



Migration and inbreeding: the importance of recipient population size for genetic management

John A. Vucetich^{1*} & Thomas A. Waite²

¹ School of Forestry, Michigan Technological University, Houghton, MI 49931, U.S.A.; ² Department of Evolution, Ecology, and Organismal Biology and Department of Anthropology, Ohio State University, Columbus, OH 43210, U.S.A. (*Author for correspondence: javuceti@mtu.edu)

Received 26 July 2000; accepted 6 October 2000

Key words: effective population size, gene flow, migration, one-migrant-per-generation

Abstract

Sewall Wright demonstrated 70 years ago that the number of migrants required to maintain specified levels of gene flow (i.e. avoid excessive inbreeding) is virtually independent of the size of the recipient population. According to conventional wisdom, this idea is valid provided population size exceeds ~ 20 . It is well known that this independence implicitly assumes that a population's effective size (N_e) is equal to its census size (N). However, it is not obvious whether independence between the required number of migrants (to avoid excessive inbreeding) and population size constitutes a reasonable assumption for real populations of conservation concern. Relying on empirical data, we demonstrate that for real populations, the assumption (i.e. $N_e = N$) is routinely violated to a degree such that the required number of migrants is strongly dependent on the size of the recipient population. Because a population's effective size (N_e) is typically much smaller than its census size (N), the number of migrants required to avoid inbreeding is actually dependent on N even when it is considerably greater than 20. For example, when $N_e/N = 0.1$, the number of migrants required to maintain the inbreeding coefficient (F) at 0.2 doubles (from 4 to 8) as N increases from 9 to 60. Similarly, when $N_e/N = 0.05$, the number of migrants required increases by 50% as N increases from 18 to 45, and increases again by 50% as N increases from 45 to 260. Thus, for populations much larger than 20, the required number of migrants increases asymptotically with N , and dramatically so when $N_e/N \ll 1$. Simple conventions regarding the requisite number of migrants may not apply to many populations of conservation concern. Genetic management should routinely rely on models that explicitly account for this and other recent considerations. Failure to do so may jeopardize the viability of populations that are sensitive to altered levels of inbreeding.

'Where m [the migration rate] is less than $1/2N$ there is a tendency toward chance fixation of one or the other allelomorph. Greater migration prevents such fixation. How little interchange would appear necessary to hold a large population together may be seen from the consideration that $m = 1/2N$ means an interchange of only one individual every other [*sic*] generation, *regardless of the size of the subgroup* [emphasis ours].' – S. Wright (1931: 127–128).

Introduction

The theory of gene flow plays a central role in the genetic management of conserved plant and animal populations (Frankham 1995a; Mills and Allendorf 1996). The most notable application of this theory

is the rule that, *regardless of their size*, populations receiving one migrant per generation will maintain an equilibrium inbreeding coefficient (F) of 0.2. The basis of this one-migrant-per-generation (OMPG) rule is the expression that approximates the equilibrium inbreeding coefficient (F) of an ideal population that

receives migrants (Futuyma 1986):

$$F \approx 1/(4Nm + 1), \quad (1)$$

where N is the size of the ideal population, m is the migration rate (migrants per generation), and Nm is the number of migrants required to maintain F at a particular value. Specifically, the OMPG rule arises because $Nm = 1$ when $F = 0.2$ in Equation (1), which depends on all of the assumptions of Wright's (1931) island model (see Mills and Allendorf [1996] for a review of these assumptions as they pertain to the OMPG rule). This somewhat arbitrary level of F is thought to represent an appropriate balance between the conflicting goals of avoiding inbreeding depression (e.g. Jimenez et al. 1994; Keller et al. 1994; Sachherri et al. 1998) and maintaining local adaptation (Mills and Allendorf 1996).

An elegant, purported property of the OMPG rule is that Nm is (virtually) independent of N . This arises because F is very close to 0.2 (i.e. within 6%) for populations receiving OMPG for all values of $N > 20$ (Figure 1; see also Figure 3 of Mills and Allendorf 1996). The deviation for populations with effective sizes of less than 20 is considered to be inconsequential since such small populations are likely to go extinct due to demographic and environmental stochasticity (Mills and Allendorf 1996). Thus, Nm is virtually independent of N under the assumptions of the OMPG rule.

