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The One-Migrant-per-Generation Rule in Conservation and Management

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Abstract: In the face of continuing habitat fragmentation and isolation, the optimal level of connectivity between populations has become a central issue in conservation biology. A common rule of thumb holds that one migrant per generation into a subpopulation is sufficient to minimize the loss of polymorphism and heterozygosity within subpopulations while allowing for divergence in allele frequencies among subpopulations. The one-migrant-per-generation rule is based on numerous simplifying assumptions that may not hold in natural populations. We examine the conceptual and theoretical basis of the rule and consider both genetic and nongenetic factors that influence the desired level of connectivity among subpopulations. We conclude that one migrant per generation is a desirable minimum, but it may be inadequate for many natural populations. We suggest that a minimum of 1 and a maximum of 10 migrants per generation would be an appropriate general rule of thumb for genetic purposes, bearing in mind that factors other than genetics may further influence the ideal level of connectivity.

La regla de Un-Migrante-Per-Generación en Conservación y Manejo

Resumen: Debido a la continua fragmentación y aislamiento de habitats, el nivel óptimo de conectividad entre poblaciones se ha convertido en un tema central en la biología de la conservación. Una regla común sostiene que un amigrante por generación en una subpoblación es suficiente para minimizar la pérdida de polimorfismo y heterocigosidad en las subpoblaciones y al mismo tiempo permite la divergencia de frecuencias alélicas entre subpoblaciones. La regla de un-migrante-por-generación se basa en numerosas suposiciones simplifican que tal vez no sucedan en poblaciones naturales. En este trabajo examinamos las bases conceptuales y teóricas de la regla y consideramos factores genéticos y no genéticos que influyen en el nivel deseado de conectividad entre subpoblaciones. Concluimos que un migrante por generación es un mínimo deseable, pero puede ser inadecuado para muchas poblaciones naturales. Surgerimos que un mínimo de uno y un máximo de diez migrantes por generación sería una regla general apropiada para fines genéticos, sin olvidar que factores no genéticos pueden influir en el nivel ideal de conectividad.

... evolution depends on a certain balance among its factors. There must be gene mutation, but an excessive rate gives an array of freaks, not evolution; there must be selection, but too severe a process destroys the field of variability, and thus the basis for further advance; prevalence of local inbreeding within a species has extremely important evolutionary consequences, but too close inbreeding leads merely to extinction. A certain amount of

crossbreeding is favorable but not too much. In this dependence on balance the species is like a living organism. At all levels of organization life depends on the maintenance of a certain balance among its factors.

—S. Wright (1932:365)

Introduction

By the 1930s Sewall Wright had clearly established—based on experiments and historical breeding records—

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that inbreeding depression in small, isolated populations typically leads to adaptive decline and extinction (Provine 1986). In Wright's view small amounts of gene flow between partially isolated demes are necessary for long-term persistence. Prompted by Wright's work, the question of how many immigrants ("migrants" in population genetics literature) are needed to prevent population differentiation became the subject of a vast body of theoretical analysis (for review see Slatkin [1985, 1987]). From this analysis emerged a genetic rule of thumb that one migrant individual per local population per generation (OMPG) is sufficient to obscure any disruptive effects of drift (Spieth 1974; see also Kimura and Ohta 1971; Lewontin 1974).

Biologists concerned with population insularization caused by habitat fragmentation began advocating the application of this principle for conservation purposes. Several of the most cited papers advocating, in some sense, the movement of one individual per generation between isolated populations for conservation purposes include Franklin (1980), Frankel and Soulé (1981), and Allendorf (1983). More recently, the OMPG concept has been widely applied by scientists and managers charged with initiating connectivity between potentially isolated populations. For example, Gogan (1990) makes the statement for mammals in general that "Immigration to a subpopulation of only one individual once every five years reduces concerns about inbreeding depression to a negligible level." Triggs et al. (1989) suggest for the critically endangered kakapo (*Strigops habroptilus*) that "In future generations, exchanges of one young kakapo per generation between populations should be made to help maintain genetic variation and reduce inbreeding."

Mace and Lande (1991) have used the OMPG rule as a criterion for fragmentation in defining threatened species categories of the World Conservation Union. In the United States nearly every recovery plan that considers genetic issues and insularization applies the OMPG rule. For example, the black-footed ferret (*Mustela nigripes*) recovery plan states that "If the effective population size is to be maintained among many smaller populations, then exchange of genetic material at the rate of one individual/generation between local populations to ensure random and adaptive divergence among populations is necessary" (U.S. Fish and Wildlife Service 1988:18).

The simplicity of the OMPG—and its widespread adoption—belies confusion over the derivation of the rule, its real generality, and the specifics of implementing it (Varvio et al. 1986). Indeed, immediately after stating that subpopulations would not become fixed for different alleles if there were "an interchange of only one individual every other generation," Wright noted that violations of simplifying assumptions may mean that "... an interchange of the order of thousands of individuals per generation between neighboring subgroups of a widely distributed species might well be insufficient to prevent

a considerable random drifting apart in their genetic compositions" (Wright 1931:128). Thus, from the outset Wright acknowledged the complicating role of the social, ecological, and genetic characteristics of immigrants; these real-world complexities are often neglected in contemporary reference to the OMPG rule.

Human-caused habitat modification is reducing many continuous populations to isolated or semi-isolated fragments (Soulé et al. 1988; Mills 1995). In light of these changes, concerns over the appropriate level of gene flow in fragments are well grounded, both because of the increased potential for demic extinction in isolated populations (Senner 1980; Soulé 1987; Lynch & Gabriel 1990; Mills & Smouse 1994) and because of potential consequences for adaptation to future disturbances (Soulé 1980; Frankel & Soulé 1981). The issue of actually prescribing gene flow in a management context is complicated, however, and it has received little empirical or theoretical consideration.

