

## LIMITING INBREEDING WITH MIGRATION

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### SUMMARY

Equations are given for the calculation of inbreeding under migration. The upper limit of inbreeding between a breed with herds interconnected by migration and a conceptual completely random mating aggregate population, allows the estimation of the number of migrants necessary to keep inbreeding within acceptable limits. The main conclusions are in the Discussion.

### THEORETICAL RESULTS

Based on results of Crow (1986), theory has been developed to calculate the inbreeding coefficient of individuals in a herd, with equiprobable migration between  $n$  herds composing a breed. Let  $N_e$  = effective population number,  $N_1$  = number of males in a single herd,  $N_2$  = number of females in a single herd,  $M_1$  = number of male migrants in a herd,  $M_2$  = number of female migrants in a herd,  $M = M_1 + M_2$  = total number of migrants,  $m_1 = M_1/N_1$ ,  $m_2 = M_2/N_2$ .

The inbreeding coefficient can be calculated from

$$F_t(1) = 1 - k\lambda_1^t - (1-k)\lambda_2^t, \quad (1)$$

with  $\lambda_1 > \lambda_2$  and  $\lambda_1, \lambda_2 = [(a_{22} + a_{11}) \pm \{(a_{22} - a_{11})^2 + 4a_{12}a_{21}\}^{1/2}]/2$  and

$$k = (1/2) + (1/2)(a_{11} + 2a_{12} - a_{22})/\{(a_{22} - a_{11})^2 + 4a_{12}a_{21}\}^{1/2} \quad (2)$$

$$\text{and } a_{11} = a(1-c); a_{12} = (1-a); a_{21} = b(1-c); a_{22} = (1-b),$$

$$a = (1-m_1)(1-m_2) + m_1m_2/(n-1); b = (1-a)/(n-1); c = 1/2N_e,$$

$$1/N_e = 1/4N_1 + 1/4N_2.$$

The inbreeding coefficient of an aggregate random mating population of effective size  $N_e n$  is given by

$$F_t(3) = 1 - (1 - 1/2N_e n)^t. \quad (3)$$

The difference in inbreeding between individuals from a single herd and from a conceptual aggregate random mating population of size  $N_e n$ , derived from (1) and (3), can be shown to be less than  $(1-k)$ ,

$$F_t(1) - F_t(3) \leq (1-k). \quad (4)$$

The value of  $(1-k)$  is, therefore, a possible criterion for the efficiency of migration in keeping inbreeding under control.

For  $n$  large, so that terms containing  $1/(n-1)$  are negligible, it follows from (2)

$$1-k = (1-m_1)(1-m_2)/[2N_e\{1 - (1-m_1)(1-m_2)\} + (1-m_1)(1-m_2)]. \quad (5)$$

With migration rates small enough to ignore higher order terms and  $m_e = (m_1 + m_2)/2$ ,

$$1-k = 1/[4m_e N_e(n+1)/(n-1) + 1]. \quad (6)$$

For  $n$  large and  $m_1 = m_2$ ,  $1-k = 1/(4M + 1)$ , equal to the limit inbreeding coefficient of Wright's (1943) island model of migration.

### MALE AND FEMALE MIGRATION

Denote the proportions of males and females in a herd by

$$p_1 = N_1/(N_1 + N_2) \text{ and } p_2 = N_2/(N_1 + N_2).$$

Substituting  $m_1N_1 = M_1$  and  $m_2N_2 = M_2$  in (6) gives

$$1-k = 1/\{8(M_1p_2 + M_2p_1)(n-1)/(n-1) + 1\} \quad (7)$$

**Conclusion:** It follows from (7) that  $(1-k)$  will be a minimum if all migrants are from the scarcer (male) sex, i.e. if  $M_1 = M$  and  $M_2 = 0$  for  $p_2 > p_1$ . Note furthermore that for  $p_1$ , small in polygamous species, it follows from (4) and (7) that female migration will be extremely inefficient in limiting inbreeding.

### PRACTICAL EXAMPLE

To illustrate the power of migration to counter inbreeding, consider the situation with  $N_2$  large enough so that  $N_2 = 4N_1$ , approximately, and with male migration only. Consider a breed with  $N_1 = 4$ ,  $n-1 = 100$ , and let there be 0; ½; 1; 2 migrant males in each herd, i.e.  $M_1 = 0; ½; 1; 2$  and  $m_1 = 0; ¼; ½; ½$ . The percentage inbreeding in a single herd, from (1), compared to an aggregate random mating population, from (3), is as follows.

**Table 1.** Inbreeding (%) under migration

Generation	$M_1 = 0$	$M_1 = ½$	$M_1 = 1$	$M_1 = 2$	Aggregate population
5	15	10	7	3	0
10	27	15	8	3	0
20	47	17	9	4	1
40	72	19	9	4	1
$1-k$ (eq. 2)	-	18	8	3	-

The aggregate random mating population has effective number  $N_e n = 4N_1 n = 1616$ . Note that keeping one migrant male of random origin in each herd halves the inbreeding for the first five generations compared to the closed herd situation. Afterwards the maximum differences in inbreeding between the aggregate random mating population and the individual herds are given by  $(1-k)$ , calculated from (2). The value of  $(1-k)$  is, therefore, clearly an important criterion for the efficiency of migration in keeping inbreeding under control.

### RECOMMENDATIONS

General recommendations for the limitation of inbreeding can be constructed from estimates of  $(1-k)$ , as follows from (4). Table 2 was calculated from (5) under the assumptions of male migration only ( $m_2 = 0$ ) and a large proportion of females ( $N_2 = 4N_1$ ).