Because it derives from Equation 1, the OMPG rule strictly applies to ideal populations, for which $N_e = N$. Thus, the OMPG should strictly be read as: regardless of their *effective* (rather than census) size, populations receiving one migrant per generation will maintain an equilibrium inbreeding coefficient (F) of 0.2. Because for most real populations $N_e < N$ (Frankham 1995b), managers are faced with the challenge of translating between effective and census population size and between effective and actual number of migrants. Although the necessity of this translation may be obvious, the consequences may be nonintuitive because of the complex properties and assumptions of Equation 1 (e.g. nonlinearity and its approximate nature) and because N_e may typically be an order of magnitude smaller than N (Frankham 1995b; Vucetich et al. 1997).

As a means of conserving genetic diversity, the OMPG rule has been advocated for general (e.g. Franklin 1980; Frankel and Soulé 1981; Allendorf 1983; Gogan 1990; Mace and Lande 1991) and specific (e.g. U.S. Fish and Wildlife Service 1988;

Triggs et al. 1989) circumstances. With a view towards providing a guide for managers, recent studies have explored the potentially misleading properties of Equation 1 (e.g. Mills and Allendorf 1996; Whitlock and McCauley 1999; Vucetich and Waite 2000). In doing so, these studies have discredited the application of the OMPG rule for management. This criticism of the OMPG rule appears to be serving an important purpose, as evidenced by the 36 citations Mills and Allendorf (1996) received between 1998 and 2000 (according to the Institute for Scientific Information[®]). Some (e.g. Kark et al. 1999), but not all, of these studies citing Mills and Allendorf reflect an improved understanding of the inadequacies of the OMPG rule for genetic management.

Building on recent efforts to clarify the application of the OMPG rule, we explore the relationship between N and Nm when the assumption $N_e = N$ is violated to the degree typical of real populations. In doing so, we show that the required number of migrants is strongly dependent on population size for real populations (i.e. where $N_e/N < 1$) and thus highlight another potentially misleading property of the OMPG rule.

Methods

To show that Nm is especially dependent on the census size of the recipient population when $N_e < N$, we begin with an exact expression for the equilibrium inbreeding coefficient of a population that receives migrants (Futuyma 1986):

$$F = \frac{(1 - m)^2}{2N - (2N - 1)(1 - m)^2}. \quad (2)$$

When $N_e < N$ (e.g. due to population fluctuation), N in Equation 2 should be replaced with N_e . The appropriateness of this substitution has been demonstrated with analytical (Rannala 1996; Hudson 1998) and simulation (Vucetich and Waite 2000) analyses. To highlight the influence of N_e/N we express N_e as αN , where α represents the N_e/N ratio. (This ratio is usually < 1 and may be estimated using a variety of demographic [e.g. Vucetich and Waite 1998] and molecular genetic techniques [e.g. Waples 1989; Jorde and Ryman 1995].) These substitutions yield:

$$F = \frac{(1 - m)^2}{2\alpha N - (2\alpha N - 1)(1 - m)^2}. \quad (3)$$

The accuracy of this model depends on the assumption that the quantity $(1-m)^2$ approximates the probability that neither of two randomly selected alleles (from within the population) comes from a migrant (Futuyma 1986). This assumption should hold when migrants are randomly selected either from an effectively infinite single source population (i.e. island-continent model) or from an effectively infinite pool of finite subpopulations (i.e. island model) (Futuyma 1986). Under these conditions, the size of the migrant pool is effectively infinite and the N_e/N ratio of the migrant pool is thus inconsequential (see Vucetich and Waite 2000). However, if the migrant pool is not effectively infinite, then our model may need to be adjusted to account for the influence of N_e/N on the migrant pool. Here, we simply point out that under such conditions the required number of migrants per generation would likely exceed the number predicted by Equation 3.