We describe the OMPG rule, present its theoretical underpinnings, and discuss its application and limitations from a genetics perspective. Finally, we make recommendations that apply both to highly manipulated systems, where managers physically move individuals, as well as to systems in which the movement rate is affected by the size and shape of available habitat or movement corridors.

The One-Migrant-per-Generation Rule

The one-migrant-per-generation rule originated in Wright's analysis of the interplay between genetic drift and gene flow in determining the expected patterns of genetic divergence among a series of subpopulations. Consider a large number of subpopulations in which genetic drift produces genetic divergence among the subpopulations at a rate inversely proportional to the local effective population size (N_e), which is assumed to equal the census size, N . Assume that in each generation a proportion m of the individuals in each subpopulation are migrants from outside that subpopulation and that the allele frequency in migrant individuals is the average allele frequency in all subpopulations. Such migration will limit the amount of divergence that will occur among subpopulations.

This model leads to the surprisingly simple result that at equilibrium the amount of divergence among subpopulations for reasonably small values of m is approximately

$$F_{ST} \approx \frac{1}{4mN + 1}, \quad (1)$$

where F_{ST} is the proportion of total gene diversity (heterozygosity) due to divergence among subpopulations. Note that because m is the proportion of migrants and N is the population size, mN is the actual number of migrants entering a subpopulation each generation.

The amount of divergence among subpopulations as measured by F_{ST} is independent of the total amount of gene diversity in a population (H_T). The F_{ST} can also be thought of as the reduction in heterozygosity within subpopulations (H_S) caused by random genetic drift and divergence among subpopulations. That is,

$$F_{ST} = 1 - \frac{H_S}{H_T}, \quad (2)$$

and F_{ST} is usually called the fixation index. In the case of more than two alleles, each allele may have a different fixation index. Nei (1973) introduced an analogous value (G_{ST} , the coefficient of genetic differentiation) that can be used to describe genetic differentiation for many loci with more than two alleles (Chakraborty & Leimar 1987).

This analysis has two notable results. First, the amount of divergence is dependent only on the number of migrants (mN) and is in a sense independent of population size. For example, we expect the same amount of divergence among subpopulations of size 1000 with 2.5% migration as we do among subpopulations of size 50 with 50% migration; in both cases there are 25 migrants per generation.

The dependence of divergence on the number of migrants, rather than the population size (N) or rate of migration (m), may at first seem counter-intuitive. Divergence, however, results from the opposing effects of migration and genetic drift. The larger the subpopulations, the slower they are diverging through drift; thus, proportionally fewer migrants are needed to counteract the effects of drift. Small subpopulations diverge rapidly through drift, and thus proportionally more migrants are needed to counteract drift.

The second notable aspect of this result is that remarkably small amounts of migration can have powerful genetic consequences on divergence among subpopulations at equilibrium; for example, OMPG is expected to yield an equilibrium F_{ST} of 0.2 (Fig. 1). If we examine the actual distribution of allele frequencies among subpopulations, it is clear that OMPG will also make it unlikely that polymorphism will be lost within subpopulations (Fig. 2; Wright 1931; Fig. 6). With at least one migrant per generation, subpopulations are unlikely to reach equilibrium gene frequencies where one allele or the other is lost (frequency of zero) or "fixed" (frequency of 1.0).

Nevertheless, substantial divergence in allele frequencies across populations is expected with one migrant per generation (Wright 1931, 1969; Allendorf & Phelps 1981). Thus, OMPG provides a desirable balance between drift and gene flow by preventing the loss of alleles and minimizing loss of heterozygosity within subpopulations but allowing genetic divergence to exist among subpopulations. Low amounts of exchange will maintain qualitative similarity among subpopulations and also allow substantial quantitative divergence in allele frequencies.

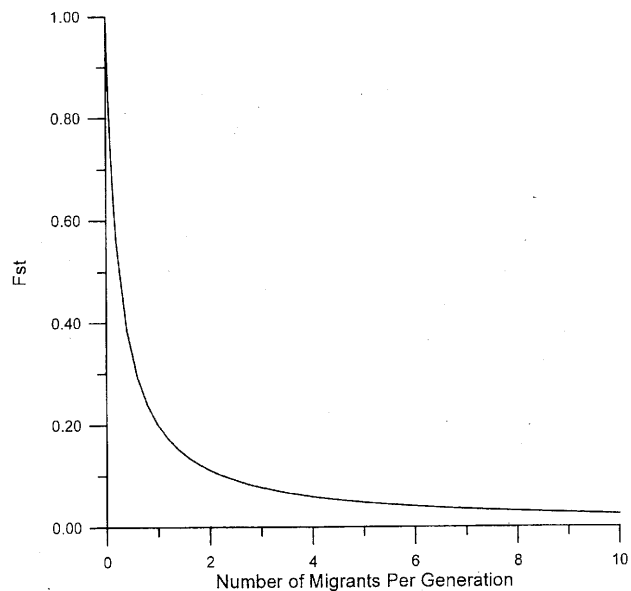


Figure 1. Relationship between number of migrants per generation (mN) and the fixation index (F_{ST}).

We want to emphasize that OMPG is not a discrete quantitative threshold and does not imply panmixia (random mating) among individuals of different populations. Rather, the basis of OMPG originates from a qualitative evaluation of tradeoffs between loss of genetic diversity within populations versus homogenization among populations.

