Countering inbreeding with migration
1. Migration from unrelated populations

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The effect of migration on inbreeding is modelled for small populations with immigrants from a large unrelated population. Different migration rates and numbers for the two sexes are assumed, and a general recursion equation for inbreeding progress derived, which can be shown to lead to an equilibrium inbreeding coefficient where the effects of genetic drift and migration balance each other. For small migration rates and large numbers of breeding animals it is shown that migration of only the scarcer sex will minimize the equilibrium inbreeding. Migration from only one sex will also be an advantage in small populations with large migration rates. In small populations with large migration rates fewer migrants are necessary for a given equilibrium inbreeding coefficient than in large populations with small migration rates. Finally, an equation is derived for situations where the number of females is so large that their contribution to inbreeding can be ignored. Simple tables are given for the equilibrium inbreeding coefficients where the number of migrants and herd sizes are taken into consideration. The general impression from these tables is that, for equal numbers of the two sexes, the provision of 2–4 migrants to a population should stabilize inbreeding. In populations with low male to female ratios, where only the inbreeding from the male side is important, one or two male migrants should stabilize the inbreeding.

Die effek van migrasie op inteling is gemodelleer vir klein bevolkings met immigrante uit 'n groot onverwante bevolking. Verskillende migrasietempo's en aantalle manlike en vroulike diere is veronderstel en 'n algemene rekursievergelyking vir die vordering van inteling is afgelei. So 'n rekursievergelyking lei tot 'n ewewigsintelingskoëffisiënt waar die uitwerking van genetiese monstering en migrasie in balans is. In die geval van klein migrasietempo's en 'n groot aantal teeldiere word daar bewys dat migrasie van die geslag met die kleinste aantal teeldiere die ewewigsinteling sal minimaliseer. Migrasie van een geslag sal ook 'n voordeel hê in klein bevolkings met groot migrasietempo's. In klein bevolkings met gepaardgaande groot migrasietempo's is minder migrante nodig vir 'n gegewe ewewigsintelingskoëffisiënt as in groot bevolkings met klein migrasietempo's. As grensgeval is 'n vergelyking afgelei waar die aantal vroulike individue so groot is dat hulle bydrae tot inteling weglaatbaar klein is. Gebruiksvriendelike tabelle vir ewewigsinteling word gegee waar kuddegroottes en die aantal migrante in ag geneem word. Die algemene indruk in hierdie tabelle is dat 2–4 migrante inteling sal beheer vir 'n gelyke aantal manlike en vroulike diere. Met groot genoeg aantalle vroulike diere, sodat hulle bydrae tot inteling negeerbaar is, behoort een of twee manlike diere inteling binne aanvaarbare grense te hou.

Keywords: Inbreeding, migration, sex differences.

Introduction

The decline in fitness associated with inbreeding in normally cross-fertilizing organisms often necessitates its avoidance in animal and plant breeding (Falconer, 1989) or conservation (Frankel & Soulé, 1981). These references also provide evidence that even a small number of migrants may serve to limit inbreeding.

Probably the simplest situation by which the effect of migration on inbreeding can be modelled is that of a small population with immigrants from a large unrelated population, the size of which is large enough so that the contribution to inbreeding from the emigrant population can be ignored. Two practical examples of this situation comes to mind. The first is that of a zoo keeping a small population of a certain species for which a great number of potential emigrants exists in a nature reserve. The second example is that of a studbreeder of a popular breed.

Equilibrium inbreeding coefficient

The generally accepted didactic device for the description of inbreeding due to finite population size is to assume a population of N diploid parents contributing gametes to the next generation. It is supposed that the offspring come from pairs of gametes drawn at random from the independently large pool of gametes to which each parent contributes equally. The following recursion equation can then be derived (Crow & Kimura, 1970)

$$F_t = 1/2N + (1 - 1/2N)F_{t-1},$$

where F_t is the inbreeding coefficient of an individual in generation t. Assume migration from a very large unrelated noninbred population, with migration rate m. Then, again following Crow and Kimura (1970),

$$F_t = [1/2N + (1 - 1/2N)F_{t-1}](1 - m)^2, \tag{1.1}$$

with $(1-m)^2$ being the probability of sampling two gametes carrying native (nonmigrant) genes.