Results and discussion

The OMPG rule is a special case of Equation 3, where $\alpha = 1$ (i.e. $N_e = N$). Thus, for the case where $N_e = N$, Nm is virtually independent of N under the assumptions of the OMPG rule. However, as N_e decreases from N (i.e. $\alpha < 1$), the value of F becomes increasingly sensitive to changes in N , for any given value of Nm (Figure 1). For example, when N_e/N is 0.1 and Nm is held constant at 10, F more than doubles as N increases from 20 to 100. To evaluate this point more formally, we derive an expression for the (actual) number of migrants by solving Equation 3 for m , multiplying both sides of the resulting expression by N , setting $F = 0.2$, and simplifying:

$$Nm = \frac{N(\alpha N + 2 - \sqrt{(\alpha N + 2)\alpha N})}{\alpha N + 2} \approx \frac{N}{\alpha N + 2}. \quad (4)$$

To characterize the behavior of this equation, we note that the numerator can be approximated as N . Inspection of this simplified expression reveals that $(N_e/N)^{-1}$ is simply the asymptotic value for Nm as N becomes large. In accordance with the OMPG rule, the number of migrants required to maintain F at the arbitrary value of 0.2 is nearly independent of N when $\alpha = 1$ (Figure 2). However, as N_e decreases from N (i.e. $\alpha < 1$), the number of migrants required to maintain F at 0.2 increases substantially as N increases. For example, when N_e/N is 0.1, the required number of migrants doubles (from 4 to 8) as the census size of

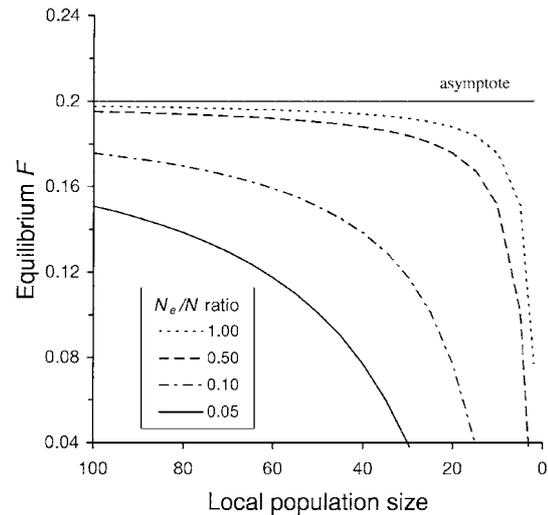


Figure 1. The equilibrium inbreeding coefficient (F) as a function of recipient population size (N). Each curve represents hypothetical populations receiving the number of migrants per generation (Nm) required to yield an asymptotic (with respect to N) F of 0.2, given the population's N_e/N ratio. For example, when $N_e/N = 0.1$, 10 migrants per generation will yield F values within 80% of 0.2, but not until $N > 60$. The curves were generated according to Equation 4. The ranges and orientation of the axes are set to facilitate direct comparison with Figure 3 in Mills and Allendorf (1996).

the local population increases from 9 to 60 individuals. Similarly, when N_e/N is 0.05, the required number of migrants increases by 50% (from 8 to 12) as the census size increases from 18 to 45, and increases again by 50% (from 12 to 18) as the census size increases from 45 to 260.

These results are significant because most real populations are characterized by a small N_e/N ratio. Based on 37 empirical estimates of N_e/N (Frankham 1995b), a typical population (i.e. median $N_e/N = 0.11$) would require some number of migrants (i.e. 9) that is strongly dependent on N for $N \lesssim 55$ (i.e. when $N = 55$, F is $< 80\%$ of the asymptotic value; Figure 3). Based on the same 37 estimates, 20% of the populations would require some number of migrants (i.e. 4) that is strongly dependent (i.e. $< 80\%$ of the asymptote) on N , but only for $N \lesssim 25$. However, at the other extreme, 20% of the populations would require some number (i.e. 28) that is strongly dependent (i.e. $< 80\%$ of the asymptote) on N , even for N as large as ~ 165 .