Assumptions of the Rule

The OMPG rule results from a simple model of population structure based upon a host of unrealistic assumptions. We consider the primary assumptions that affect the applications of the results of this basic model to conservation.

(1) *Island model of migration*: A migrant is equally likely to come from any subpopulation so that there is no geographical pattern to gene flow. The assumption is also usually made that there are an infinite number of subpopulations of equal size.

(2) *Selective neutrality and no mutation*: There are no selective differences among genotypes, and no new mutations enter the population. That is, gene-frequency dynamics are determined entirely by the interaction between genetic drift and gene flow.

(3) *Ideal populations*: The subpopulations have the characteristics of an ideal genetic population, so that the census number of individuals equals the effective population size. For general purposes, the ideal population consists of a constant number of N diploid individuals ($N/2$ females and $N/2$ males) in which all parents have

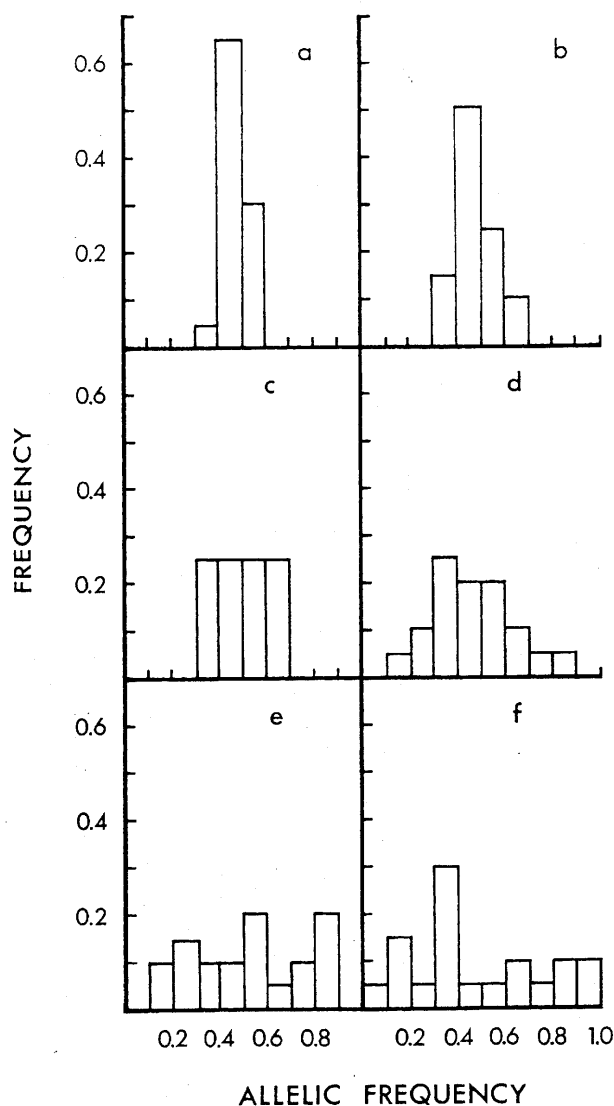


Figure 2. Distribution of allele frequencies in 20 subpopulations ($N = N_e = 200$ each) with different amounts of migration, based upon computer simulations of the island model for two alleles at a single locus (Allendorf & Phelps 1981). For panels a-e, number of migrants per generation decreases and F_{ST} increases, as follows: $mN = 25$, $F_{ST} = 0.0080$ (a); $mN = 10$, $F_{ST} = 0.0175$ (b); $mN = 5$, $F_{ST} = 0.0509$ (c); $mN = 2$, $F_{ST} = 0.1104$ (d); $mN = 1$, $F_{ST} = 0.2513$ (e); and $mN = 0.5$, $F_{ST} = 0.3221$ (f).

equal probability of contributing an offspring to the next generation.

(4) *Demographic equality*: Immigrants have the same demographic attributes, in terms of survival and reproduction probabilities, as resident individuals.

(5) *Equilibrium*: The subpopulations persist long enough to reach steady-state or equilibrium conditions with respect to gene frequencies.

Limitations of the Rule

What are the consequences of violating the simplistic assumptions of the OMPG rule? We consider how population size may affect the predicted effects of OMPG, then evaluate each of its assumptions. In each case we determine whether each complicating factor is expected to increase or decrease the effectiveness of OMPG or whether "it depends."

Census Population Size

As noted in the derivation of the OMPG rule, one of its interesting and attractive features is that it is independent of population size, as long as gene dynamics are driven entirely by drift and gene flow (mutation and selection play no role). There are, however, at least two caveats to this generalization. First, mN migrants into a small population will represent a larger proportion of the population than if they had entered a larger population; any disruptive social or mating system effects of the immigration will therefore be magnified in smaller populations (Frankel & Soulé 1981; Frankel 1983).

Second, the usual formulation for the loss of genetic variation under drift-migration equilibrium (Eq. 1) is an approximation of the exact equation and holds true only when m (migration rate) is "small" (Wright 1969:291). For a fixed mN , such as one migrant, m becomes large with small population size. For example, when $N = 2$, $m = 0.5$, a large value that leads to less loss in variation (smaller F_{ST}), with the exact equation than expected with the approximation (Fig. 3). We note, however, that the overestimation of F_{ST} with the approximate equation is insignificant with subpopulation sizes large enough to be likely to persist in the face of demographic stochasticity for even relatively short periods of time. For example, for $N = 20$, the exact F_{ST} is 94% of the approximation.

Both of these issues imply that when populations become quite small less migration may be appropriate, both because of possible social disruption and because very small populations are not losing variation as fast as predicted by the F_{ST} approximation. Other factors, such as Allee effects and demographic or environmental stochasticity, lead to the opposite conclusion, with immigrants initiating an important "rescue effect" (Brown & Kodric-Brown 1977).

