

Countering inbreeding with migration

2. Migration from related populations

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In conservation and breeding, large populations are important for evolutionary viability and selection progress. On the other hand, practical and economic reasons may exist for population subdivision. These populations (islands) may be tied together to form effectively a single population (archipelago) by migration rates of acceptable magnitude. The acceptability of migration rates is judged by the maximum difference $(1 - k)$ in inbreeding between a subpopulation, of size N , and a conceptual aggregate random mating population of size Nn , with n equal to the number of subpopulations. For small migration rates (m) and large subpopulation sizes this maximum difference $(1 - k)$ is equal to $1/\{4M(n + 1)/(n - 1) + 1\}$, where $M = mN$, the number of migrants in each subpopulation. For large n this result is equivalent to the standard result of the limit inbreeding coefficient of a subpopulation (single island) with migration from a very large noninbred population, $1/(4M + 1)$. The recommendations for the limitation of inbreeding are, therefore, equivalent to the single island situation for a large number of subpopulations, while a small number of subpopulations (n) requires less migration than a large number. For large migration rates and small subpopulation sizes exact results are available. The general conclusion is that these situations require less migration for a given maximum difference $(1 - k)$ than small rates and large population sizes. The rules for different male and female migration rates are the same as for migration from a large unrelated population (single island situation). Indeed, adjustment with a factor of $(n - 1)/(n + 1)$ allows most conclusions on number of migrants and maximum difference $(1 - k)$ in inbreeding coefficients to carry over from the single island to the archipelagic situation.

In bewaring en teling is groot bevolkings nodig vir evolusionêre oorlewing en seleksievordering. Aan die anderkant mag daar praktiese en ekonomiese redes wees vir die onderverdeling van bevolkings. Onderverdeelde bevolkings (eilande) kan saamgebind word vir 'n enkele bevolking (argipel) deur migrasietempo's van aanvaarbare grootheidsordes. Die aanvaarbaarheid van migrasietempo's word gemeet aan die maksimum verskil $(1 - k)$ in inteling tussen 'n subbevolking met N lede en 'n konseptuele samegevoegde panmiktiese bevolking met Nn lede, waar n gelyk is aan die aantal subbevolkings. Vir klein migrasietempo's (m) en groot subbevolkings is die maksimum verskil $(1 - k)$ gelyk aan $1/\{4M(n + 1)/(n - 1) + 1\}$, waar $M = mN$, die aantal migrante in elke subbevolking. As n groot is, is hierdie resultaat gelyk aan die limiet van die intelingskoëffisiënt van 'n subbevolking (eiland) met migrasie vanaf 'n baie groot onverwante bevolking, $1/(4M + 1)$. In die geval van 'n groot aantal subbevolkings is die aanbevelings vir die beperking van inteling dus gelyk aan die standaard aanbevelings wat afgelei kan word vir 'n enkele bevolking terwyl 'n klein aantal subbevolkings (n) minder migrante nodig het. In die geval van groot migrasietempo's en klein subbevolkings is eksakte afleidings beskikbaar. Die algemene gevolgtrekking is dat hierdie situasie minder migrante nodig het as die teenoorgestelde geval van klein migrasietempo's en groot aantalle in die subbevolkings. Die reëls vir geslagverskille in migrasietempo's is dieselfde as vir migrasie vanaf 'n groot onverwante bevolking na 'n enkele eiland. As die aantal migrante in die maksimum verskil $(1 - k)$ met 'n faktor $(n - 1)/(n + 1)$ aangepas word, kan die meeste gevolgtrekkings oor die enkeleilandmodel oorgedra word na die argipelmodel.

Keywords: Inbreeding, migration, sex differences.

Introduction

Among reasons given for the subdivision of populations into smaller breeding groups are those related to economics, space, facilities, health and exposure to a wider public, as in zoos, where the subdivision may also contain the spread of epidemics. In conservation biology and animal breeding, on the other hand, evolutionary and entrepreneurial arguments may be raised for the integration of geographically separated subpopulations into larger breeding units, with the ultimate aim of being able to treat a whole race, breed or species as a single breeding unit. The migration rates necessary to integrate subpopulations into an effectively single breeding population then become of major importance. Inbreeding is a reflection of effective population size. Hence, one way of achieving an effectively single breeding population is to keep inbreeding in the subpopulations within specified limits from that of a single conceptual aggregate random mating population.

