is an integral power of two. Cockerham (1970) briefly discussed cyclical matings as a class of mating systems which do not form permanent sublining. Beilharz (1982) used a cyclical mating system and computed the inbreeding coefficient of the first 25 generations in a population of size 40 by the method of co-ancestry, and found a pattern of rises and falls in the inbreeding coefficient.

The objective of this study was to compute the theoretical rate of inbreeding and inbreeding effective population size under a cyclical mating system. It is assumed that the generations do not overlap, and each pair leaves only two progeny per generation, and, therefore, the population size remains constant.

Cyclical mating system

Suppose one male and one female are selected from each of the n families per generation (population size $N = 2n$). The foundation pairs are given a family number from 1 to n. One of the mates, say male, is

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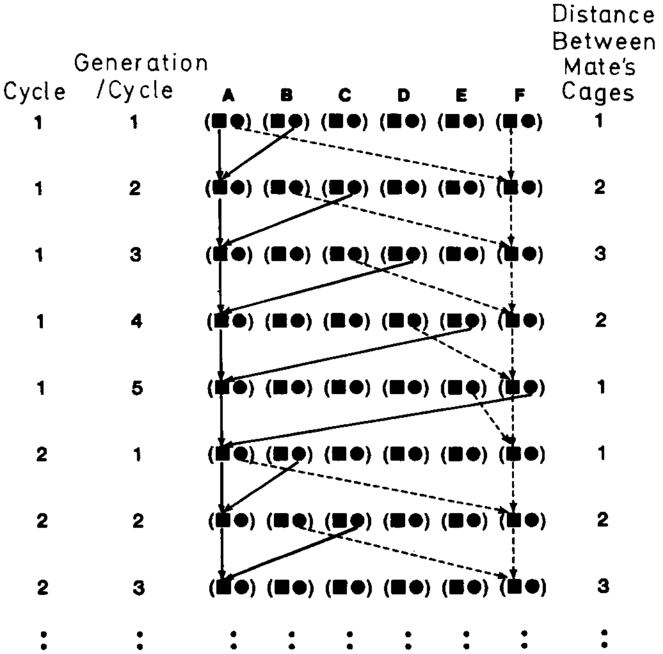

Fig. 1. Cyclical mating system in a population of size 12. Only the parents of individuals born in cages A and F are shown

given the family number of his sire in each generation, while his mate comes from another family, varying systematically in different generations. Males of the r-th family in generations $1, 2, 3, \ldots, t'$ within each cycle $(t' = n - 1)$ mates with females from families $r + 1$, $r + 2$, $r + 3, \ldots, r + t'$ to produce generations $2, 3, 4, \ldots, t' + 1 = 1$, respectively. The cycle is repeated after each $n - 1$ generations. Figure 1 shows the cyclical mating system for a population with six pairs. This system is, of course, one of many possible types of cyclical matings (Cockerham 1970).

Recurrence equations

When two individuals A and B are related, they may carry identical copies of genes received from their common ancestors at any randomly selected locus, i.e., the genes are identical by descent (Malecot 1969). The coefficient of identity of individuals A and B, $\Phi(A, B)$, is defined as the probability that a gene taken at random from A is identical by descent with a gene at the same locus taken at random from B. The coefficient of identity of an individual by itself, $\Phi(A, A)$, is the probability that two genes randomly selected, one after the other, from the same locus in individual A, are identical by descent. The coefficient of inbreeding of individual $A\,(f(A))$ is the probability that the two genes at a randomly selected locus in individual A are identical by descent. Considering a neutral autosomal gene in a dioecious organism in which Mendelian segregation occurs, the basic equations defining the genetic relationship between individuals are:

$$f(A) = \Phi(F_1, M_1) \tag{1}$$

$$\Phi(A, A) = (1/2)[1 + \Phi(F_1, M_1)] = (1/2)[1 + f(A)] \tag{2}$$

$$\begin{aligned}\Phi(\text{Full-sibs}) = {}& (1/4)[2\,\Phi(F_1, M_1) + \Phi(F_1, F_1) \\ & + \Phi(M_1, M_1)] = (1/2)\,\{(1/2)[f_{(t-1)} + 1] + \Phi(F_1, M_1)\}\end{aligned} \tag{3}$$

$$\begin{aligned}\Phi(A, B) = {}& (1/4)[\Phi(F_1, F_2) + \Phi(F_1, M_2) \\ & + \Phi(M_1, M_2) + \Phi(M_1, F_2)]\end{aligned} \tag{4}$$

Where F_1, F_2, M_1 and M_2 are fathers and mothers of individuals A and B respectively. For the unrelated individuals, or those in the original generation whose genealogical relationships are not known, it is assumed that $\Phi(A, B) = 0$, and $\Phi(A, A) = 1/2$.

The recurrence equations 1 to 4 connecting homozygosity (f) and coefficients of identity (Φ) in successive generations were applied to populations of various sizes subjected to continued cyclical mating system. The results showed that the equations for f and Φ's are not the same in all generations, but two cyclic patterns were detected. Firstly, the set of equations are repeated after a cycle length of $j = n - 1$ generations, i.e., equations for generations 1 to $n - 1$, n to $2n - 2$, $2n - 1$ to $3n - 3$, etc., are the same. Secondly, there is a symmetry for the recurrence equations within each cycle. Considering the cages as points on a circle, and "k" as the shortest distance between any two points, then the maximum number of steps between any two cages is $m = n/2$ if n is even and $m = (n - 1)/2$ if n is odd. The coefficients of identity between any two individuals "k" steps (cages) apart, either to the right or to the left, are the same in each generation. The equations for generations $1, 2, 3, \ldots, m$ within each cycle are the same as those for generations $n - 1, n - 2, n - 3, \ldots, m$, respectively. The homozygosity of an individual for any one of the possible alleles at a locus at generation t is:

$$f_t(A) = \Phi_{t-1}(i) \tag{5}$$

$$\begin{aligned} i &= t' && \text{if } 1 \leqq t' \leqq m \\ i &= n - t' && \text{if } m < t' \leqq n - 1\,. \end{aligned}$$