Island Model: Pattern of Migration

The immigrants in Wright's infinite island model are randomly chosen from the pool of an infinite number of subpopulations. If individuals in the real world come from nearby populations, their gene frequencies would differ little from the target population, so more immigrants would be necessary to prevent loss of variation

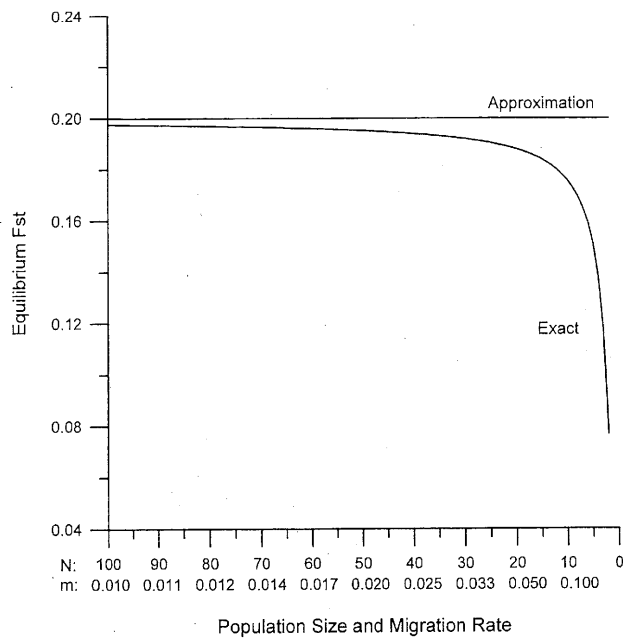


Figure 3. Expected F_{ST} at equilibrium for one migrant per generation ($mN = 1$) using the exact equation (from Eq. 12.2 in Wright 1969) and the commonly used approximation (Eq. 1). Unlike the approximation, which assumes small m , the exact equation changes as m changes.

(Wright 1931; Levin 1988). Crow and Aoki (1984) conclude, however, that unless the number of populations is very large, this neighborhood effect is relatively small; in a finite population model, migrants from neighboring groups are about half as effective in their genetic effects. Kin-structured migration—in which individuals disperse in the company of relatives—will also have the effect of requiring more immigrants for the same effect on genetic drift (Levin 1988).

Directional movement patterns are an important and widespread exception to the assumption of the island migration model. In many situations migrants from a relatively large subpopulation may be moved into a smaller subpopulation that is isolated; this is referred to as a continent-island pattern of migration (Hedrick 1983:278). For example, grizzly bears (*Ursus arctos*) from the Yellowstone National Park region are isolated from other populations. The recovery plan for grizzly bears includes regularly moving bears from more northern populations in Montana that are contiguous with grizzly bear populations in Canada into the Yellowstone region (U.S. Fish and Wildlife Service 1993).

The genetic effects of this type of directional movement pattern are compatible with the OMPG rule. The isolated population can be considered one subpopulation of the island model in which migrants from the larger population represent the migrant pool of the is-

land model. Thus, the predictions of the OMPG rule will be valid as long as the donor population is large so that genetic drift is minimal. Weishampel (1990) cautions that if the donor population has lower genetic variation than the receiving population, migration can actually decrease genetic variation in the population of interest.

Another characteristic of the pattern of migration is the interval between immigrants. In its simplest form the island model assumes that probability of migration per generation is constant. Will 1 migrant per generation have the same effect as 10 migrants every 10 generations? Lacy (1987:153) concludes that sporadic immigration should be just as effective as a steady supplementation, provided that the same long-term average rate is maintained. On the other hand, Levin (1988:645) concludes that “a variable migration rate homogenizes neutral allele frequencies less than a uniform migration rate with the same mean.” This effect is quite small, however, based upon theory (Nagylaki 1979). Experimental work offers no insight into this question. In many cases the driving criteria for the timing of immigrants will probably not be genetic calculations but logistical concerns (transplanting one animal per generation will often be impractical) and behavioral and social considerations whereby groups of immigrants are more likely to experience successful reproduction.

In short, real-world deviations from the simple pattern of migration used to derive the OMPG rule mean that somewhat more than one migrant per generation may be necessary to achieve the desired genetic goals; the necessary increase will depend on particular circumstances, but it is probably small.

Island Model: Number of Subpopulations

The expected value of F_{ST} at equilibrium can be corrected as shown below to take into account a finite number (n) of subpopulations (Slatkin 1995):

$$F_{ST} \approx \frac{1}{4mNa + 1}, \quad (3)$$

where

$$a = \left(\frac{n}{n-1} \right)^2. \quad (4)$$

Total gene diversity (H_T) can be partitioned into within- and between-subpopulation components. Isolation causes a decrease in within-subpopulation variation (H_S), whereas fixation for different alleles maintains total gene diversity (H_T). As long as the subpopulations are connected by gene flow, an allele will eventually be lost from all subpopulations (and therefore the entire population) by genetic drift if there are a finite number of subpopulations. If the subpopulations are isolated, however, then different alleles will drift to fixation in differ-

ent populations, so more alleles will be maintained in the entire population.

There may be merit (Chesser 1983) in maintaining isolated populations so that more alleles can be retained in the entire population. Nevertheless, these benefits must be weighed against increased probability of extinction due to within-population inbreeding depression (Varvio et al. 1986; Mills & Smouse 1994). In short, the tradeoff between within- and among-population variation may dictate more or less migration than the OMPG rule does (Figs. 1 & 2).