In the first article of this series (Roux, 1995) inbreeding in a subpopulation was described for a system of migration of individuals from a large unrelated population, or from a large

number of unrelated subpopulations of equal size. In this situation inbreeding in a finite subpopulation is arrested by unrelated migrants. In contrast, small total population sizes will cause subpopulations to become related as a consequence of migration. One way in which such a situation can be described is by the finite island model (Crow, 1986), in contradistinction to that of the first article, which can be described as the infinite island model. Perhaps more apt terms would be the archipelago and single island models of migration and inbreeding.

Chesser *et al.* (1993) derived recursion formulas for the archipelagic situation for dioecious organisms from which the progress in inbreeding can be calculated. Unfortunately, the mathematically explicit solutions to the recursion equations are too complex to gain understanding of the dynamics of the situation. Chesser *et al.* (1993) circumvented the problem by the device of deriving effective population numbers. However, using the relevant effective population numbers to calculate the progress in inbreeding is only slightly less tedious than numerical iterations based on the full recursion equations (Chesser *et al.*, 1993).

In this article the problem will be simplified by an extension of the standard monoecious approximation to the dioecious situation. Both Kempthorne (1969) and Crow & Kimura (1970) show that this approximation is very good, even for small population sizes. Furthermore, extensions to migration in the dioecious situation will be validated by comparison to the special case of a very large number of islands for which an exact solution is available from Roux (1995).

Recursion equations and their solutions for monoecious organisms in the archipelagic situation have been obtained by Latter (1973) in terms of the degree of heterozygosity in subpopulations or islands. As this is inconvenient for the calculation of inbreeding coefficients and the comparison of conclusions with the conventional approach, Latter's (1993) results will be transcribed from heterozygosities to inbreeding coefficients in terms of the development found in Li (1976) and also to be found in Crow (1986). The solutions to the recursion equations will then be used for an exploration of the dynamics of inbreeding under migration for the purpose of development of useful rules of thumb for countering inbreeding by migration. Important extensions approximating the dioecious case will be indicated for differences between the sexes in number and migration rate and validated by comparisons to solutions from Chesser *et al.* (1993) and Roux (1995).

The correction for migration in the finite island model effectively precludes self-fertilization (Crow & Kimura, 1970). The formulas for a truly monoecious situation in which self-fertilization is included will also be indicated.

Recursion equations and their solutions

Exact solutions

Consider n islands in an archipelago, each with a population of size N , so that the total population number is equal to Nn . On each island there is a proportion of m migrants, arriving with equal probability from the other $(n - 1)$ members of the archipelago. Let

$$c = 1/2N,$$

a = the probability that two random individuals from the same population were on the same island a generation earlier;

b = the probability that two random individuals from different islands were on the same island a generation earlier. Therefore, $1 - a$ and $1 - b$ are the probabilities that two individuals were on different islands a generation earlier. Furthermore, let F_t be the probability in generation t that two alleles on the same island are identical by descent, and f_t the probability in generation t that two alleles on different islands are identical by descent.

The natural extension of the single island equation (Crow, 1986),

$$F_t = (1 - m)^2[c + (1 - c)F_{t-1}], \quad (2.1)$$

to the archipelagic situation is then

$$\begin{aligned} F_t &= a[c + (1 - c)F_{t-1}] + (1 - a)f_{t-1} \\ f_t &= b[c + (1 - c)F_{t-1}] + (1 - b)f_{t-1}. \end{aligned} \quad (2.2)$$

Crow (1986) provides a proof that

$$a = (1 - m)^2 + m^2/(n - 1), \quad b = (1 - a)/(n - 1).$$

For further development it is more convenient to work with the panmictic coefficients $P_t = 1 - F_t$ and $Q_t = 1 - f_t$. Equations (2.2) then transform to

$$\begin{aligned} P_t &= a_{11}P_{t-1} + a_{12}Q_{t-1} \\ Q_t &= a_{21}P_{t-1} + a_{22}Q_{t-1}, \end{aligned} \quad (2.3)$$

with

$$\begin{aligned} a_{11} &= a(1 - c), \quad a_{12} = 1 - a \\ a_{21} &= b(1 - c), \quad a_{22} = (1 - b). \end{aligned}$$