Where t' and i stand for generation within each cycle $(t' = 1 + [(t - 1) \bmod n - 1])$, and type of equation, respectively. In this case, type of equation "i" in each generation is the same as the number of steps "k" between cages. The general formula for the probability that the homologous genes taken one from each of the two individuals born in the same cage (zero step apart, $k = 0$) in generation t be identical by descent is:

$$\Phi_t(0) = (1/2)\,\{(1/2)[1 + f_{t-1}] + \Phi_{t-1}(i)\} \tag{6}$$

$$\begin{aligned} i &= t' && \text{if } 1 \leqq t' \leqq m \\ i &= n - t' && \text{if } m < t' \leqq n - 1\,. \end{aligned}$$

Let $\Phi_t(k)$ be the probability that any two randomly chosen homologous genes in two individuals k $(1 \leqq k \leqq m)$ cages apart are identical by descent in generation t. Then the recurrence equations for individuals 1, 2, ..., k cages apart are:

$$\Phi_t(1) = (1/4)\,[\Phi_{t-1}(i-1) + 2\,\Phi_{t-1}(1) + \Phi_{t-1}(i+1)] \quad (7)$$

$$\Phi_t(2) = (1/4)\,[\Phi_{t-1}(|i-2|) + 2\,\Phi_{t-1}(2) + \Phi_{t-1}(i+2)] \quad (8)$$

. . . .

$$\Phi_t(k) = (1/4)\,[\Phi_{t-1}(|i-k|) + 2\,\Phi_{t-1}(k) + \Phi_{t-1}(p)] \quad (9)$$

$i = t'$ if $1 \leqq t' \leqq m$

$i = n - t'$ if $m < t' \leqq n-1$

$p = i + k$ if $i < m - k + 1$

$p = n - i - k$ if $i \geqq m - k + 1$

t' = generation within cycle $= 1 + [(t-1) \bmod n-1]$.

It is more convenient to use heterozygosity $(H_t = 1 - f_t)$ and coefficient of non-identity $(\Psi_t(k) = 1 - \Phi_t(k))$. Equations 5, 6 and 9 then take the following forms:

$$H_t = \Psi_{t-1}(i) \quad (10)$$

$$\Psi_t(0) = (1/4)\, H_{t-1}(i) + (1/2)\,\Psi_{t-1}(i) \quad (11)$$

$$\Psi_t(k) = (1/4)\,[\Psi_{t-1}(|i-k|) + 2\,\Psi_{t-1}(k) + \Psi_{t-1}(p)]\,. \quad (12)$$

Detailed information on the derivation of the recurrence equations is given by Farid (1986).

Generation matrices

The recurrence equations (10, 11, 12) can be easily presented in matrix form. There are $j = n - 1$ generation (transition probability) matrices within each cycle which are of m different types. Examples of the generation matrices are presented in Appendix 1. There are some differences between intracyclic patterns of matrices, depending on whether n is even or odd. The generation matrices for the odd values of n have the size $s = (n+3)/2$ and appear in the following pattern within each cycle:

$$\Omega = \mathbf{G}_1\,\mathbf{G}_2\,\mathbf{G}_3 \ldots \mathbf{G}_{m-1}\,\mathbf{G}_m\,\mathbf{G}_m\,\mathbf{G}_{m-1} \ldots \mathbf{G}_3\,\mathbf{G}_2\,\mathbf{G}_1\,.$$

The matrices for even n's have size $s = (n+4)/2$ and appear in the following form for each cycle:

$$\Omega = \mathbf{G}_1\,\mathbf{G}_2\,\mathbf{G}_3 \ldots \mathbf{G}_{m-1}\,\mathbf{G}_m\,\mathbf{G}_{m-1} \ldots \mathbf{G}_3\,\mathbf{G}_2\,\mathbf{G}_1\,.$$

The first and the last matrix in each cycle $(\mathbf{G}_1)$ is the same as the generation matrix of the circular pair mating (Kimura and Crow 1963). Many of the matrices for each population size can be transformed to each other using a permutation matrix. The eigenvalues of the matrices which can be transformed to each other are the same. The relationships between the generation matrices and the form of the permutation matrices are discussed in Appendix 2.

Rate of inbreeding and effective population size

When a cyclical mating system has been continued for several generations (after the second cycle for $N > 16$), the proportional change in heterozygosity per cycle (H c) becomes equal to a constant value for each population size.

$$Hc = (H_{t+j}/H_t) = \lambda\,.$$

Where j is the cycle length and λ is the largest eigenvalue of Ω (the generation matrices for one cycle). The values for the rate of change of heterozygosity per cycle (1 − H c) are presented in Table 1.

The decrease in heterozygosity (H_t/H_0) with a continued cyclical mating system shows a repeating pattern of rises and falls from generation to generation, which is in contrast to all other regular mating systems that have been reported so far. The amount of heterozygosity in successive generations in a population of

Table 1. Rate of decrease of heterozygosity per cycle (1 − H c), average rate of inbreeding per generation (ΔF), and average effective population size (N e) under cyclical mating system in populations of size 8 to 52

N[a]	j[b]	(1 − H c)	ΔF	N e
8	3	0.104080	0.035971	13.90
10	4	0.106905	0.027870	17.94
12	5	0.109442	0.022915	21.82
14	6	0.110483	0.019323	25.88
16	7	0.112063	0.016836	29.70
18	8	0.112116	0.014754	33.89
20	9	0.113236	0.013264	37.69
22	10	0.113319	0.011955	41.82
24	11	0.113853	0.010928	45.75
26	12	0.113947	0.010031	49.85
28	13	0.114433	0.009304	53.74
30	14	0.114236	0.008627	57.96
32	15	0.114778	0.008095	61.77
34	16	0.115813	0.007663	65.24
36	17	0.115718	0.007208	69.37
38	18	0.115995	0.006826	73.25
40	19	0.115992	0.006468	77.30
42	20	0.116046	0.006148	81.32
44	21	0.116100	0.005859	85.33
46	22	0.116225	0.005600	89.28
48	23	0.116134	0.005353	93.41
50	24	0.116287	0.005138	97.32
52	25	0.116252	0.004931	101.40