Natural Selection and Mutation

The theoretical model upon which the OMPG rule is based assumes selective neutrality—that is, there are no differences in fitness among genotypes. Nevertheless, the OMPG rule itself does take into account natural selection. The OMPG rule was chosen because it is sufficient to avoid the loss of alleles in subpopulations caused by genetic drift but will allow the allele frequencies within subpopulations to respond to local selective pressures.

Even weak natural selection can have a major effect on the amount of genetic divergence among populations (Allendorf 1983). The effects of natural selection will be greater in larger subpopulations because of the reduced effects of drift in larger populations. In general, natural selection will not have a major effect on the distribution of allele frequencies if the selection coefficient (s) is less than the migration rate (m) (Wright 1940). Thus, natural selection will have less effect on allele frequency divergence among subpopulations with smaller subpopulations for the same amount of migration (mN) (Allendorf 1983).

The effect of selection upon the expected amount of divergence with a given amount of gene flow depends upon the pattern of selection. Similar selection in different subpopulations will tend to reduce divergence, whereas different selective conditions will increase divergence among subpopulations (Allendorf 1983). It is likely that both of these patterns of selection will occur at different loci within the same population. Thus, the OMPG rule seems appropriate when we consider the potential effects of natural selection.

Mutation is expected to have little effect on the application of the OMPG rule. The expected amount of divergence at equilibrium for G_{ST} (the multiple-allele form of F_{ST}) is independent of the mutation rate and the number of alleles, as long as the migration rate is much greater than the mutation rate (Hartl & Clark 1989). This condition will be met for all loci in which migration rates are on the order of one per generation ($mN = 1$) or greater.

Ideal Populations and Demographic Equality

The ratio of effective population size to census population size is expected to affect the consequences of vary-

ing migration rates. Wright (1931:128, 1969:292) noted that the smaller N_e is relative to the census N , the larger the number of migrants necessary to minimize differentiation. This is because as N_e decreases below N the population loses variation faster via drift, and a given migrant contributes less to the breeding population, than when N_e equals N . Therefore, populations with highly skewed N_e/N ratios, as is often the case in wild vertebrates (Frankham 1995), may require more than one migrant per generation. How many more are necessary is uncertain; presumably it will depend on why N_e is less than N (for example, because of skewed sex ratio or variance in family size) and on the reproductive characteristics of the immigrants.

Demographic equality also assumes that immigrants are equivalent to residents. To the extent that an immigrant is more or less likely to survive and breed relative to individuals in the target population, it may count as more or less than one migrant. It seems unlikely that immigrants will be demographically equivalent to resident individuals in most situations. In the case in which immigration is imposed by moving captured individuals, there are a variety of reasons to expect immigrants to be less likely to survive and reproduce than residents.

There are also a few situations in which immigrants may be more successful than residents. For example, individuals with rare genotypes have a reproductive advantage in plant species with self-incompatibility systems (Charlesworth 1985). Thus, immigrants from a genetically different subpopulation may have a reproductive advantage in this case.

Because deviations from ideal population structure will tend to compromise the effectiveness of migration relative to expectations, including social structure and taking into account the relative reproductive success of immigrants will mean that more than one migrant per generation may be necessary.

Equilibrium

The OMPG rule is based upon the assumption of equilibrium between the effects of migration and genetic drift. Equilibrium will be reached more quickly with smaller population sizes and higher migration rates (Varvio et al. 1986). Thus, greater migration may be initially desirable with larger subpopulations in order to reach equilibrium more quickly. Equilibrium between gene flow and drift is approached fairly quickly with small population sizes (Table 1; see also Allendorf & Phelps 1981; Table 2).

Before the population reaches equilibrium, the restorative effect of immigration is initially greater for small populations than for large because they have drifted to lower levels of variation (Lacy 1987). This implies that increases above OMPG may well be beneficial when migration is initiated for the first time.

Table 1. Observed and expected genetic divergence among five subpopulations of Leadbeater's opossum connected by gene flow in a simulation study (Lindenmayer & Lacy 1995).*

mN	H_s	Expected F_{ST}	Observed F_{ST}		
			20 yr	50 yr	100 yr
0	0.28	1.000	0.170	0.309	0.509
0.7	0.60	0.186	0.105	0.128	0.130
1.5	0.70	0.096	0.074	0.068	0.079
7.4	0.80	0.021	0.021	0.022	0.024

*The mN values were calculated with the annual migration rate (m) used in the simulations, a generation interval of 3.71 years and an N of 40 based on carrying capacity (see text for discussion of using N versus N_e). H_s values represent observed mean heterozygosity within subpopulations at 100 years. Expected F_{ST} at equilibrium was calculated using Eq. 3 and the actual mN values used in the simulations. Observed F_{ST} values were calculated using Eq. 2.

Implicit in the equilibrium assumption is that populations all persist long enough to reach equilibrium. McCauley (1993) reviews the consequences of relaxing this assumption: incorporating extinction and recolonization dynamics can either increase or decrease genetic differentiation, depending on how high population turnover rates are, where the migrants originate, how many migrants move together, and whether the migrants settle in unoccupied or occupied patches. Extinction and recolonization dynamics tend to accentuate population differentiation most when migrant individuals move into established populations more than colonizing new patches. Therefore, if conspecific attraction (Reed & Dobson 1993) tends to increase the likelihood of a dispenser settling in an already occupied area rather than an unoccupied area in a metapopulation, then those migrants will be less effective at minimizing differentiation in the metapopulation; if they settle more in empty patches, then extinction and recolonization dynamics predict that fewer migrants are needed to prevent differentiation (McCauley 1993).

