

# Is one migrant per generation sufficient for the genetic management of fluctuating populations?

John A. Vucetich<sup>1</sup> and Thomas A. Waite<sup>2</sup>

<sup>1</sup>School of Forestry, Michigan Technological University, Houghton, MI 49931, USA

<sup>2</sup>Department of Evolution, Ecology, and Organismal Biology and Department of Anthropology, Ohio State University, Columbus, OH 43210, USA

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## Abstract

Small isolated populations may face an increasing risk of extinction due to the loss of genetic diversity. This increasing risk, though, may be offset by gene flow, provided the population receives an adequate number of migrants per generation. We show that as temporal fluctuation in population size (FPS) increases, so too does the required number of immigrants. This increase in the requisite number of immigrants arises because the ratio of census size to effective population size decreases with increasing FPS. Because all populations fluctuate, our work extends a recent challenge to the widely adopted one migrant per generation rule, which refers to the supposedly requisite number of immigrants. In a sample of 44 animal populations, ~60% of the populations fluctuated enough to require >10 immigrants per generation to avoid a substantial loss of genetic diversity, and ~25% fluctuated enough to require >20 immigrants per generation. We thus recommend that estimation of the requisite number of immigrants take into account fluctuation in population size.

Although genetic deterioration is a potentially important component of extinction risk for isolated populations (e.g. Allendorf & Leary, 1987; Frankham, 1995a; Czech & Krausman, 1997; Newman & Pilson, 1997; Vucetich & Waite, 1999), extensive theoretical analysis has suggested that just one migrant per generation (OMPG) typically may be sufficient to offset genetic deterioration within subpopulations (e.g. Wright, 1931; Slatkin, 1987), which could avert elevated extinction risk due to genetic deterioration (Saccheri *et al.*, 1998). The elegance of this guideline has probably contributed to its adoption as a general rule for the genetic management of conserved populations. Unfortunately, 'several compelling real-world factors ... suggest more than [OMPG] may be necessary to achieve genetic goals' (Mills & Allendorf, 1996). The OMPG rule strictly applies only in the unrealistic (ideal) case where genetically effective population size ( $N_e$ ) equals actual population size ( $N$ ). Because real populations are not ideal (i.e. not characterized by random mating, even sex ratio, constant population size and discrete generations (Wright, 1931)),  $N_e$  is usually less than  $N$  (Frankham, 1995c), and hence, the *actual* number of migrants required for genetic management routinely exceeds one. Considering this and other limitations, Mills & Allendorf (1996) recently concluded that 'a minimum of 1 and a

maximum of 10 migrants per generation would be an appropriate general rule of thumb for genetic purposes.' Whitlock & McCauley (1999) discuss similar issues from a population genetics point of view.

Here, we evaluate this recommendation, recognizing that temporal fluctuation in population size acting in concert with other factors frequently causes  $N_e$  to be much less than  $N$  (Frankham, 1995c; Vucetich, Waite & Nunney, 1997). For example, fluctuations alone can reduce  $N_e/N$  to below 0.2 in approximately one-third of the 44 natural animal populations analyzed (see Figure 1 in Vucetich *et al.*, 1997). Our consideration of fluctuations suggests that 1–10 migrants per generation may often be inadequate. We provide managers with a method for determining when >10 migrants per generation may be required.

## N-MPG FOR FLUCTUATING POPULATIONS

The OMPG rule is based on the assumption that each subpopulation in a metapopulation is ideal and hence  $N_e = N$ . To evaluate the importance of this restrictive assumption, consider the inbreeding coefficient (homozygosity) ( $F$ ) of an isolated local population assumed to be ideal (Hartl & Clark, 1989):

$$F_t = \frac{1}{2N} + (1 - \frac{1}{2N})F_{t-1}, \quad (1)$$

where  $N$  is the size of the subpopulation. If the popula-

All correspondence to: J. A. Vucetich. Tel: (906) 497-1711; E-mail: javuceti@mtu.edu.