[a] Population size

[b] Number of generation per cycle

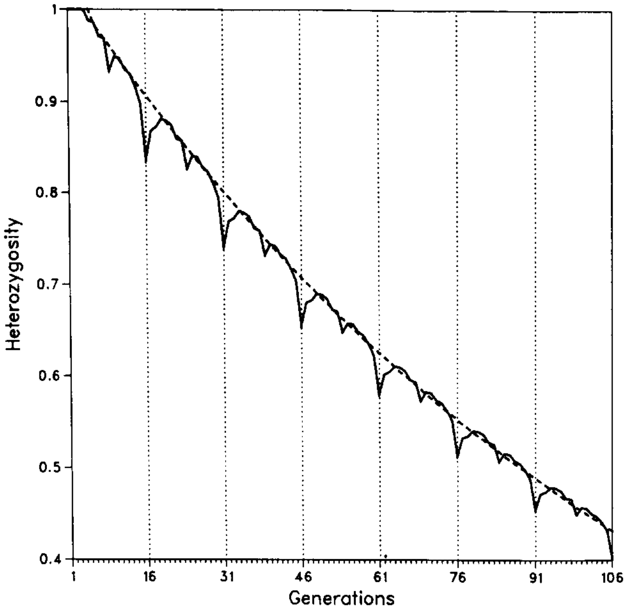

Fig. 2. Decrease in heterozygosity in a population of size 32 for the cyclical mating (*solid line*) and maximum avoidance of inbreeding (*broken line*)

size N = 32 is shown in Fig. 2. A corresponding plot for the maximum avoidance (Wright 1921) in a population of the same size is also presented for comparison. The cyclical mating system precludes inbreeding for the first four generations when population size is larger than 18.

Under the cyclical mating system, the rate of change of inbreeding in each generation of the second cycle is exactly similar to the corresponding generations in all the succeeding cycles. There is large variation in ΔF from generation to generation within each cycle for the cyclical mating, as shown in Table 2. The intracyclic pattern is, however, constant from cycle to cycle. The rate of inbreeding is more than 6.4% in the first generation of each cycle regardless of the population size. In populations where the number of families (n) is odd, a large positive value of ΔF (> 6%) also occurs in the $(j + 2)/2$th generation within each cycle. When n is even, the second largest positive value of inbreeding rate occurs in the $(j + 3)/2$th generation within each cycle. The large positive value of ΔF is followed by a large negative value, indicating that

Table 2. Rate of change of inbreeding per generation (X100) in populations of size 8 to 52

Generation within cycle	Population size											
	8	10	12	14	16	18	20	22	24	26	28	30
1	7.170	7.767	6.442	7.669	6.733	7.217	6.774	6.931	6.939	6.878	6.962	6.887
2	−1.879	−2.462	−3.216	−3.580	−3.595	−3.557	−3.749	−3.747	−3.774	−3.852	−3.876	−3.848
3	5.268	7.767	2.871	0.946	0.335	0.144	−0.030	−0.126	−0.240	−0.266	−0.321	−0.350
4		−2.462	2.806	7.240	1.424	1.575	0.135	−0.486	−0.720	−0.849	−0.957	−1.021
5			2.312	−3.071	4.129	6.355	2.336	2.170	2.623	0.994	0.930	0.483
6				1.789	−0.859	−3.725	2.974	6.227	−0.018	1.580	1.048	1.953
7					3.261	1.939	−1.116	−3.544	3.550	6.232	0.986	−0.084
8						1.288	2.106	−0.378	−1.462	−3.848	3.393	6.513
9							2.154	2.449	2.173	−0.509	−1.635	−3.902
10								1.874	0.302	1.552	0.475	−0.772
11									2.230	1.391	1.702	2.210
12										2.131	1.043	−0.063
13											1.941	1.297
14												2.125
15												
16												
17												
18												
19												
20												
21												
22												
23												
24												
25												

(continued overleaf)

Table 2 (continued)

Generation within cycle	Population size										
	32	34	36	38	40	42	44	46	48	50	52
1	6.926	6.897	6.908	6.877	6.918	6.884	6.897	6.893	6.898	6.894	6.888
2	−3.880	−3.870	−3.883	−3.902	−3.905	−3.911	−3.906	−3.914	−3.917	−3.919	−3.921
3	−0.388	−0.409	−0.415	−0.433	−0.443	−0.451	−0.462	−0.469	−0.473	−0.479	−0.482
4	−1.076	−1.118	−1.148	−1.175	−1.196	−1.210	−1.226	−1.239	−1.248	−1.258	−1.265
5	0.271	0.171	0.101	0.045	0.006	−0.025	−0.053	−0.074	−0.091	−0.107	−0.120
6	0.530	0.279	0.305	−0.156	−0.218	−0.361	−0.440	−0.488	−0.523	−0.552	−0.575
7	1.680	1.483	1.941	0.926	0.687	0.605	0.689	0.263	0.162	0.139	0.002
8	0.292	0.422	−0.443	1.335	1.191	1.875	0.299	0.596	0.495	0.316	0.529
9	3.565	6.536	0.814	−0.007	0.258	−0.429	1.415	1.153	1.899	0.520	0.230
10	−1.662	−3.968	3.563	6.643	0.849	0.348	−0.237	0.165	−0.574	1.395	1.156
11	0.181	−0.805	−1.730	−3.895	3.472	6.704	0.944	0.389	0.207	−0.316	0.157
12	1.288	0.360	0.079	−0.955	−1.786	−3.960	3.547	6.667	0.939	0.539	0.131
13	0.578	1.972	1.770	0.232	−0.006	−0.933	−1.793	−3.974	3.549	6.657	0.980
14	1.429	−0.022	−0.226	1.522	0.267	0.056	−0.071	−0.983	−1.786	−3.985	3.519
15	1.990	1.529	0.912	0.385	1.536	2.161	−0.036	0.012	−0.117	−0.998	−1.817
16		2.026	1.064	0.683	−0.039	−0.482	1.410	0.537	−0.146	−0.049	−0.136
17			2.108	1.236	0.854	0.381	0.263	1.546	1.982	0.431	−0.212
18				2.142	1.339	0.930	0.682	−0.286	−0.392	1.195	0.436
19					1.982	1.188	0.488	0.675	0.114	0.233	1.548
20						2.115	1.270	0.692	0.775	0.153	−0.339
21							2.091	1.305	0.639	0.786	0.639
22								2.064	1.319	0.626	0.431
23									2.045	1.234	0.632
24										2.084	1.296
25											2.082