In general, then, violation of the equilibrium assumption means that somewhat more than one migrant per generation may be beneficial. Extinction and recolonization dynamics could either increase or decrease the desirable number.

Empirical and Simulation Results

What insights can be gained from field studies, laboratory experiments, and comprehensive computer studies of natural populations that violate many of the above assumptions at the same time? Because it is not possible to test the predictions of the OMPG rule within a reasonable time frame for most species of interest, empirical tests will initially come from model genetic species with short generation times.

Little experimental work considers the issue of how many migrants are optimal in natural—or even captive—populations. The most direct experimental work is that of Spielman and Frankham (1992). They found strong and significant increases in reproductive fitness in 10 replicate inbred lines of *Drosophila melanogaster* that received only a single immigrant per generation. On average, OMPG restored nearly 50% of that fitness lost under isolation. Newman (1996) has found similar results with experimental populations of the plant *Brassica campestris*. One migrant per generation among 10 subpopulations had a significantly positive effect for five of six fitness components measured. In contrast to these results, Backus et al. (1995) found no increase in fitness associated with a single immigrant (although higher levels of gene flow did increase fitness) among five subpopulations of the housefly (*Musca domestica*).

Studies that use simulations or analytical approaches incorporating actual life-history information for long-lived species also provide insight into how effective OMPG is expected to be in the face of real-world deviations from the simplifying assumptions. For example, Hedrick (1995) used a variety of theoretical population genetic models to test the validity of the OMPG rule in the case of the Florida panther (*Felis concolor coryi*). The report of a workshop for genetic restoration of the Florida panther recommended an initial influx of 20% of the population, followed by gene flow of one animal per generation. Hedrick's models included various combinations of gene flow and genetic drift. He also examined several violations of the assumptions of the basic model: natural selection, directional gene flow, and nonequilibrium initial conditions. Despite these complicating factors, he concluded that this recommendation was sufficient to eliminate lowered fitness due to inbreeding depression and to retain adaptive alleles in the Florida population.

Allendorf et al. (1991) used simulations with the computer program GAPPs (Harris et al. 1986; Harris & Allendorf 1989) to examine the effects of immigration on effective population size and the rate of loss of genetic variation in an isolated population of grizzly bears in the Rocky Mountains. These simulations used a directional (continent-island) pattern of gene flow in a discrete-time, stochastic computer program that followed each individual bear from birth to death. The estimated effective population size of the isolated population was approximately 30% of the census population size. Their results are in general agreement with those expected with the basic model: the introduction of a few bears per generation greatly reduced the rate of loss of variation in the isolated population. The introduction of males had a greater effect than the introduction of females in the model, but this effect may be outweighed by the reduced likelihood of males being incorporated in the breeding population into which they are introduced be-

cause of the behavioral differences between males and females (Allendorf et al. 1991; U.S. Fish and Wildlife Service 1993).

Dobson et al. (1991) used GAPPS to simulate the viability of isolated populations of black rhinos (*Diceros bicornis*) in Kenya. They used an island-continent pattern of migration and demographic data obtained from black rhino sanctuaries. They also included the effects of inbreeding depression in some of their simulations. They found that one immigrant every 10 years had a major effect on the population size and persistence of isolated populations.

The most realistic test of the OMPG rule using simulations that we are aware of was done by Lindenmayer and Lacy (1995) with Leadbeater's possum (*Gymnobelideus leadbeateri*). They used the computer program VORTEX (Lacy 1993) to model the viability of metapopulations with subpopulations occupying a small number of habitat patches of varying sizes. They used values for life-history parameters drawn from extensive field studies, allowed local subpopulations to become extinct, and included the effects of inbreeding depression. Dramatic effects of migration were observed in their largest metapopulation, which consisted of five subpopulations of 40 individuals each (Table 1).

The results for Leadbeater's possum also can be used to quantitatively test the predictions in a system that violates many of the assumptions upon which the OMPG is based. The observed amount of genetic divergence among the five subpopulations estimated from the data of Lindenmayer and Lacy (1995) is similar to that predicted by the simple equilibrium model (Table 1). As expected, near-equilibrium values were obtained more rapidly with greater amounts of gene flow. Even with $mN = 1.5$, however, the observed F_{ST} value was nearly 75% of that expected at equilibrium after approximately five generations.

Recommendations for Implementing Gene Flow

When connectivity is implemented for genetic purposes, we are interested in finding the middle ground between loss of alleles in local populations (fixation, or loss in heterozygosity) and uniformity of allele frequencies across local populations. One migrant per generation is an appropriate lower limit to the amount of gene flow that is desirable. Nevertheless, sometimes more than an average of one migrant per generation will be necessary because of deviations in real populations from the ideal conditions assumed in developing the OMPG rule.

We hesitate to give "cookbook" prescriptions, but an increase in migration above the mean of one migrant per generation may be desirable under the following conditions: (1) inbreeding depression is thought to be a problem in the local population; (2) migrants are closely related to each other or to the local population; (3) social,

behavioral, or logistical factors prevent single individuals from immigrating, so that movement is in pulses of several animals every several generations; (4) N_e is much less than total population size; (5) migrants are likely to be at a disadvantage in terms of survival and breeding success; (6) the receiving population has been isolated for many generations; and (7) demographic or environmental variation indicates a high danger of extinction without aggressive supplementation.