The characteristic roots of the 2×2 matrix associated with (2.3) are

$$\lambda_1, \lambda_2 = [(a_{22} + a_{11}) \pm \{(a_{22} - a_{11})^2 + 4a_{12}a_{21}\}^{1/2}]/2. \quad (2.4)$$

The intrapopulation solution to (2.3) is

$$P_t = k\lambda_1^t + (P_0 - k)\lambda_2^t, \quad (2.5)$$

with

$$k = (P_1 - P_0\lambda_2)/(\lambda_1 - \lambda_2)$$

and

$$P_1 = a_{11}P_0 - a_{12}Q_0.$$

Assume that $P_0 = Q_0 = 1$, then

$$k = (1/2) + (1/2)(a_{11} + 2a_{12} - a_{22})/\{(a_{22} - a_{11})^2 + 4a_{12}a_{21}\}^{1/2}, \quad (2.6)$$

if $\lambda_1 > \lambda_2$ from (2.4). The theory behind (2.4–2.6) is available from Crow and Kimura (1970). Equations (2.4), (2.5) and (2.6) are equivalent to Li's (1976) (5a) and (5b), but simplify the notational complexities employed by him to accommodate the possibility of a balance between mutation and migration in the limit values of P and Q .

Asymptotic and approximate solutions

Define

$$m' = mn/(n - 1). \quad (2.7)$$

Assuming m and $1/N$ small enough so that squares and products are negligible and that $16m'N/n$ is small in comparison to $(1 + 4m'N)^2$, it follows from Latter (1973) that

$$\lambda_1 = 1 - \{1/2N(n - 1)\}\{4m'N/(4m'N + 1)\}, \quad (2.8)$$

for the larger root in (2.4). In a more symmetrical form (2.8) is equal to

$$\lambda_1 = 1 - (1/2Nn)\{4m'N/(4m'N + 1)\}. \quad (2.9)$$

The same assumptions as (2.8), and including only the dominant terms, give the second root in (2.4) as, approximately,

$$\lambda_2 = 1 - (1/2N)\{1 + 4m'N\}. \quad (2.10)$$

Numerical calculations show that, for small sizes of n ,

$$\lambda_1 = 1 - 1/2Nn \quad (2.11)$$

provides adequately accurate approximations to (2.4). For example, for $N = 32$, $n = 2$, $mN = 2$, the difference between (2.4) and (2.9) = -2.6×10^{-4} , and between (2.4) and (2.11) = 2.0×10^{-4} .

The excellent performance of (2.11) for small n , suggests approximating the term $4Nm'/(4Nm' + 1)$ by unity, and replacing the factor $1/(n - 1)$ in all terms by $1/n$ so that analogous to the derivation of (2.9), (2.6) simplifies to

$$k = 4m'N/\{4m'N + (n - 1)/(n + 1)\} \quad (2.12)$$

If the factor $1/(n - 1)$ [v (2.8)] is retained in all terms of (2.6), it simplifies to

$$k = 4m'N/[4m'N + \{(n - 1)/n\}^2], \quad (2.13)$$

instead of (2.12). For large n both (2.12) and (2.13) become

$$k = 4m'N/(4m'N + 1). \quad (2.14)$$

Asymptotic behaviour of panmictic indices

Asymptotically the system (2.5) is determined by the larger root. It is therefore of interest to compare the behaviour of

$$P_t(15) = k(1 - k/2Nn)^t, \tag{2.15}$$

for large n , from (2.9), and $k = 4mN/(4mN + 1)$ to the panmictic index of an aggregate random mating population

$$P_t(16) = (1 - 1/2Nn)^t. \tag{2.16}$$

Since $1 - k/2Nn \geq 1 - 1/2Nn$, it is clear that it may be true that $P_t(15) > P_t(16)$ for t large enough.

Using exponential approximations it turns out that

$$t > (-lnk)(2Nn)/(1 - k), \tag{2.17}$$

for $P_t(15) > P_t(16)$. Since $-lnk > (1 - k)$ for $0 < k < 1$, (2.17) implies that the smaller the value of k , the longer the time before $P_t(15) > P_t(16)$ and, furthermore, the time must be of order $2Nn$ before $P_t(15) > P_t(16)$. Since Nn must be large for (2.15) to hold, the value of t from (2.17) may be too large to be of practical importance for animal breeding and conservation. For t smaller than $2Nn$ it would be better to control inbreeding by choosing k as near to unity as is practically possible, since $P_t(15) \rightarrow P_t(16)$ for $k \rightarrow 1$.