The equilibrium between the opposing effects of migration and restricted population size on the degree of genic identity by descent can be quantified by the equilibrium inbreeding coefficient, $F = F_t = F_{t-1}$. Solving for the equilibrium F from (1.1) gives

$$F = (1 - m)^2 / \{2N[1 - (1 - m)^2] + (1 - m)^2\}. \tag{1.2}$$

For small m, $(1 - m)^{-2} = 1 + 2m$, approximately, and (1.2) becomes

$$F = 1/(4mN + 1). \tag{1.3}$$

Equation (1.3) is the standard approximation (Crow & Kimura, 1970) for the equilibrium inbreeding coefficient, showing that the limitation of inbreeding by migration depends mainly on $mN = M$, the number of migrants in a population, independent of the population size.

Sex differences in numbers and migration rates

By solving the relevant recursion equations it can be shown (Crow & Kimura, 1970) that with $m = 0$, equation (1.1) gives a fair approximation to the progress in inbreeding with different numbers of two separate sexes in a small population by assuming

$$1/N_e = 1/4N_1 + 1/4N_2, \text{ or } N_e = 4N_1N_2/(N_1 + N_2),$$

where N_1 = number of males and N_2 = number of females in a population with size $N = N_1 + N_2$, and where N_e is the so-called effective population number which can be substituted in (1.1) in place of N to describe inbreeding due to finite population size.

From the equal genic contribution to offspring by the sexes, it is natural to define the effective migration rate (m_e) as equal to the mean of the male and female migration rates,

$$m_e = (m_1 + m_2)/2. \tag{1.4}$$

Substituting $m_e = (m_1 + m_2)/2$ and $N_e = 4N_1N_2/(N_1 + N_2)$ in (1.3), and writing $p_1 = N_1/(N_1 + N_2)$; $p_2 = N_2/(N_1 + N_2)$ for male and female frequencies respectively, and $m_1N_1 = M_1$ = number of male migrants and $m_2N_2 = M_2$ = number of female migrants gives

$$F = 1/\{8(p_1M_2 + p_2M_1) + 1\}, \tag{1.5}$$

but still based on die assumption of small migration rates.

From equation (1.5) two important conclusions follow:

Conclusion 1: With equal numbers of the two sexes in the population, the equilibrium inbreeding coefficient depends asymptotically only on the total number of migrants, regardless of their sex.

Proof: With $p_1 = p_2 = \frac{1}{2}$ (1.5) becomes $F = 1/[4(M_1 + M_2) + 1]$, equivalent to (1.3) with $M_1 + M_2 = M$, M being the total number of migrants.

Conclusion 2: With unequal numbers of the two sexes in the population, the equilibrium inbreeding coefficient will be minimized if, for a fixed number of migrants, all migrants are from the scarcer sex.

Proof: Assume $p_2 > p_1$ and write, from $M_1 = M - M_2$,

$$p_1M_2 + p_2M_1 = p_1M + M_1(p_2 - p_1).$$

Then, since M is fixed and $(p_2 - p_1)$ positive, it is clear that $p_1M_2 + p_2M_1$ is a maximum if M_1 is as large as possible, that is, $M_1 = M$. If $p_1M_2 + p_2M_1$ is a maximum, then F must be a minimum.

The foregoing two conclusions seem of great enough theoretical interest and practical importance to justify modelling a more realistic biological situation than the one portrayed by random union between an array of an infinite number of gametes from a finite set of parents. Additionally, it seems important to determine if the definition of effective migration rate can also be substantiated from inbreeding considerations, in addition to the gene frequency considerations employed in the derivation of (1.4).

Different migration rates and numbers for the two sexes

In the general formulation N_1, N_2, m_1, and m_2 will be defined as before, with the subscripts 1 referring to males and 2 to females. The development is closely analogous to the development of the formulas for inbreeding due to small populations with different proportions of the two sexes. The arguments will, therefore, be given in outline only. Details can easily be filled in from derivations of Crow and Kimura (1970).