some of the heterozygosity which was lost in the previous generation is immediately recovered. The sharp fluctuation in the rate of inbreeding is important when inbreeding depression is being studied. Beilharz (1982) reported that the overall reproductive performance of a population of mice under a cyclical mating system dropped in those generations in which inbreeding rose sharply.

The average rate of change in inbreeding per generation ($\Delta\bar{F}$), i.e., the constant rate of change which would have resulted in the same amount of inbreeding over the period of j generations, was computed from the relationship:

$$Hc = (1-\Delta\bar{F})^j = \prod_{i=1}^{j} (1-\Delta F_i)$$

where, j is the number of generations in each cycle and ΔF_i ($i = 1, 2, \ldots j$) is the rate of inbreeding per generation. When the stage of steady decay is reached, $\Delta\bar{F}$ will have a constant value. The average rate of inbreeding per generation and the average inbreeding effective population size ($\bar{N}e = 1/2\Delta\bar{F}$) for populations of size 8 to 52 are presented in Table 1. The average rate of inbreeding per generation and the average inbreeding effective population size are close to $1/[4N-(\log_2 N+1)]$ and $2N-((\log_2 N+1)/2)$ respectively, which are the values for the maximum avoidance of inbreeding for population size which is an integral power of 2 (Robertson 1964; Wright 1965). The average rate of inbreeding is the asymptotic value around which the actual rates oscillate. The inbreeding effective population size is approximately $2N-2$.

When effective population size is not constant over generations, the harmonic mean

$$\left(1/\bar{N}e = 1/t \sum_{i=1}^{t} (1/N e_i)\right)$$

is often used as the approximate solution to the equation $(1-1/2\bar{N}e)^t = \prod_{i=1}^{t} (1-1/2 N e_i)$. In the present case, however, it was found that the harmonic mean of effective population size over each cycle is larger than that obtained from the exact solution. This is in agreement with the findings of Karlin (1968) and Motro and Thomson (1982) who dealt with the population sizes that were changing cyclically.

In practice, when $\Delta\bar{F}$ is computed from the relationship $(1-1/2\bar{N}e)^t = \prod_{i=1}^{t} (1-1/2 N e_i)$, which is

Table 3. The average rate of inbreeding per generation computed by different methods[a] in a population of size 18, and percent deviation of the computed from the asymptotic value

Cycle	Generation no.[b]	Methods 1		Method 2		Method 3	
		ΔF	%dev.[c]	ΔF	%dev.	ΔF	%dev.
6	41	0.015447	4.70	0.015148	2.67	0.014780	0.17
6	42	0.014233	−5.53	0.013880	−5.92	0.014760	0.04
6	43	0.013930	−5.58	0.013577	−7.98	0.014701	−0.36
6	44	0.013973	−5.29	0.013629	−7.53	0.014662	−0.63
6	45	0.015128	2.54	0.014790	0.24	0.014760	0.04
6	46	0.013994	−5.15	0.013607	−7.77	0.014711	−0.29
6	47	0.014111	−4.36	0.013736	−6.90	0.014681	−0.49
6	48	0.014085	−4.53	0.013717	−7.03	0.014652	−0.69
7	49	0.015332	3.91	0.014961	1.40	0.014770	0.11
7	50	0.014318	−2.95	0.013908	−5.73	0.014760	0.04
7	51	0.014062	−4.69	0.013654	−7.46	0.014721	−0.22
7	52	0.014096	−4.46	0.013696	−7.17	0.014681	−0.49
7	53	0.015071	2.15	0.014673	−0.55	0.014760	0.04
7	54	0.014109	−4.37	0.013675	−7.31	0.014721	−0.22
7	55	0.014207	−3.71	0.013783	−6.58	0.014701	−0.36
7	56	0.014182	−3.87	0.013766	−6.70	0.014681	−0.49
8	57	0.015249	3.36	0.014828	0.50	0.014770	0.11
8	58	0.014379	−2.54	0.013928	−5.60	0.014760	0.04
8	59	0.014158	−4.04	0.013709	−7.08	0.014730	−0.16
8	60	0.014185	−3.86	0.013744	−6.85	0.014701	−0.36
8	61	0.015029	1.86	0.014588	−1.12	0.014760	0.04
8	62	0.014193	−3.80	0.013724	−6.98	0.014730	−0.16
8	63	0.014277	−3.23	0.013817	−6.35	0.014711	−0.29
8	64	0.014255	−3.38	0.013802	−6.45	0.014701	−0.36

[a] Method 1: $(1-1/2\bar{N}e)^t = \Pi_{i=1}^{t}(1-1/2Ne_i)$, or $1-F_t=(1-\Delta\bar{F})^t$
Method 2: $1/\bar{N}e = 1/t\,\Sigma_{i=1}^{t}(1/Ne_i)$
Method 3: Regression of $\log(1-F_t)$ on generation number