For n large (2.15) and (2.16) indicate that the relative asymptotic difference (*rad*) in the panmictic indices of a subpopulation of size N relative to a single aggregate random mating population of size Nn is

$$rad \leq (1 - k), \tag{2.18}$$

with the equality holding for n small, from (2.11).

Maximum difference between inbreeding coefficients

Denote λ_1 from (2.11) by $\lambda_1(11)$ and λ_1 from (2.9) by $\lambda_1(9)$. From (2.5) and (2.16) the asymptotic difference (d) in inbreeding coefficients of an island subpopulation of size N and a single random mating aggregate population of size nN is

$$d = \lambda_1'(11) - k\lambda_2'(9) - (1 - k)\lambda_2'. \tag{2.19}$$

Hence, since $\lambda_1(9) \geq \lambda_1(11)$

$$d \leq (1 - k)(\lambda_1'(9) - \lambda_2'). \tag{2.20}$$

Furthermore $1 > \lambda_1 > \lambda_2$, so that (2.20) implies

$$d < (1 - k)\lambda_1'(9), \tag{2.21}$$

or

$$d < (1 - k). \tag{2.22}$$

λ_1 may often be near enough to unity and λ_2 small enough for (2.22) to provide a useful upper limit for the difference in inbreeding coefficients for moderate t . This can be confirmed by first order approximations to binomial expansions of $\lambda_1(9)$ and $\lambda_1(11)$ and by the example in Table 3. That equation (2.22) is also applicable to small population sizes and large migration rates will be illustrated by a comparison between Tables 1 and 2.

Controlling inbreeding in subpopulations

Rationale

In many breeding or conservation situations, considerations involving resource restrictions, evolutionary viability (Frankel & Soulé, 1981) or probability of selection gain (Nicholas, 1980) would probably fix the total population size (Nn). In such situations (2.18), (2.21) and (2.22) indicate that inbreeding can be controlled in subpopulations by migration of such a nature that

the maximum difference $(1 - k)$, between a subpopulation of size N and a conceptual aggregate random mating population of size Nn , is acceptably small. Since the variance in gene frequencies between subpopulations is a function of the inbreeding coefficient of a population (Crow & Kimura, 1970) it is clear that controlling subpopulation inbreeding is equivalent to controlling subpopulation divergence.

An additional consideration could be to limit inbreeding in the subpopulations to a rate that would allow its effects to be countered by natural selection. Guidelines for this approach are available from Frankel & Soulé (1981). In such a situation, adding approximations of the maximum difference $(1 - k)$ to the conceptual total population inbreeding coefficient can provide a quick first approximation to the rate of inbreeding, indicating the range of migration rates necessary for a desired result. This preliminary range can then be fine-tuned for a desired time interval by exact calculations from (2.5).

Approximations

Exact calculations from (2.6) for N large show that $(1 - k)$ from (2.12) is the best estimate of a upper limit for $(1 - k)$. Hence, from (2.12)

$$1 - k = 1/\{4mN(n + 1)/(n - 1) + 1\}. \tag{2.23}$$

For n large enough so that terms involving $1/(n - 1)$ can be ignored in relation to the others, (2.6) allows simplification to

$$1 - k = (1 - m)^2/[2N\{1 - (1 - m)^2\} + (1 - m)^2], \tag{2.24}$$

precisely equal to (1.2) in Roux (1994), the equilibrium inbreeding coefficient in the single or infinite island situation.

Representative examples

Table 1 gives values of $(1 - k)$ calculated for a representative set of parameters. It was calculated in the following way:

1. $M = 1, M = 2$ indicates one or two migrants per subpopulation of either sex. Equal numbers for the two sexes are assumed.
2. The columns involving $N = 4, 8, 32$ were calculated from (2.6) for $n \leq 101$. The columns involving the limit values were calculated from (2.23). The row for $n - 1 = \infty$ was calculated from (2.24).