Recursion equation

The probability that two genes in different individuals in generation t are both derived from the same native individual in generation $(t - 1)$ *is*

$$(1 - m_1)/4N_1 + (1 - m_2)/4N_2. \tag{1.6}$$

The probability of both genes derived from the same migrant individual in generation $(t - 1)$ is

$$m_1/4N_1 + m_2/4N_2. \tag{1.7}$$

The probability that two genes in different individuals in generation t are derived from different native males in generation $(t - 1)$ is

$$[(1 - m_1)^2 - (1 - m_1)/N_1]/4 \tag{1.8}$$

and, likewise, from different native females,

$$[(1 - m_2)^2 - (1 - m_2)/N_2]/4. \tag{1.9}$$

The probability that two genes are derived from native males and females is

$$(1 - m_1)(1 - m_2)/2. \tag{1.10}$$

The probability that two genes in different individuals in generation t are derived from different native individuals in generation $(t - 1)$ is, therefore, the sum of (1.8), (1.9) and (1.10), namely,

$$\{[(1 - m_1) + (1 - m_2)]^2 - (1 - m_1)/N_1 - (1 - m_2)/N_2\}/4. \tag{1.11}$$

The probabilities of native and migrant combinations are not necessary for further development since it is assumed that native and migrant individuals are unrelated.

Let G_t be the coefficient of consanguinity of two random native individuals in generation t, with the coefficient of consanguinity being the probability of a random gene from one individual being identical by descent to a random gene from the other. It follows by definition that

$$F_t = (1 - m_1)(1 - m_2)G_{t-1}, \tag{1.12}$$

since $(1 - m_1)(1 - m_2)$ is the probability of a mating between natives, and the coefficient of consanguinity between natives and migrants, and of migrants alone, are assumed equal to zero.

The probability that two genes from different individuals, derived from the same individual in the previous generation, are identical by descent must be

$$1/4 + 1/4 + (1/2)F_{t-1} = (1/2)(1 + F_{t-1})$$

for natives in generation t, and 1/2 for migrants, since migrants are assumed noninbred. Combining these probabilities of identity by descent with (1.6), (1.7) and (1.11) gives

$$G_t = [(1 - m_1)/N_1 + (1 - m_2)/N_2](1 + F_{t-1})/8 + (m_1/N_1 + m_2/N_2)/8 + \{[(1 - m_1) + (1 - m_2)]^2 - (1 - m_1)/N_1 - (1 - m_2)/N_2\} G_{t-1}/4. \tag{1.13}$$

Substituting (1.12) in (1.13) gives a recursion equation that can be solved to describe the progress in inbreeding of natives.

Equilibrium equation

Migration is likely to be used for the limitation of inbreeding, and the limiting or equilibrium inbreeding coefficient is, therefore, of greater interest than the recursion equation. Putting $F_t = F_{t-1} = F_{t-2} = F$ with F, the equilibrium inbreeding coefficient, in (1.12) and (1.13) then gives

$$F = (1 - m_1)(1 - m_2)/\{2N_e[1 - (1 - m_e)^2] + (1 - p_1m_2 - p_2m_1) \times$$
$$[2 - (1 - m_1)(1 - m_2)]\}, \tag{1.14}$$

with all terms as defined for (1.5).

Equation (1.14) does not appear to be directly amenable to the development of general rules for the limitation of inbreeding. Therefore, a number of special cases of general interest will be considered.

Small migration rates and large numbers of breeding animals

Assume m_1, $m_2 \rightarrow 0$, while the numbers of male and female migrants remain constant. Then (1.14) simplifies to

$$F = 1/[4m_eN_e + 1], \tag{1.15}$$

which immediately justifies the definition of the effective migration rate, $m_e = (m_1 + m_2)/2$, conjectured in (1.4). Hence the two important conclusions on male and female migrants, which follows from (1.5), hold in general under the assumptions on which (1.15) are based.

Equal migration rates and numbers

The restriction of separate sexes on the completely random union of gametes was ignored in the derivation of (1.2). Therefore, a situation with separate sexes is worth exploring, even if $m_1 = m_2 = m$. Under this assumption (1.14) reduces to

$$F = (1 - m)^2/\{2N_e[1 - (1 - m)^2] + (1 - m)[2 - (1 - m)^2]\}. \tag{1.16}$$

For m small (1.16) is approximately equal to (1.3). Denote the equilibrium F from (1.16) by $F(16)$ and that from (1.3) by $F(3)$. By straightforward but tedious algebra it can be shown that $F(16) \leq F(3)$, that is to say that equation (1.3) gives an upper limit to the solution to equation (1.16). This conclusion is also illustrated in Table 1, which is a tabulation of (1.16) in terms of numbers of migrants and herd size, with equal numbers for the two sexes (i.e. $N_1 = N_2 = N/2$). The limit value is the value obtained from (1.3), for a given number of migrants. This table may be of value for very small herds, for which even a small number of migrants represent a large migration rate. For example, for a herd size of eight or less, two migrants per generation may be adequate, and four migrants per generation may only be under consideration for herd sizes of more than 16.