[b] The last generation included in the computation

[c] Percent deviation of the computed from the asymptotic value of $\Delta F = 0.014754$

equivalent to and gives the same results as the equation $1-F_t=(1-\Delta\bar{F})^t$, or equation $1/\bar{N}e = 1/t\sum_{i=1}^{t}(1/Ne_i)$, the value of $\Delta\bar{F}$ would be above or below the average asymptotic rate if the last generation of inbreeding is taken in those generations in which it is maximum or minimum within each cycle respectively. The method of regression of $\log(1-F_t)$ on generation number ($\Delta\bar{F} = 1-\exp(b)$) gives estimates which are less fluctuating with the final value of F. The numerical values for the average rate of inbreeding per generation computed by the different methods, and the percentage deviations of the computed and the asymptotic values in the case of $N=18$ are presented in Table 3. All methods are sensitive to the value of t; the larger the number of generations of inbreeding, the closer the estimate of average inbreeding to its asymptotic value. Nevertheless, the dependency of the rate of inbreeding on t computed from the regression method is far less than those computed from the other methods.

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Appendix 1. Generation matrices for population of size 32 (n = 16, m = 8)

$$\mathbf{G}_1$$

$$\begin{vmatrix} H_t \\ \Psi_t(0) \\ \Psi_t(1) \\ \Psi_t(2) \\ \Psi_t(3) \\ \Psi_t(4) \\ \Psi_t(5) \\ \Psi_t(6) \\ \Psi_t(7) \\ \Psi_t(8) \end{vmatrix} = \begin{vmatrix} 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.25 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.25 & 0.5 & 0.25 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.25 & 0.5 & 0.25 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.25 & 0.5 & 0.25 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.25 & 0.5 & 0.25 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.25 & 0.5 & 0.25 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.25 & 0.5 & 0.25 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.25 & 0.5 & 0.25 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0.5 \end{vmatrix} \begin{vmatrix} H_{t-1} \\ \Psi_{t-1}(0) \\ \Psi_{t-1}(1) \\ \Psi_{t-1}(2) \\ \Psi_{t-1}(3) \\ \Psi_{t-1}(4) \\ \Psi_{t-1}(5) \\ \Psi_{t-1}(6) \\ \Psi_{t-1}(7) \\ \Psi_{t-1}(8) \end{vmatrix}$$

$$\mathbf{G}_2$$

$$\begin{vmatrix} H_t \\ \Psi_t(0) \\ \Psi_t(1) \\ \Psi_t(2) \\ \Psi_t(3) \\ \Psi_t(4) \\ \Psi_t(5) \\ \Psi_t(6) \\ \Psi_t(7) \\ \Psi_t(8) \end{vmatrix} = \begin{vmatrix} 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.25 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.75 & 0 & 0.25 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.25 & 0 & 0.5 & 0 & 0.25 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.25 & 0 & 0.5 & 0 & 0.25 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.25 & 0 & 0.5 & 0 & 0.25 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.25 & 0 & 0.5 & 0 & 0.25 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.25 & 0 & 0.5 & 0 & 0.25 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.25 & 0 & 0.75 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0.5 \end{vmatrix} \begin{vmatrix} H_{t-1} \\ \Psi_{t-1}(0) \\ \Psi_{t-1}(1) \\ \Psi_{t-1}(2) \\ \Psi_{t-1}(3) \\ \Psi_{t-1}(4) \\ \Psi_{t-1}(5) \\ \Psi_{t-1}(6) \\ \Psi_{t-1}(7) \\ \Psi_{t-1}(8) \end{vmatrix}$$

$$\mathbf{G}_3$$

$$\begin{vmatrix} H_t \\ \Psi_t(0) \\ \Psi_t(1) \\ \Psi_t(2) \\ \Psi_t(3) \\ \Psi_t(4) \\ \Psi_t(5) \\ \Psi_t(6) \\ \Psi_t(7) \\ \Psi_t(8) \end{vmatrix} = \begin{vmatrix} 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0.25 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.5 & 0.25 & 0 & 0.25 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.25 & 0.5 & 0 & 0 & 0.25 & 0 & 0 & 0 \\ 0 & 0.25 & 0 & 0 & 0.5 & 0 & 0 & 0.25 & 0 & 0 \\ 0 & 0 & 0.25 & 0 & 0 & 0.5 & 0 & 0 & 0.25 & 0 \\ 0 & 0 & 0 & 0.25 & 0 & 0 & 0.5 & 0 & 0 & 0.25 \\ 0 & 0 & 0 & 0 & 0.25 & 0 & 0 & 0.5 & 0.25 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.25 & 0 & 0.25 & 0.5 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0.5 \end{vmatrix} \begin{vmatrix} H_{t-1} \\ \Psi_{t-1}(0) \\ \Psi_{t-1}(1) \\ \Psi_{t-1}(2) \\ \Psi_{t-1}(3) \\ \Psi_{t-1}(4) \\ \Psi_{t-1}(5) \\ \Psi_{t-1}(6) \\ \Psi_{t-1}(7) \\ \Psi_{t-1}(8) \end{vmatrix}$$

$$\mathbf{G}_4$$

$$\begin{vmatrix} H_t \\ \Psi_t(0) \\ \Psi_t(1) \\ \Psi_t(2) \\ \Psi_t(3) \\ \Psi_t(4) \\ \Psi_t(5) \\ \Psi_t(6) \\ \Psi_t(7) \\ \Psi_t(8) \end{vmatrix} = \begin{vmatrix} 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0.25 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.5 & 0 & 0.25 & 0 & 0.25 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.75 & 0 & 0 & 0 & 0.25 & 0 & 0 \\ 0 & 0 & 0.25 & 0 & 0.5 & 0 & 0 & 0 & 0.25 & 0 \\ 0 & 0.25 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0.25 \\ 0 & 0 & 0.25 & 0 & 0 & 0 & 0.5 & 0 & 0.25 & 0 \\ 0 & 0 & 0 & 0.25 & 0 & 0 & 0 & 0.75 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.25 & 0 & 0.25 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0.5 \end{vmatrix} \begin{vmatrix} H_{t-1} \\ \Psi_{t-1}(0) \\ \Psi_{t-1}(1) \\ \Psi_{t-1}(2) \\ \Psi_{t-1}(3) \\ \Psi_{t-1}(4) \\ \Psi_{t-1}(5) \\ \Psi_{t-1}(6) \\ \Psi_{t-1}(7) \\ \Psi_{t-1}(8) \end{vmatrix}$$