Table 2 was calculated to illustrate that equation (2.22) represents a useful estimate of the difference between the inbreeding coefficients of an aggregate population and that of subpopulations connected by migration. Note the remarkable agreement of

Table 1 Percentage values of $(1 - k)$ for different numbers (n) of subpopulations, different subpopulation sizes (N) and different numbers of migrants per subpopulation (M)

$n - 1$	$N = 4$		$N = 8$		$N = 32$		Limit	
	$M = 1$	$M = 2$	$M = 1$	$M = 2$	$M = 1$	$M = 2$	$M = 1$	$M = 2$
∞	13.8	4.0	17.0	7.4	19.2	10.2	20.0	11.1
100	13.6	3.9	16.7	7.3	19.0	10.0	19.7	10.9
10	11.6	2.9	14.6	6.0	16.9	8.6	17.2	9.4
5	9.7	2.0	12.6	4.9	14.8	7.4	15.2	8.2
3	7.7	1.2	10.4	3.8	12.6	6.1	13.0	7.0
2	5.8	0.6	8.3	2.9	10.3	4.8	11.1	5.9
1	2.4	0.0	4.4	1.1	6.0	2.7	7.7	4.0

Table 2 Percentage inbreeding coefficients at generation 10 ($t = 10$) for different numbers (n) of subpopulations of size $N = 8$, with one or two migrants per generation (M) compared to an aggregate population of size Nn ($M = N(n - 1)/n$), together with the differences between aggregate and subpopulations

$(n - 1)$	Inbreeding coefficient			Difference	
	$M = 1$	$M = 2$	$M = N(n - 1)/n$	$M = 1$	$M = 2$
	100	17	8	1	16
10	18	11	6	12	5
5	20	14	10	10	4
3	22	17	15	7	2
2	24	21	19	5	2
1	29	28	27	2	1

approximately one to three percentage points between the differences in Table 2 and the corresponding values for $N = 8$ of $(1 - k)$ in Table 1. This is also true for the other values of N in Table 1, indicating that (2.22) is also applicable to small population sizes and large migration rates.

Specific example

Perhaps a more extensive example than the ones in Table 2 will be worth while, especially since it gives an illustration of the possible strength and utility of migration between subpopulations. Consider the percentage inbreeding from (2.4), (2.5) and (2.6) in the situation with subpopulation size $N = 32$, number of subpopulations $n - 1 = 100$, number of migrants $M = 0, 1/2, 1, 2$, compared to the inbreeding in a single aggregate population with $Nn = 3232$, given in Table 3.

Table 3 Percentage inbreeding in a subpopulation of size $N = 30$ compared to a single aggregate population of size $Nn = 3232$

Generation	Number of migrants				Single population
	0	1/2	1	2	$M = N(n - 1)/n$
10	15	13	11	8	0
30	38	15	18	10	1
50	55	30	19	11	1
$1 - k$	-	33	19	10	from(2.6)

Note the high percentage of inbreeding in a population of size $N = 32$ with no migration in generation 50, and how two migrants per generation effectively controls it. Furthermore, for all migration numbers $(1 - k)$ is an excellent estimate of the maximum differences with the single aggregate population.

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)? The answer is in Table 4, which was constructed from Table 1 by interpolation. For $Nn < 100$ and $M = 2$ the best values of Nn are

Table 4 Percentage values of $(1 - k)$ for different total population sizes (Nn) different subpopulation sizes (N) and different numbers of migrants per subpopulation (M)

Nn	$M = 1$			$M = 2$		
	$N = 4$	$N = 8$	$N = 32$	$N = 4$	$N = 8$	$N = 32$
24	10	8	-	2	3	-
64	12	15	6	3	6	3
96	12	15	10	3	6	5
192	13	16	15	3	6	7
352	14	16	17	4	7	9
3200	14	17	19	4	7	10

along both edges, that is, either as small or as large values as possible for N , if $N = 2$ is excluded, as from (2.24) $(1 - k)$ might be equal to zero. The disadvantage of the middle values is probably small enough, though, so that other considerations, like transport cost, protection against epidemics, etc., could be decisive. For $Nn > 100$ the lowest values of $(1 - k)$ occur for $N = 4$, and with an increase in Nn the values of $1 - k$ will approximate the limit (first) line in Table 1.