It is of interest to note that (1.2) is an excellent approximation of (1.16). For example, if the first line of Table 1 is computed from (1.2), total agreement will be found for figures rounded to whole percentage values.

Table 1 Percentage inbreeding at equilibrium between the effects of migration and restricted population size with equal numbers of the two sexes

| Migrant number | Herd size | | | | | |
	2	4	6	8	16	Limit
2	0	3.6	5.8	7.0	8.9	11.1
4		0	1.0	1.9	3.7	5.9
6			0	0.4	1.9	4.0
8				0	1.0	3.0
16					0	1.5

Males only

Migrants all males and equal population numbers in the two sexes

Equal migration rates and equal numbers for the two sexes imply that only even numbers can appear in Table 1. Uneven numbers of migrants can best be handled by assuming migrants are all of the same sex. Consider only male migrants, that is, assume $m_2 = 0$. Then, with $N_1 = N_2 = N/2$, so that $p_2 = 1/2$, (1.14) reduces to

$$F = (1 - m_1)/\{m_1N_1(4 - m_1) + (2 - m_1)(1 + m_1)/2\}. \tag{1.17}$$

Table 2 is a tabulation of (1.17) in terms of numbers of male migrants $M_1 = N_1m_1$ and herd size. A comparison with Table 1 shows an advantage in inbreeding limitation in very small populations with migrants all of the same sex, even when the numbers of animals in the two sexes are equal. Otherwise the conclusions emanating from Tables 1 and 2 are equivalent.

Table 2 Percentage inbreeding at equilibrium between the effects of migration and restricted population size with equal numbers of the two sexes and with only male migration

| Male migrant number | Herd size | | | | | |
	2	4	6	8	16	Limit
1	0	10.8	14.0	15.5	17.7	20.0
2		0	4.2	6.2	8.7	11.1
3			0	2.3	5.2	7.7
4				0	3.3	5.9
8					0	3.0

Fewer breeding males

Conclusion 2, emanating from equation (1.5), suggests that for fewer breeding males than females only male migrants need to be considered. If the number of females is much larger than the number of males, it follows that

$$N_e = 4N_1, p_2 = N_2/(N_1 + N_2) = 1 \text{ and } p_1 = N_1/(N_1 + N_2) = 0, \tag{1.18}$$

approximately. Substituting (1.18) and $m_2 = 0$ in (1.14) results in

$$F = (1 - m_1)/[2N_1m_1(4 - m_1) + (1 - m_1^2)]. \tag{1.19}$$

For $m_1 \rightarrow 0$ and m_1N_1 constant (1.19) becomes

$$F = 1/(8m_1N_1 + 1). \tag{1.20}$$

Equation (1.20) is equivalent to (1.5) for $1/N_2$ negligible. Since all terms are positive it is immediately obvious that $F(19) < F(20)$ where $F(19)$ and $F(20)$ refer to equilibrium values from (1.19) and (1.20) respectively.

Even for a small number of migrants the migration rate may be large for a small number of males in the herd. Hence, Table 3 from equation (1.19) for large migration rates and a small number of males in the herd may be of value. For practical convenience it is in terms of numbers of males in the herd and migrant numbers. A manager can decide on a tolerable degree of inbreeding and decide, for example, that one or two migrant males should always be kept among the male members of the herd. The limit values in Table 3 are from (1.20).

Table 3 Percentage inbreeding at equilibrium between the effects of migration and restricted population size with male migration and large numbers of females

Migrant number	Number of males in herd						
	1	2	3	4	5	10	Limit
1	0	6.5	8.1	8.9	9.3	10.2	11.1
2		0	2.4	3.4	3.9	5.0	5.9
3			0	1.3	1.9	3.1	4.0
4				0	0.8	2.0	3.0
5					0	1.4	2.4
10						0	1.2

Emigration from a large number of equally inbred populations

Instead of emigration from a large unrelated population, one can consider emigration from a large number of equivalent small populations. The assumption is, therefore, that all members of a population are equally inbred, but all migrants are unrelated to each other and to members of the native population. This situation can be handled by a modification of (1.13) to

$$G_t = [1/N_1 + 1/N_2](1 + F_{t-1})/8$$
$$+ \{[(1 - m_1) + (1 - m_2)]^2 - (1 - m_1)/N_1 - (1 - m_2)/N_2\}G_{t-1}/4, \quad (1.21)$$

while (1.12) remains the same.