**Table 2.** Estimates of  $(1-k)\%$  with male migration and a large proportion of females

Migrant Numbers	Numbers of males in herd						
	1	2	3	4	5	10	LARGE
1	0	7	8	9	9	10	11
2		0	2	3	4	5	6
3			0	1	2	3	4
4				0	1	2	3
5					0	1	2
10						0	1

For a small number of herds ( $n$ ), the same values of  $(1-k)$  can be obtained with fewer migrants: the number of migrants can be adjusted by a factor of  $(n-1)/(n+1)$ . This follows since the correction from (6) applied to (5) often approximates the exact (2) adequately. For example, with  $n = 3$ ,  $(n-1)/(n+1) = 1/2$  so that one migrant will give  $(1-k) = 3$  for  $N_1 = 4$  instead of  $(1-k) = 9$  in Table 2. The correction  $(n-1)/(n+1)$  can also be applied to  $(1-k)$  itself, as a quick first approximation, except for  $N_e = 4$ .

Even with equal numbers in the two sexes,  $N_1 = N_2 = N/2$ , migration from a single sex will give smaller values of  $(1-k)$  than equal migration rates for males and females. With an equal number of migrants in both situations,

$$m_1 N/2 + m_2 N/2 = \{(m_1 + m_2)/2\}N = mN.$$

However,

$$(1-m_1)(1-m_2) \leq \{1 - (m_1 + m_2)/2\}^2,$$

with equality only if  $m_1 = m_2$ . Hence (5) gives a lower value for  $(1-k)$  if  $m_1 > m_2$  (or  $m_2 > m_1$ ) than if  $m_1 = m_2$ . For large migration rates, which may often occur in very small herds, the difference may be appreciable. With equal numbers for the two sexes and only male migration ( $m_2 = 0$ ) the values of  $(1-k)$  from (5) are given by Table 3.

**Table 3.** Estimates of  $(1-k)\%$  with male migration and equal numbers of males and females

Male Migrant Numbers	Herd size					
	2	4	6	8	16	LARGE
1	0	11	14	16	18	20
2		0	4	6	9	11
3			0	2	5	8
4				0	3	6
8					0	3

Corrections for small  $n$  are the same as for Table 2.

Table 4 was calculated from (5) for equal migration rates and equal numbers of males and females.

**Table 4.** Estimates of  $(1-k)\%$  with equality between the sexes

Migrant Numbers	Herd size					
	2	4	6	8	16	LARGE
2	0	4	6	7	9	11
4		0	1	2	4	6
6			0	0	2	4
8				0	1	3
16					0	2

Corrections for small  $n$  are the same as for Table 2.

### OPTIMAL DECOMPOSITION

One question of some importance remains. For constant total population size ( $Nn$ ), what is the optimal decomposition into number of subpopulations ( $n$ ) and subpopulation size ( $N$ )? An attempted answer is given in Table 5, which was directly calculated from (2), assuming either one male migrant ( $M_1 = 1$ ) or two migrants of either sex per herd ( $M = 2$ ), with equal numbers of the two sexes.

Table 5. Values of  $(1-k)\%$  according to number of migrants, breed ( $Nn$ ) and herd ( $N$ ) size

$Nn$	$M_1 = 1$			$M = 2$		
	$N = 4$	$N = 8$	$N = 32$	$N = 4$	$N = 8$	$N = 32$
24	7	7	-	2	3	-
64	9	13	6	3	6	3
96	9	13	9	3	6	5
192	10	14	15	3	6	7
352	11	14	17	4	7	9
3200	11	16	19	4	7	10

For  $Nn < 100$  the lowest values tend to be along the edges of the table. That is, the lowest  $(1-k)$  values are for  $N$  either as small or as large as possible, if  $N = 2$  is excluded, as similar to (5),  $(1-k)$  might then be equal to zero. For  $M = 2$  the disadvantage of the middle values is probably small enough, however, so that other considerations, like transport cost or protection against epidemics could be decisive. For  $Nn > 100$  the lowest values of  $(1-k)$  occur for  $N = 4$ , while an increase in the values of  $Nn$  together with the concomitant increase in  $n$ , will cause an approximation to (5). This is reflected in the correspondence between the last line of Table 5 with the first lines of Tables 3 and 4.

#### DISCUSSION

As follows from (4), sufficient migrants for a satisfactory value of  $(1-k)$  will cause the progress of inbreeding in a breed to be determined by its total effective population size ( $N_e n$ ). The general conclusion from Table 2 must be that, with a large proportion of females, one or two migrant males per herd are enough to ensure that any breed can effectively be a single breeding unit. With equal numbers between the sexes, Tables 3 and 4 show that one to four migrants are enough for the same conclusion, if the correction  $(n-1)/(n+1)$  for a small number of herds, suggested by (6), is borne in mind. For very small values of  $N_e$  it may be wise to confirm the adequacy of the correction of  $(n-1)/(n+1)$  to the number of migrants or to  $(1-k)$ , suggested for Tables 2,3 and 4, by direct calculation from (2).

Reductions in  $(1-k)$  due to constant offspring numbers can be accommodated by the usual adjustments of  $N_e$ .

With  $Nn < 100$  the results in Table 5 indicate small differences in  $(1-k)$  for two migrants in the decomposition of total breed size ( $Nn$ ) into number of herds ( $n$ ) and herd size ( $N$ ). For  $Nn > 100$  the indications are for small herd sizes with as many herds as possible.

Depending on the sex ratio in breeding animals, single sex migration from the scarcer sex may be drastically more efficient for the limitation of inbreeding than bisexual migration. Even with equal numbers of the sexes, single sex migration may be advantageous for large migration rates, which may often occur in very small populations.

#### REFERENCES

- CROW, J.F. (1986) Basic concepts in population, quantitative and evolutionary genetics.  
 WRIGHT, S. (1943). Genetics 28, 114-138.