Discussion

Approximations to binomial expansions involving (2.5), (2.9) and (2.10), confirmed by the numerical calculations for $N = 32$ in the specific example (Table 3), show that the pattern of response in inbreeding in a island population is characterized by a relatively sharp initial increase under the influence of subpopulation size (N), followed by a slower increase determined mainly by total archipelagic population size (Nn). The initial increase in inbreeding is faster than that of an aggregate panmictic population of size Nn , while the increase may be slightly slower in the later phase.

At any given generation the inbreeding coefficient of an island subpopulation will always be larger than that of an aggregate panmictic population of size nN . However, it follows from the inequality (2.22) that this difference (d) will always be less than $(1 - k)$ for small migration rates and large subpopulation sizes, with k defined by (2.6). However, the results from Table 2 strongly suggest that (2.22) is applicable to all situations.

Large subpopulation sizes

For large subpopulation size (N), a large number of islands (n) and small migration rates (m) the value of the maximum difference $1 - k$ (2.23) depends only on the number of migrants, $1 - k = 1/(4M + 1)$. From the following table

Number of migrants	1	2	3	4	5	6	8	12	25
$(1 - k)\%$	20	11	8	6	5	4	3	2	1

it is clear that as few as two to six migrants per subpopulation per generation will go a long way to limit inbreeding of subpopulations to a value near to that of a panmictic population of size Nn .

For a small number of subpopulations n , the difference in inbreeding coefficients between the subpopulations and aggregate population will be less than (2.23). It follows that fewer migrants will be required for a given value of $(1 - k)$ if the

number of subpopulations decreases. For $n = 3$, the number of migrants needed for a given $(1 - k)$ will be half that required for a very large value of n .

Small subpopulation sizes

For small subpopulation sizes migrant rates can be large. In this situation Table 1 provides values of $(1 - k)$ in the somewhat restricted situation of one or two migrants for a representative set of values for population size (N) and number of subpopulations (n). From Table 1 it is clear that the adjustment in migration number for constant $(1 - k)$ from (2.23) holds to a fair approximation for all values of N . For example, for $N = 8$, $n - 1 = \infty$, $M = 2$, $(1 - k)$ is equal to 7.4%, and this is close to the 8.3% from $M = 1$, $n - 1 = 2$, as one would expect from $(n - 1)/(n + 1) = 2$, in (2.23). For $N = 32$ the approximation is very good.

From (2.23)

$$(1 - k) = \{(n - 1)/(n + 1)\} \{1/(4M + 1)\}, \quad (2.25)$$

approximately. This suggests that (2.24) might be adjusted to

$$(1 - k) = \{(n - 1)/(n + 1)\} (1 - m)^2 / [2N\{1 - (1 - m)^2 + (1 - m)^2\}] \quad (2.26)$$

as a quick first approximation for $(1 - k)$ with small values of n . This can be verified for $N \geq 6$ from Table 1 and from additional computations. Since the equivalent equations (2.24) and (1.2) (from Roux, 1995) can be approximated by the first table in Roux (1995), this table can be used for quick first approximations of $(1 - k)$ by adjusting the limit inbreeding coefficient $[= (1 - k)]$ by a factor of $(n - 1)/(n + 1)$ according to (2.26).

Conclusion

The foregoing can be summarized by the following conclusion. As the equilibrium inbreeding coefficient (F) and maximum difference in inbreeding between the subpopulations and a random mating total population ($1 - k$) are equivalent for a large number of subpopulations (n) (equations 2.24, 1.2), the same conclusions hold for $(1 - k)$ in this article as for equilibrium F in the previous article (Roux, 1995). For small values of n , both the number of migrants (M) and $(1 - k)$ can be adjusted by $(n - 1)/(n + 1)$ to excellent approximations, except for $N = 4$ in the case of $(1 - k)$.

Including self-fertilization

The correction in $(1 - m)^2$ in (2.1) effectively precludes self-fertilization (Crow & Kimura, 1970). The inclusion of self-fertilization with random mating can be achieved by changing (2.1) to

$$F_t = c + [(1 - m)^2 - (1 - m)c]F_{t-1}. \quad (2.27)$$

Where $c = 1/2N =$ probability of drawing two gametes carrying copies of the same gene and $(1 - m)^2 - (1 - m)/2N =$ probability of drawing two gametes carrying copies of two different native genes. It is assumed that native and migrant genes cannot be identical by descent and that migrants are completely unrelated and noninbred. The extension of (2.27) to the archipelagic situation would change a_{11} in (2.3) to

$$a_{11} = a - c, \quad (2.28)$$

with a_{12} , a_{21} , and a_{22} remaining the same.