From (1.21) and (1.12) the equilibrium inbreeding coefficient is

$$F = (1 - m)^2/\{2N_e[1 - (1 - m)^2] + (1 - m^2)\}, \quad (1.22)$$

under the same assumptions as (1.16). Since $N \geq 2$, it is apparent that (1.22), (1.16) and (1.2) are close approximations to each other.

The conclusion is, therefore, that migration from a large number of more or less equally inbred, unrelated populations can be approximated from Tables 1, 2 and 3, which were constructed for migration from a single large population. In practice this probably approximates the situation for a studbreeder in a large breed. The likely situation for endangered species and smaller breeds will be modelled in the companion article (Roux, 1995).

Differences between alternative solutions

To justify developments in the companion article (Roux, 1995), it is important to know if the naive generalizations of (1.1) to the situation of different numbers for the two sexes,

$$F_t = [1/2N_e + (1 - 1/2N_e)F_{t-1}](1 - m_e)^2 \quad (1.23)$$

or

$$F_t = [1/2N_e + (1 - 1/2N_e)F_{t-1}](1 - m_1)(1 - m_2), \quad (1.24)$$

with all terms defined as for (1.5), can have equilibrium solutions approximately equal to the general (1.14).

Analogous to (1.2) the equilibrium solutions to (1.23) and (1.24) are

$$F = (1 - m_e)^2/\{2N_e[1 - (1 - m_e)^2] + (1 - m_e)^2\} \quad (1.25)$$

and

$$F = (1 - m_1)(1 - m_2)/\{2N_e[1 - (1 - m_1)(1 - m_2)] + (1 - m_1)(1 - m_2)\}. \quad (1.26)$$

Certainly for m_1, $m_2 \to 0$ and m_1N_1, m_2N_2 constant (1.25) and (1.26), like (1.14), are approximately equal to (1.15). However, for m_1 or $m_2 \to 1$ (1.26) is clearly a better approximation to (1.14) than (1.25). This suggests that (1.26) should be preferred above (1.25) as an approximation to (1.14), if $m_1 \neq m_2$. For $m_1 = m_2$, (1.25) = (1.26). If Tables 2 and 3 are rounded to whole percentage values, calculations from (1.26) instead of (1.17) or (1.19) give equivalent results.

Equation (1.26) is comparable to a specialization from a more complex and general model presented by Chesser et al. (1993). For exactly two offspring per female and the variance in the number of females mated to a male equal to the mean, their equation (49) and (1.26) are approximately equal to each other.

Discussion

The equation (1.2), representing the equilibrium between the effects of migration and restricted population size, dates back to Wright's (1943) work on population structure in what he termed the island model. In this article Wright's formula (1.2) for the equilibrium inbreeding coefficient was generalized to accommodate sex differences in population numbers and migration rates with practical application in conservation and animal breeding in view. Nevertheless, this generalization remains of limited value as the requirement of unrelated migrants may be difficult to achieve in many practical situations. However, in the context of equiprobable migration between subpopulations, the maximum difference $(1 - k)$ in inbreeding coefficients of such populations and a conceptual aggregate random mating population can be shown to be asymptotically equal to the equilibrium inbreeding coefficient. The development of this approach is the topic of the second article in this series (Roux, 1995), in which the results from the present article will be important for the justification of generalizations allowing practical application in conservation and animal breeding. Even the tables will present important baselines for the maximum difference $(1 - k)$ mentioned above.

References

CHESSER, R.K., RHODES, O.E., SUGG, D.W. & SCHNABEL, A. 1993. Effective sizes for subdivided populations. Genetics 135, 1221.

CROW, J.F. & KIMURA, M. 1970. An introduction to population genetics theory. Harper and Row, New York.

FALCONER, D.S. 1989. Introduction to quantitative genetics. Third Edition. Longman, Harlow.

FRANKEL, O.H. & SOULÉ, M.E. 1981. Conservation and evolution. University Press, Cambridge.

ROUX, C.Z. 1995. Countering inbreeding with migration. 2. Migration from related populations. S. Afr. J. Anim. Sci., 25, 44

WRIGHT, S. 1943. Isolation by distance. Genetics 28, 114.