Appendix 1 (continued)

$\mathbf{G}_5$

$$\begin{vmatrix} H_t \\ \Psi_t(0) \\ \Psi_t(1) \\ \Psi_t(2) \\ \Psi_t(3) \\ \Psi_t(4) \\ \Psi_t(5) \\ \Psi_t(6) \\ \Psi_t(7) \\ \Psi_t(8) \end{vmatrix} = \begin{vmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0.25 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0.5 & 0 & 0 & 0.25 & 0 & 0.25 & 0 & 0 \\ 0 & 0 & 0 & 0.5 & 0.25 & 0 & 0 & 0 & 0.25 & 0 \\ 0 & 0 & 0 & 0.25 & 0.5 & 0 & 0 & 0 & 0 & 0.25 \\ 0 & 0 & 0.25 & 0 & 0 & 0.5 & 0 & 0 & 0.25 & 0 \\ 0 & 0.25 & 0 & 0 & 0 & 0 & 0.5 & 0.25 & 0 & 0 \\ 0 & 0 & 0.25 & 0 & 0 & 0 & 0.25 & 0.5 & 0 & 0 \\ 0 & 0 & 0 & 0.25 & 0 & 0.25 & 0 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0.5 \end{vmatrix} \begin{vmatrix} H_{t-1} \\ \Psi_{t-1}(0) \\ \Psi_{t-1}(1) \\ \Psi_{t-1}(2) \\ \Psi_{t-1}(3) \\ \Psi_{t-1}(4) \\ \Psi_{t-1}(5) \\ \Psi_{t-1}(6) \\ \Psi_{t-1}(7) \\ \Psi_{t-1}(8) \end{vmatrix}$$

$\mathbf{G}_6$

$$\begin{vmatrix} H_t \\ \Psi_t(0) \\ \Psi_t(1) \\ \Psi_t(2) \\ \Psi_t(3) \\ \Psi_t(4) \\ \Psi_t(5) \\ \Psi_t(6) \\ \Psi_t(7) \\ \Psi_t(8) \end{vmatrix} = \begin{vmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0.25 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.5 & 0 & 0 & 0 & 0.25 & 0 & 0.25 & 0 \\ 0 & 0 & 0 & 0.5 & 0 & 0.25 & 0 & 0 & 0 & 0.25 \\ 0 & 0 & 0 & 0 & 0.75 & 0 & 0 & 0 & 0.25 & 0 \\ 0 & 0 & 0 & 0.25 & 0 & 0.5 & 0 & 0.25 & 0 & 0 \\ 0 & 0 & 0.25 & 0 & 0 & 0 & 0.75 & 0 & 0 & 0 \\ 0 & 0.25 & 0 & 0 & 0 & 0.25 & 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 & 0.25 & 0 & 0 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0.5 \end{vmatrix} \begin{vmatrix} H_{t-1} \\ \Psi_{t-1}(0) \\ \Psi_{t-1}(1) \\ \Psi_{t-1}(2) \\ \Psi_{t-1}(3) \\ \Psi_{t-1}(4) \\ \Psi_{t-1}(5) \\ \Psi_{t-1}(6) \\ \Psi_{t-1}(7) \\ \Psi_{t-1}(8) \end{vmatrix}$$

$\mathbf{G}_7$

$$\begin{vmatrix} H_t \\ \Psi_t(0) \\ \Psi_t(1) \\ \Psi_t(2) \\ \Psi_t(3) \\ \Psi_t(4) \\ \Psi_t(5) \\ \Psi_t(6) \\ \Psi_t(7) \\ \Psi_t(8) \end{vmatrix} = \begin{vmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0.25 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 \\ 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0.25 & 0 & 0.25 \\ 0 & 0 & 0 & 0.5 & 0 & 0 & 0.25 & 0 & 0.25 & 0 \\ 0 & 0 & 0 & 0 & 0.5 & 0.25 & 0 & 0.25 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.25 & 0.5 & 0.25 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.25 & 0 & 0.25 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0.25 & 0 & 0.25 & 0 & 0 & 0.5 & 0 & 0 \\ 0 & 0.25 & 0 & 0.25 & 0 & 0 & 0 & 0 & 0.5 & 0 \\ 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 \end{vmatrix} \begin{vmatrix} H_{t-1} \\ \Psi_{t-1}(0) \\ \Psi_{t-1}(1) \\ \Psi_{t-1}(2) \\ \Psi_{t-1}(3) \\ \Psi_{t-1}(4) \\ \Psi_{t-1}(5) \\ \Psi_{t-1}(6) \\ \Psi_{t-1}(7) \\ \Psi_{t-1}(8) \end{vmatrix}$$

$\mathbf{G}_8$

$$\begin{vmatrix} H_t \\ \Psi_t(0) \\ \Psi_t(1) \\ \Psi_t(2) \\ \Psi_t(3) \\ \Psi_t(4) \\ \Psi_t(5) \\ \Psi_t(6) \\ \Psi_t(7) \\ \Psi_t(8) \end{vmatrix} = \begin{vmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0.25 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 \\ 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.5 & 0 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.5 & 0 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 \\ 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 \end{vmatrix} \begin{vmatrix} H_{t-1} \\ \Psi_{t-1}(0) \\ \Psi_{t-1}(1) \\ \Psi_{t-1}(2) \\ \Psi_{t-1}(3) \\ \Psi_{t-1}(4) \\ \Psi_{t-1}(5) \\ \Psi_{t-1}(6) \\ \Psi_{t-1}(7) \\ \Psi_{t-1}(8) \end{vmatrix}$$

Appendix 2

The relationships between generation matrices

An algorithm to transform the generation matrices into each other is desirable as it would make the computations easier. Since matrices can be transformed into each other only if their eigenvalues are the same, the generation matrices with similar eigenvalues were grouped together and presented in Appendix Table 1. This table shows the number of unit eigenvalues (if they exist) and the largest non-unit eigenvalue of the generation matrices for populations of size 8 to 52, and clearly demonstrates the matrices which can be transformed into each other. Ignoring the first two rows of the generation matrices, many of them are circulants (Davis 1979), suggesting that there are permutation matrices which can be used to transform one to the other. The type of transformation of one matrix to another, and the corresponding permutation matrices share some similarities depending on whether n or n/2 is odd or even.