If one migrant per generation is not enough in many circumstances, then the next question is how much gene flow may be too much to maintain the balance we are seeking. This question is difficult to answer without extensive genetic and demographic information on the population under consideration. Concerns over local adaptation and outbreeding depression dictate that, under some conditions of phenotypic or genotypic dissimilarity, immigration into an isolated population should be minimized (for cogent discussions see Templeton [1986] and Leberg [1990]). Frankel and Soulé (1981) proposed an upper limit of 5 migrants per generation because of concerns with disruptive effects on social structure in small populations. We suggest that up to 10 migrants per generation is not likely to tip the balance too far by causing uniformity of allele frequencies across subpopulations (Fig. 2).

The characteristics of the migrants is as important as the number of migrants. Social, behavioral, and demographic characteristics that affect the likelihood of survival and reproduction of migrants may overwhelm genetic considerations in assessing the "ideal" candidates to recruit as migrants (Kleiman 1989; Stanley-Price 1989; Short et al. 1992). Likewise, considerations of mating system and social structure will affect the genetic impact of an immigrant. Greater numbers of randomly chosen migrants may be necessary to achieve the same genetic effect as fewer migrants chosen to maximize contribution to the effective population size.

Finally, we stress that criteria other than genetic variation will often play pivotal roles in determining the appropriate level of connectivity between semi-isolated fragments. For example, small populations subject to blinking out due to demographic or environmental stochasticity can experience a "rescue effect" (Brown & Kodric-Brown 1977), with immigrants increasing numbers away from the boundary of zero. In this case more migrants increase population persistence, regardless of genetic considerations. On the other hand, contagious diseases have been raised as a factor decreasing the benefits of connectivity (Wilson et al. 1994; Hess 1994).

Conclusions

The OMPG rule has provided much-needed guidance in management and has illuminated the need for genetic

connectivity among isolated populations. Like many theoretical applications in conservation, its utility is strongest when its complexity is appreciated (Doak & Mills 1994). We have seen several compelling real-world factors that suggest more than one migrant per generation may be necessary to achieve genetic goals, and some situations (albeit fewer) in which less connectivity is desirable. One key to practical decision making is to define clearly the desired genetic outcome, as well as other objectives and constraints of the supplementation program (Lacy 1987).

One migrant per generation is an acceptable minimum, but it may be inadequate for many natural populations. Different levels and schedules of supplementation are appropriate under different environmental conditions and with different species. Nevertheless, we suggest that a minimum of 1 and a maximum of 10 migrants per generation would be an appropriate general rule of thumb for genetic purposes.

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Literature Cited

- Allendorf, F. W. 1983. Isolation, gene flow, and genetic differentiation among populations. Pages 51-65 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, editors. *Genetics and conservation: a reference for managing wild animal and plant populations*. Benjamin/Cummings, Menlo Park, California.
- Allendorf, F. W., and S. R. Phelps. 1981. Use of allelic frequencies to describe population structure. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1507-1514.
- Allendorf, F. W., R. B. Harris, and L. H. Metzgar. 1991. Estimation of effective population size of grizzly bears by computer simulation. Pages 650-654 in E. C. Dudley, editor. *The unity of evolutionary biology*. Dioscorides Press, Portland, Oregon.
- Backus, V. L., E. H. Bryant, C. R. Hughes, and L. M. Meffert. 1995. Effect of migration or inbreeding followed by selection on low-founder-number populations: implications for captive breeding programs. *Conservation Biology* 9:1216-1224.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445-449.
- Chakraborty, R., and O. Leimar. 1987. Genetic variation within a subdivided population. Pages 89-120 in N. Ryman and F. Utter, editors. *Population genetics and fishery management*. University of Washington Press, Seattle.
- Charlesworth, D. 1985. Distribution of dioecy and self-incompatibility in angiosperms. Pages 237-268 in J. J. Greenwood and M. Slatkin, editors. *Evolution—essays in honor of John Maynard Smith*. Harvard University Press, Cambridge, Massachusetts.
- Chesser, R. K. 1983. Isolation by distance: relationship to the management of genetic resources. Pages 66-77 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, editors. *Genetics and conservation: a reference for managing wild animal and plant populations*. Benjamin/Cummings, Menlo Park, California.
- Crow, J. F., and K. Aoki. 1984. Group selection for a polygenic behavioral trait: estimating the degree of population subdivision. *Proceedings of the National Academy of Sciences (U.S.A.)* 81:6073-6077.
- Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. *Ecology* 75:615-626.
- Dobson, A. P., G. M. Mace, J. Poole, and R. A. Brett. 1991. *Conservation biology: the ecology and genetics of endangered species*. Pages 405-430 in R. J. Berry, T. J. Crawford, and G. M. Hewitt, editors. *Genes in ecology*. Blackwell Scientific, Oxford, United Kingdom.
- Frankel, O. H. 1983. The place of management in conservation. Pages 1-14 in C. M. Schonewald Cox, S. M. Chambers, B. MacBryde, and L. Thomas, editors. *Genetics and conservation: a reference for managing wild animal and plant populations*. Benjamin/Cummings, Menlo Park, California.
- Frankel, O. H., and M. E. Soulé. 1981. *Conservation and evolution*. Cambridge University Press, Cambridge, United Kingdom.
- Frankham, R. 1995. Effective population size/adult population size ratios in wildlife: a review. *Genetical Research* 66:95-107.
- Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135-149 in M. Soulé and B. Wilcox, editors. *Conservations biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts.
- Gogan, P. J. P. 1990. Considerations in the reintroduction of native mammalian species to restore natural ecosystems. *Natural Areas Journal* 10:210-217.
- Harris, R. B., and F. W. Allendorf. 1989. Genetically effective population size of large mammals: an assessment of estimators. *Conservation Biology* 3:181-191.
- Harris, R. B., L. H. Metzgar, and C. D. Bevins. 1986. GAPPs—Generalized animal population projection system. Montana Cooperative Wildlife Research Unit, Missoula.
- Hartl, D. L., and A. G. Clark. 1989. *Principles of population genetics*. 2nd edition. Sinauer Associates, Sunderland, Massachusetts.
- Hedrick, P. W. 1983. *Genetics of populations*. Science Books International, Boston.
- Hedrick, P. W. 1995. Gene flow and genetic restoration: the Florida panther as a case study. *Conservation Biology* 9:996-1007.
- Hess, G. R. 1994. Conservation corridors and contagious disease: a cautionary note. *Conservation Biology* 8:256-262.
- Kimura, M., and T. Ohta. 1971. *Theoretical aspects of population genetics*. Princeton University Press, Princeton, New Jersey.
- Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation. *Bioscience* 39:152-161.
- Lacy, R. C. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. *Conservation Biology* 1:143-158.
- Lacy, R. C. 1993. VORTEX: a computer simulation model for use in population viability analysis. *Wildlife Research* 20:45-65.
- Leberg, P. L. 1990. Genetic considerations in the design of introduction programs. *Transactions of the North American Wildlife and Natural Resource Conference* 55:609-619.
- Levin, D. A. 1988. Consequences of stochastic elements in plant migration. *American Naturalist* 132:643-651.