tion receives immigrants, then  $F_t$  must be modified accordingly (Hartl & Clark, 1989):

$$F_t = \left(\frac{1}{2N} + (1 - \frac{1}{2N})F_{t-1}\right)(1-m)^2, \quad (2)$$

where  $m$  is the immigration rate. This expression is valid when selection and mutation are unimportant, patterns of migration are random (i.e. each individual has a constant probability of moving among subpopulations) among an infinite number of subpopulations, and migrant and resident individuals have equal fitness (see Mills & Allendorf, 1996; Whitlock & McCauley, 1999). Collectively, these assumptions describe Wright's (1931) island model. Solving eqn (2) for the equilibrium value yields (Hartl & Clark, 1989):

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

when  $m$  is small. Since local populations are typically not ideal, a more appropriate expression is:

$$F_{ST} \approx \frac{1}{(4N_e m + 1)}, \quad (4a)$$

where  $N_e$  is the long-term effective size of the subpopulation that receives immigrants. Because this expression represents the equilibrium value of  $F_{ST}$ ,  $N_e$  represents the long-term effective population size and should account for fluctuations in population size. The appropriateness of applying this equation to fluctuating populations is supported by a recent coalescent analysis (Hudson 1998; see also Rannala, 1996).

Theoretical analysis suggests that maintaining  $F_{ST}$  at 0.2 adequately conserves genetic diversity while allowing for sufficient differentiation among subpopulations (e.g. Varrio, Chakraborty & Nei, 1986; Mills & Allendorf, 1996; but see Lacy, 1987). Since  $N_e m$  represents the effective number of migrants per generation, the OMPG rule obtains when  $F_{ST}$  is set at 0.2. The effective number of migrants per generation is the actual number of migrants per generation that would be required to maintain  $F_{ST}$  at some specified level, if the subpopulation under consideration were ideal (see Mills & Allendorf, 1996 for further discussion). In principle,  $N_e$  can be expressed as  $\alpha N$ , where  $\alpha$  represents the long-term  $N_e/N$  ratio, where the denominator ( $N$ ) is naturally represented by the average population size (see eqn (9), below). This ratio is usually  $<1$  and may be estimated using a variety of demographic (e.g. Vucetich & Waite, 1998) and molecular genetic techniques (e.g. Waples, 1989; Jorde & Ryman, 1995). Thus, eqn (4a) can be rewritten as:

$$F_{ST} \approx \frac{1}{(4N_e \alpha m + 1)}, \quad (4b)$$

When  $F_{ST}$  is set to 0.2, the actual number of migrants,  $Nm$ , is equal to  $1/\alpha = (N_e/N)^{-1}$ . We emphasize that this result relies on all of the assumptions of the OMPG rule, except that  $N_e$  does not necessarily equal  $N$  in the local population.

Quantifying the relationship between the effective and

actual numbers of migrants is essential for the genetic management of real populations. Here, we aim to quantify this relationship on the basis of realistic models for the long-term  $N_e/N$  value of the local population. Equations (1)–(4) show that the relationship between the effective and actual numbers of migrants depends on the relationship between the effective and actual sizes of the local population. This property suggests that OMPG will often be inadequate (Mills & Allendorf, 1996), since  $N_e$  is much less than  $N$  for most real populations (Frankham, 1995b; Vucetich *et al.*, 1997).