Appendix Table 1. The number of unit eigenvalues (No. $\lambda = 1$) and the largest non-unit eigenvalue (λ_m) of the generation matrices ($\mathbf{G}_i$) for populations of size 8 to 52

n	m	i	No. $\lambda = 1$	λ_m
4	2	1	0	0.965252
		2	1	0.919643
5	2	1, 2	0	0.973696
6	3	1	0	0.979163
		2	1	0.950647
		3	1	0.919643
7	3	1, 2, 3	0	0.982968
8	4	1, 3	0	0.986752
		2	1	0.965252
		4	1	0.919643
9	4	1, 2, 4	0	0.987868
		3	1	0.950647
10	5	1, 3	0	0.989521
		2, 4	1	0.973696
		5	2	0.919643
11	5	1, 2, 3, 4, 5	0	0.990843
12	6	1, 5	0	0.991920
		2	1	0.979163
		3	1	0.965252
		4	2	0.950647
		6	3	0.919643
13	6	1, 2, 3, 4, 5, 6	0	0.992811
14	7	1, 3, 5	0	0.993557
		2, 4, 6	1	0.982968
		7	3	0.919643
15	7	1, 2, 4, 7	0	0.994190
		3, 6	1	0.973696
		5	2	0.950647
16	8	1, 3, 5, 7	0	0.994732
		2, 6	1	0.985752
		4	2	0.965252
		8	4	0.919643
17	8	1, 2, 3, 4, 5, 6, 7, 8	0	0.995199
18	9	1, 5, 7	0	0.995606
		2, 4, 6	1	0.987868
		3	1	0.979163
		6	3	0.950647
		9	4	0.919643
19	9	1, 2, 3, 4, 5, 6, 7, 8, 9	0	0.995962
20	10	1, 3, 7, 9	0	0.996276
		2, 6	1	0.989521
		4, 8	2	0.973696
		5	2	0.965252
		10	5	0.919643
21	10	1, 2, 4, 5, 8, 10	0	0.996554
		3, 6, 9	1	0.982968
		7	3	0.950647
22	11	1, 3, 5, 7, 9	0	0.996802
		2, 4, 6, 8, 10	1	0.990843
		11	5	0.919643
23	11	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11	0	0.997023
24	12	1, 5, 7, 11	0	0.997222
		2, 10	1	0.991920
		3, 9	1	0.985752
		4	2	0.979163
		6	3	0.965252
		8	4	0.950647
		12	6	0.919643
25	12	1, 2, 3, 4, 6, 7, 8, 9, 11, 12	0	0.997402
		5, 10	2	0.973696
26	13	1, 3, 5, 7, 9, 11	0	0.997564
		13	6	0.919643
		2, 4, 6, 8, 10, 12	1	0.992811

n and m are number of pairs of breeding individuals and different types of matrices, respectively

A-Cases where n is odd: The permutation matrix (**P**) when n is odd has the following general form:

$$\begin{vmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdot & \cdot \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdot & \cdot \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & \cdot & \cdot \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & \cdot & \cdot \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & \cdot & \cdot \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & \cdot & \cdot \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & \cdot & \cdot \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & \cdot & \cdot \end{vmatrix}$$

The column number in which 1's appear in the first, second, third, ... $s-3$, $s-2$, $s-1$, and s-th rows (s is the size of the matrix and is equal to $(n+3)/2$ in this case) are 1, 2, 4, 6, 8, ... 9, 7, 5, 3. This permutation matrix can be partitioned as:

$$\left|\begin{array}{c|c} \mathbf{I} & \mathbf{0} \\ \hline \mathbf{0}' & \mathbf{Q} \end{array}\right| .$$

Where **I** is a 2×2 identity matrix, **Q** is a $m \times m$ matrix, **0** is a $2 \times m$ null matrix, and **0**′ is transpose of **0**. Thus permutations of the form $\mathbf{P}'\mathbf{G}\mathbf{P}$ do not shift the first and second rows and columns of **G**, but other rows and columns (3, 4, ... m) are permutated by **Q**, which corresponds to $\mathbf{Q}(1) = 2$, $\mathbf{Q}(2) = 4$, $\mathbf{Q}(3) = 6$, ... $\mathbf{Q}(m-2) = 5$, $\mathbf{Q}(m-1) = 3$, $\mathbf{Q}(m) = 1$. The correspondence between the sequence of permutation described above and the position of one's in the matrix **Q** is apparent. The above discussion in the matrix notation means that the matrix **Q** can be factored into a product of disjoint cycles, and this factorization is unique up to the arrangement of factors. For example; for $N = 22$ ($n = 11$, $m = 5$), the permutation corresponds to $\mathbf{Q}(1) = 2$, $\mathbf{Q}(2) = 4$, $\mathbf{Q}(3) = 5$, $\mathbf{Q}(4) = 3$, $\mathbf{Q}(5) = 1$, which produces the full cycle $1 \Rightarrow 2 \Rightarrow 4 \Rightarrow 3 \Rightarrow 5 \Rightarrow 1$. This permutation matrix is called primitive since its factorization consists of one cycle of full length m (Davis 1979). For $N = 30$ ($n = 15$, $m = 7$), the permutation corresponds to $\mathbf{Q}(1)=2$, $\mathbf{Q}(2)=4$, $\mathbf{Q}(3)=6$, $\mathbf{Q}(4)=7$, $\mathbf{Q}(5)=5$, $\mathbf{Q}(6)=3$, $\mathbf{Q}(7)=1$, showing that it is factorized into three disjoint cycles; $(1 \Rightarrow 2 \Rightarrow 4 \Rightarrow 7 \Rightarrow 1)$, $(3 \Rightarrow 6 \Rightarrow 3)$ and $(5 \Rightarrow 5)$. In general, when n is an odd prime, and one of its least positive or least negative primitive roots is even, i.e., $n = 5, 7, 11, 13, 19$, etc. (Abramowitz and Stegun 1970), then the corresponding permutation matrix is primitive. The transformation $\mathbf{P}'\mathbf{G}_x\mathbf{P} = \mathbf{G}_z$ gives exactly the same sequence of transformation of $\mathbf{G}_x$ to $\mathbf{G}_z$ within each cycle as shown above. For odd values of n, the general form of transformation of $\mathbf{G}_x$ to $\mathbf{G}_z$, where $x = 1, 2, \ldots, m$, is $z = \text{Minimum } [2x, n-2x]$, which gives both the number of groups and the sequence of transformation.