The asymptotic solutions (2.9), (2.10) and (2.13) remain the same, since the asymptotic values of a_{11} in (2.28) and (2.3) are equivalent. The results in Tables 1, 2 and 3, however, are no longer applicable. In general, it appears that $(1 - k)$ from (2.28) and (2.6) is larger than (2.23) instead of smaller as with self-fertilization excluded. If random mating with the inclusion of self-

fertilization is important, exact calculations from (2.28), (2.4), (2.5) and (2.6) are recommended for m large and n, N small.

Sex differences in migration rates and population numbers

In the derivation of (2.24) it was noted that, for a large number of subpopulations, $(1 - k)$ of this article is equivalent to the comparable equilibrium F in Roux (1995). In Roux (1995) a general equilibrium F was derived for sex differences in migration rates and population numbers. Denote male and female migration rates and population numbers by m_1 , m_2 and N_1 , N_2 , and define $1/N_e = 1/4N_1 + 1/4N_2$. In the discussion of (1.26) of Roux (1995) it was noted that replacement of N by N_e and $(1 - m)^2$ by $(1 - m_1)(1 - m_2)$ in (2.24) or (1.2) resulted in good approximations to the general (1.14). This suggests that sex differences in numbers be taken in consideration in (2.2) from

$$a = (1 - m_1)(1 - m_2) + m_1 m_2 / (n - 1) \text{ and } c = 1/2N_e. \quad (2.29)$$

Values for $(1 - k)$ can be approximated from Tables 2 and 3 in Roux (1995) in the same way as indicated for Table 1 from (2.26). The adjustment by $(n - 1)/(n + 1)$ to migration numbers for constant $(1 - k)$ is also the same.

Substituting (2.29) in (2.24) is approximately equal to Chesser *et al.*'s (1993) equation (49), with the approximation involving only the effective population number, N_e . If there are exactly two offspring per female and if the variance in the number of females mated to a male is equal to the mean, Chesser *et al.*'s (1993) terms involving numbers of males and females per subpopulation would approximate N_e .

Constant family size

The accommodation of different numbers of the two sexes in (2.29) suggests that $c = 1/2N$ in (2.2) can be generally replaced by $c = 1/2N_e$ to handle all sorts of deviations from simplistic initial assumptions. In the present context the most important is to note that the maximum difference $(1 - k)$, from (2.22) and (2.23), also depends on N_e . For instance, with constant family sizes $N_e = 2N$, approximately, with N equal here to the census number (Falconer, 1989). This implies that (2.23) with $mN = M$ changes to $1 - k = 1/\{8M(n - 1)/(n - 1) + 1\}$, an appreciable gain over the situation of variable family sizes. If a sire is replaced by a son, and a dam by a daughter, $1/N_e = 3/16N_1 + 1/16N_2$ (Falconer, 1989). With N_2 large and only male migration, the formula $m_e = (m_1 + m_2)/2$ in Roux (1994) gives $1 - k = 1/\{(32/3)M_1(n + 1)/(n - 1) + 1\}$, instead of $1 - k = 1/\{8M_1(n + 1)/(n - 1) + 1\}$, for (2.23) with $M_1 =$ number of male migrants.

Relationship of $(1 - k)$ to G_{ST}

The coefficient of gene differentiation, G_{ST} , is a measure of subpopulation differentiation explicated by Nei (1975). With an equilibrium between drift, mutation and migration

$$G_{ST} = 1/[4mN\{n/(n - 1)\}^2 + 1], \quad (2.30)$$

for mutation rates much smaller than migration rates (Takahata & Nei, 1984; Crow, 1986). This equilibrium value of G_{ST} is precisely equal to $(1 - k)$ from (2.13). The equivalence between (2.30) and $(1 - k)$ from (2.13) ultimately derives from a general correspondence between the definitions of the relative asymptotic difference in (2.18) and Nei's G_{ST} .

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