Analysis of the conventional one-migrant-per-generation rule reinforces recent claims that OMPG will rarely be adequate to meet goals for the genetic management of real populations (Mills and Allendorf 1996; Vucetich and Waite 2000; this study). Previ-

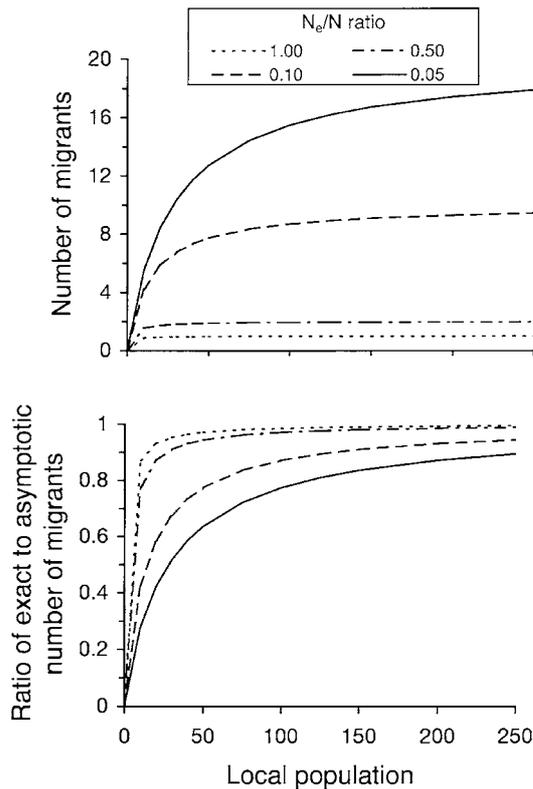


Figure 2. (a) The number of migrants per generation (Nm in Equation 4) required to maintain the equilibrium inbreeding coefficient (F) at 0.2 as a function of local population size for various values of N_e/N (i.e. α in Equation 4). (b) The curves presented in panel (a) are rescaled to facilitate comparison across N_e/N ratios.

ously, we explored how decreases in N_e/N lead to increases in the actual number of migrants required to maintain F at a given level (Vucetich and Waite 2000). Specifically, we indicated that when F is set to 0.2, $Nm = 1/\alpha = (N_e/N)^{-1}$, which implies that for a typical value of N_e/N (i.e. ~ 0.1 ; Frankham 1995b) the maintenance of F at 0.2 would require ~ 10 migrants per generation. According to conventional wisdom (Hartl and Clark 1986), these results should not apply when N_e is small (i.e. $\lesssim 20$ Mills and Allendorf 1996). This apparent limitation has not been of concern because such small populations are prone to rapid extinction due to nongenetic factors (see also Vucetich and Waite 1999). However, empirical considerations indicate that because the effective size of real populations is often much smaller than the census size, the requisite number of migrants may typically depend on population (census) size even when it is on the order of 200. Thus, for real populations of conservation

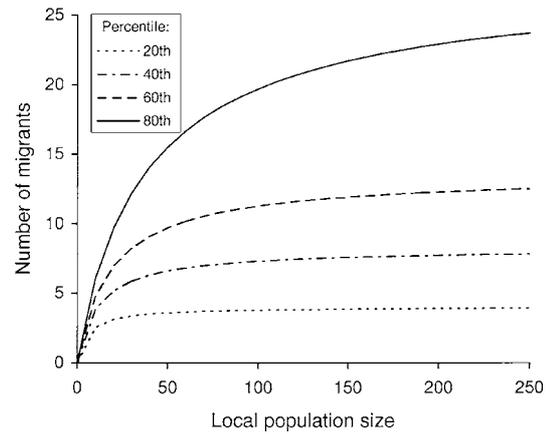


Figure 3. The number of migrants per generation (Nm) required to maintain the equilibrium inbreeding coefficient (F) at 0.2 as a function of population size (N). Each curve corresponds to a percentile of an empirical distribution of N_e/N representing 37 animal populations (Frankham 1995b). For example, since the 80th percentile of this distribution corresponds to $N_e/N = 0.036$, the curve labeled '80th percentile' represents values of Nm (i.e. Equation 4) over a range of local population sizes (N) where $\alpha = N_e/N \geq 0.036$.

concern, it will seldom be appropriate to assume that the number of migrants required to avoid inbreeding is independent of the size of the recipient population. For real populations, the actual required number of migrants depends on N_e/N (Vucetich and Waite 2000), recipient population size (this study), and other important factors (Mills and Allendorf 1996; Whitlock and McCauley 1999). Therefore, simple conventions like the OMPG rule may be inappropriate for the genetic management of many populations.