In addition to the above form of sequential transformation, any of the matrices in one group can be transformed to another matrix in the same group. There is an integer "d" which satisfies the relationship $\mathbf{P}^d = \mathbf{I}$ for all the permutation matrices. The operation $\mathbf{P}^y\mathbf{G}_x\mathbf{P}^{y\prime} = \mathbf{G}_z$ or $\mathbf{P}^{y\prime}\mathbf{G}_x\mathbf{P}^y = \mathbf{G}_z$, where $y = 1, 2, \ldots, d-1$, will perform this transformation. Another property of the permutation matrices of this sort is $\mathbf{P}^y = \mathbf{P}^{(d-y)\prime}$. When n is an odd prime, and one of its least positive or least negative primitive roots is even (i.e. the corresponding permutation matrix is primitive) then $d = m$, and all the matrices for that population size can be transformed to each other. In other cases, $d < m$ and the matrices form two or more groups.

B-Cases when n is even and n/2 is odd: The column number in which 1's appear in the first, second, ... $s-3$, $s-2$, $s-1$ and s-th rows of the permutation matrix are 1, 2×1, $s-2\times 1$, 2×3, $s-2\times 3$, 2×5, $s-2\times 5$, 2×7 ... $s-2\times 6$, 2×6, $s-2\times 4$, 2×4, $s-2\times 2$, 2×2, s; i.e., 1 in the odd rows are in columns $1, s-2, s-6, s-10, \ldots s-12, s-8, s-4, s$, and in even rows are on columns $2, 6, 10, 14, \ldots 12, 8, 4$.

The matrix $\mathbf{Q}$ corresponds to the permutation $\mathbf{Q}(1) = m-2$, $\mathbf{Q}(2)=4$, $\mathbf{Q}(3)=m-6$, $\mathbf{Q}(4)=8$, $\mathbf{Q}(5)=m-10$, ... $\mathbf{Q}(m-3)=6$, $\mathbf{Q}(m-2)=m-4$, $\mathbf{Q}(m-1)=2$ and $\mathbf{Q}(m) = m$. When n/2 is odd, "d" which satisfies $\mathbf{P}^d = \mathbf{I}$ is equal to $(n-2)/4$ if n/2 is an odd prime and one of its least positive or least negative primitive roots is even. In such cases, the matrices form three distinct groups; $(1, 3, 5, \ldots, m-2)$, $(2, 4, 6, \ldots, m-1)$ and (m). In other cases $d < (n-2)/4$, and the matrices form more than three groups.

C-Cases where n and n/2 are even: The general form of permutation matrices for the cases where both n and n/2 were even could not be found. The position of 1's in the permutation matrices for the populations of up to size 40 ($n = 20$) are shown below ($\mathbf{P}_{i,j}$ is the element in the i-th row and j-th column of the matrix).

$n = 4$ $\mathbf{P}_{1.1}\,\mathbf{P}_{2.2}\,\mathbf{P}_{3.3}\,\mathbf{P}_{4.4}$

$n = 8$ $\mathbf{P}_{1.1}\,\mathbf{P}_{2.2}\,\mathbf{P}_{3.5}\,\mathbf{P}_{4.4}\,\mathbf{P}_{5.3}\,\mathbf{P}_{6.6}$

$n = 12$ $\mathbf{P}_{1.1}\,\mathbf{P}_{2.2}\,\mathbf{P}_{3.7}\,\mathbf{P}_{4.4}\,\mathbf{P}_{5.5}\,\mathbf{P}_{6.6}\,\mathbf{P}_{7.3}\,\mathbf{P}_{8.8}$

$n = 16$ $\mathbf{P}_{1.1}\,\mathbf{P}_{2.2}\,\mathbf{P}_{3.5}\,\mathbf{P}_{4.8}\,\mathbf{P}_{5.9}\,\mathbf{P}_{6.6}\,\mathbf{P}_{7.3}\,\mathbf{P}_{8.4}\,\mathbf{P}_{9.7}\,\mathbf{P}_{10.10}$

$n = 20$ $\mathbf{P}_{1.1}\,\mathbf{P}_{2.2}\,\mathbf{P}_{3.5}\,\mathbf{P}_{4.8}\,\mathbf{P}_{5.11}\,\mathbf{P}_{6.10}\,\mathbf{P}_{7.7}\,\mathbf{P}_{8.4}\,\mathbf{P}_{9.3}\,\mathbf{P}_{10.6}\,\mathbf{P}_{11.9}\,\mathbf{P}_{12.12}$

The number of groups of matrices in this case is larger than those for the cases where n or n/2 were odd, indicating that many of them cannot be transformed to each other.