To quantify this relationship between  $N_e$  and  $N$ , we begin by considering the factors that tend to influence the  $N_e$  of a local subpopulation. The  $N_e$  of a subpopulation is depressed by greater fluctuations in population size (FPS), by variance in fecundity, by skew in sex ratio and by a lesser overlap between generations. The influence of these factors on the long-term  $N_e$  of a subpopulation is described by (Vucetich *et al.*, 1997):

$$N_e = \frac{\bar{N}(N_{e,t}/N_t)}{\{1 + (1/2)(\ln(10)\sigma_n)^2\}} \quad (5)$$

where  $\bar{N}$  is the arithmetic mean of the population size, and FPS is measured by  $\sigma_n$ , the standard deviation of the logarithm of population counts over a series of years (or other intervals). In this equation,  $N_{e,t}/N_t$  should be replaced with a representative value for the short-term ratio of effective size to census size (i.e. a value that accounts for the influence of sex ratio, generation overlap and variance in fecundity on  $N_e/N$ ). Such a short-term ratio is given by (Nunney, 1991):

$$N_e/N_t = \frac{4r(1-rT)}{rA_f(1+I_{Af}) + (1-r)A_m(1+I_{Am}) + (1-r)I_{bf} + rI_{bf}} \quad (6)$$

where  $r$  is the sex ratio,  $T$  is the average generation time,  $A_f$  and  $A_m$  are the average adult life spans for females and males,  $I_{Af}$  and  $I_{Am}$  are the standardized variances in adult life span, and  $I_{bf}$  and  $I_{bm}$  are the standardized variances in reproductive success. If available, the harmonic mean of a series of such ratios would be appropriate. (Vucetich & Waite (1998:1028) were incorrect to state that the arithmetic mean could be used for this purpose.) Practical considerations for estimating the parameters of eqns (5) and (6) are described elsewhere (Nunney & Elam, 1994; Vucetich & Waite, 1998). Equation (5) holds if the processes that govern eqn (6) are independent of the processes that govern FPS, or if  $N_e/N$  can reasonably be estimated as the product of the short-term  $N_e/N$  ratio (i.e. eqn (6)) and the  $N_e/N$  ratio calculated from the influence of FPS alone. The degree to which real populations may violate this assumption has not been evaluated. Equation (5), also based on the harmonic mean, has been shown to approximate the harmonic mean estimator (see Figure 3 in Vucetich *et al.*, 1997 for comparisons between eqn (5) and harmonic mean

estimates of  $N_e/N$  for real animal populations). An advantage of eqn (5) is that, in contrast to the harmonic mean estimator, we have some knowledge about the distribution of  $\sigma_n$  for natural populations (Fig. 1).

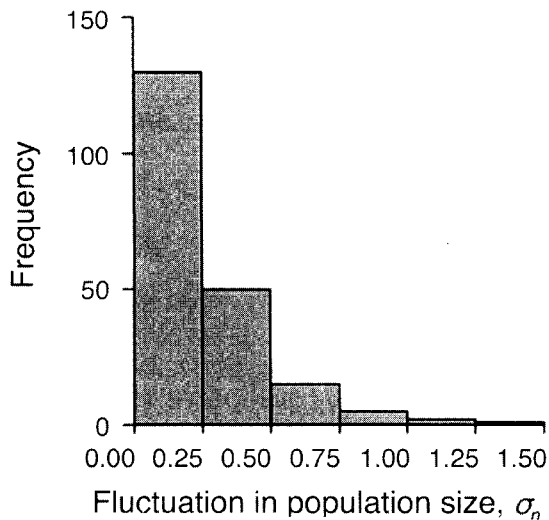
To obtain an expression for the average (actual) number of immigrants required to maintain  $F_{ST}$  at 0.2, we substitute the right side of eqn (5) (an expression for the long-term  $N_e$  of the local population) for  $N_e$  in eqn (4a), and then solve for  $\bar{Nm}$ :

$$\bar{Nm} = \frac{(2 + (1n(10)\sigma_n)^2)^2 (1 - F)}{16(N_{e,t}/N_t)F} \quad (7)$$

This equation relies on a more realistic model for the  $N_e$  of the local population than does the OMPG rule. Otherwise, eqn (7) relies on the same set of restrictive assumptions. For example, when the immigrant pool is represented by a finite number of subpopulations,  $m$  is scaled downward by the factor  $(s/(s-1))^2$ , where  $s$  is the number of subpopulations (Mills & Allendorf, 1996).