- Lewontin, R. C. 1974. The genetic basis of evolutionary change. Columbia University Press, New York.
- Lindenmayer, D. B., and R. C. Lacy. 1995. Metapopulation viability of leadbeater's possum, *Gymnobelideus leadbeateri*, in fragmented old-growth forests. *Ecological Applications* 5:164-182.
- Lynch, M., and W. Gabriel. 1990. Mutation load and the survival of small populations. *Evolution* 44:1725-1737.
- Mace, G. M., and R. Lande. 1991. Assessing extinction threats: toward a reevaluation of the IUCN threatened species categories. *Conservation Biology* 5:148-157.
- McCauley, D. E. 1993. Genetic consequences of extinction and recolonization in fragmented habitats. Pages 217-233 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts.
- Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. *Conservation Biology* 9:395-403.
- Mills, L. S., and P. E. Smouse. 1994. Demographic consequences of inbreeding in remnant populations. *American Naturalist* 144:412-431.
- Nagylaki, T. 1979. The island model with stochastic migration. *Genetics* 91:163-176.
- Nei, M. 1973. Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences (U.S.A.)* 70:3321-3323.
- Newman, D. K. 1996. Importance of genetics on survival of small populations: genetic drift, inbreeding, and migration. Ph.D. dissertation. University of Montana, Missoula.
- Provine, W. B. 1986. Sewall Wright and evolutionary biology. University of Chicago Press, Chicago.
- Reed, J. M., and A. P. Dobson. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution* 8:253-256.
- Senner, J. W. 1980. Inbreeding depression and the survival of zoo populations. Pages 209-224 in M. E. Soulé and B. A. Wilcox, editors. *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts.
- Short, J., S. D. Bradshaw, J. Giles, R. I. T. Prince, and G. R. Wilson. 1992. Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia: a review. *Biological Conservation* 62:189-204.
- Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* 16:393-430.
- Slatkin, M. 1985. A measure of population subdivision based on microsatellite allele frequencies. *Genetics* 139:457-462.
- Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. *Science* 236:787-792.
- Soulé, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151-169 in M. E. Soulé and B. A. Wilcox, editors. *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts.
- Soulé, M. E. 1987. Where do we go from here? Pages 175-184 in M. E. Soulé, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Soric, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75-92.
- Spielman, D., and R. Frankham. 1992. Modeling problems in conservation genetics using captive *Drosophila* populations: improvement of reproductive fitness due to immigration of one individual into small partially inbred populations. *Zoo Biology* 11:343-351.
- Spieth, P. T. 1974. Gene flow and genetic differentiation. *Genetics* 78:961-965.
- Stanley-Price, M. R. 1989. Animal re-introductions: the Arabian oryx in Oman. Cambridge University Press, Cambridge, United Kingdom.
- Templeton, A. R. 1986. Coadaptation and outbreeding depression. Pages 105-116 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Triggs, S. J., R. G. Powlesland, and C. H. Daugherty. 1989. Genetic variation and conservation of kakapo (*Stigops habroptilus*: Psittaciformes). *Conservation Biology* 3:92-96.
- U.S. Fish and Wildlife Service. 1988. Black-footed ferret recovery plan.
- U.S. Fish and Wildlife Service. 1993. Grizzly bear recovery plan. Missoula, Montana.
- Varvio, S., R. Chakraborty, and M. Nei. 1986. Genetic variation in subdivided populations and conservation genetics. *Heredity* 57:189-198.
- Weishampel, J. F. 1990. Maintaining genetic variation in a one-way, two island model. *Journal of Wildlife Management* 54:676-682.
- Wilson, M. H., C. B. Kepler, N. F. R. Snyder, S. R. Derrickson, F. J. Dein, J. W. Wiley, J. M. Wunderle, Jr., A. E. Lugo, D. L. Graham, and W. D. Toone. 1994. Puerto Rican parrots and potential limitations of the metapopulation approach to species conservation. *Conservation Biology* 8:114-123.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97-259.
- Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proceedings of the Sixth International Congress of Genetics* 1:356-366.
- Wright, S. 1940. Breeding structure of populations in relation to speciation. *American Naturalist* 74:232-248.
- Wright, S. 1969. Evolution and the genetics of populations. Volume 2. The theory of gene frequencies. University of Chicago Press, Chicago.