Acknowledgements

We thank Kristin Field and Scott Mills for helpful comments on the ms. This work was supported by a McIntire-Stennis grant to TAW.

References

- Allendorf FW (1983) Isolation, gene-flow, and genetic differentiation among populations. In: *Genetics and Conservation: a reference for managing wild animal and plant populations* (eds. Schonewald-Cox cm, Chambers SM, MacBryde B, Thomas WL), pp. 51–65. Benjamin/Cummings, Menlo Park, California.
- Frankel OH, Soulé ME (1981) *Conservation and Evolution*. Cambridge University Press, Cambridge, United Kingdom.
- Frankham R (1995a) Conservation genetics. *Ann. Rev. Gen.*, **29**, 305–327.
- Frankham R (1995b) Effective population size/adult population size ratios in wildlife: a review. *Gen. Res.*, **66**, 95–107.

- Franklin IR (1980) Evolutionary change in small populations. In: *Conservation Biology: an evolutionary-ecological perspective* (eds. Soulé M, Wilcox B), pp. 135–149. Sinauer, Sunderland, MA.
- Futuyma DJ (1986) *Evolutionary Biology*, 2nd edn. Sinauer, Sunderland, MA.
- Gogan PJP (1990) Considerations in the reintroduction of native mammalian species to restore natural ecosystems. *Natural Areas Journal*, **10**, 210–217.
- Hartl DL, Clark AG (1989) *Principles of Population Genetics*, 2nd edn. Sinauer, Sunderland, MA.
- Hudson RR (1998) Island models and the coalescent process. *Mol. Ecol.*, **7**, 413–418.
- Jimenez JA, Hughes KA, Alaks G, Graham L, Lacy RC (1994) An experimental study of inbreeding depression in a natural habitat. *Science*, **266**, 271–273.
- Jorde PE, Ryman N (1995) Temporal allele frequency change and estimation of effective size in populations with overlapping generations. *Genetics*, **139**, 1077–1090.
- Kark S, Alkon PU, Safriel UN, Randi E (1999) Conservation priorities for chukar partridge in Israel based on genetic diversity across an ecological gradient. *Con. Biol.*, **13**, 542–552.
- Keller LF, Arcese P, Smith JN, Hochachka WM, Stearns SC (1994) Selection against inbred song sparrows during a natural population bottleneck. *Nature*, **372**, 356–357.
- Mace GM, Lande R (1991) Assessing extinction threats: toward a reevaluation of the IUCN threatened species categories. *Conserv. Biol.*, **5**, 148–157.
- Mills LS, Allendorf FW (1996) The one-migrant-per-generation rule in conservation and management. *Conserv. Biol.*, **10**, 1509–1518.
- Rannala B (1996) The sampling theory of neutral alleles in an island population of fluctuating size. *Theor. Pop. Biol.*, **50**, 91–104.
- Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I (1998) Inbreeding and extinction in a butterfly metapopulation. *Nature*, **392**, 491–494.
- Triggs SJ, Powlesland RG, Daugherty, CH (1989) Genetic variation and conservation of kakao (*Stigops habroptilus*: Psittaciformes). *Conserv. Biol.*, **3**, 92–96.
- U.S. Fish and Wildlife Service (1988) Black-footed ferret recovery plan.
- Vucetich JA, Waite TA (1998) The number of censuses required for demographic estimation of effective population size. *Conserv. Biol.*, **12**, 1023–1030.
- Vucetich JA, Waite TA (1999) Erosion of heterozygosity in fluctuating populations. *Conserv. Biol.*, **13**, 860–868.
- Vucetich JA, Waite TA (2000) Is one-migrant-per-generation sufficient for the genetic management of fluctuating populations? *Animal Conserv.*, **3**, 261–266.
- Vucetich JA, Waite TA, Nunney L (1997) Fluctuating population size and the ratio of effective to census population size (N_e/N). *Evol.*, **51**, 2015–2019.
- Waples RS (1989) A generalized approach for estimating effective population size from temporal changes in allele frequency. *Genetics*, **121**, 379–391.
- Whitlock MC, McCauley DE (1999) Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. *Heredity*, **82**, 117–125.
- Wright S (1931) Evolution in Mendelian populations. *Genetics*, **16**, 97–259.