Extensive demographic data are required to estimate  $\bar{Nm}$  from eqns (6) and (7). For example, an ongoing 38-year study of the isolated wolf (*Canis lupus*) population in Isle Royale National Park provides estimates of population size, sex ratio, survivorship and fecundity (e.g. Peterson *et al.*, 1998). These data yield estimates of 0.17 for  $N_{e,t}/N_t$  and, coincidentally, 0.17 for  $\sigma_n$ . Based on these values, eqn (7) predicts that 6.8 migrants per generation are required to maintain  $F_{ST}$  at 0.2.

Such extensive demographic data are rarely available and so management of conserved populations must be based on the best information available. Unfortunately, a common practice is to adopt the OMPG rule. Given its dependence on the unrealistic assumption that

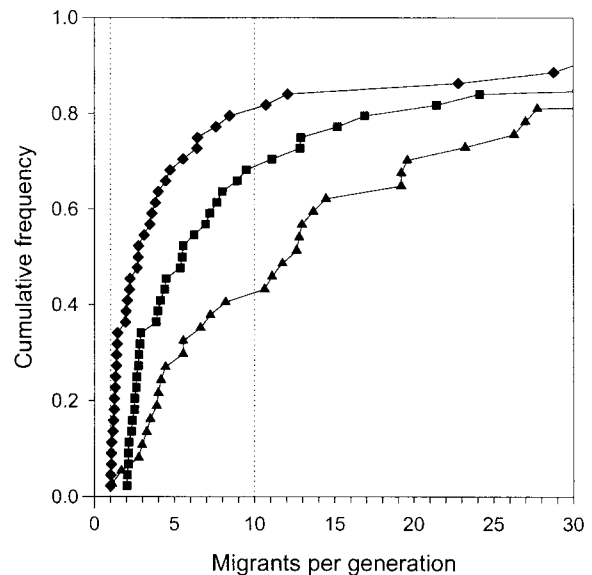


**Fig. 1.** Frequency distribution of  $\sigma_n$  for a sample of 202 real animal populations (data from Figure 3.1 in Pimm, 1991). This distribution provides the context for interpreting the  $x$ -axis of Figures 2,3 and 4.

$N_e = N$ , this approach is inadequate. Empirical evidence suggests that, on average,  $N_e \approx N/10$  (Frankham, 1995c). When no information is available, it may be tempting to assume that  $N_e \approx N/10$ , which corresponds to  $\sim 10$  immigrants per generation (obtained by replacing  $N_e$  in eqn (4) with  $N/10$  and solving for  $Nm$ ). Based on this single assumption and comprehensive estimates of  $N_e$  for 37 animal populations (Frankham, 1995c), we estimate that about 60% of animal populations require  $>10$  migrants per generation and that only about 5% require  $<3$  migrants per generation (Fig. 2).

FPS is often the most important factor influencing long-term  $N_e$  (Frankham, 1995c; Vucetich *et al.*, 1997). Fortunately, FPS can be estimated even if the only data available are a series of census counts. In such cases, though, information about  $N_{e,t}/N_t$  will often be lacking. It is clearly inappropriate, given the current state of knowledge, to suppose that  $N_{e,t}/N_t = 1$  (i.e. the population is ideal in every way except for temporal fluctuation in size). In the absence of information about  $N_{e,t}/N_t$ , a crude but clearly more reasonable assumption is that  $N_{e,t}/N_t = 0.5$  (e.g. Nunney, 1991, 1993, 1996; Nunney & Elam, 1994). Applying this assumption to eqn (7) yields:

$$\bar{Nm} = \frac{(2 + (1n(10)\sigma_n)^2)^2 (1 - F)}{8F} \quad (8)$$



**Fig. 2.** Cumulative frequency distribution of the number of migrants ( $\bar{Nm}$ ) required to maintain an equilibrium inbreeding coefficient of 0.2 under three sets of assumptions. [◆], eqn (7) ( $N_{e,t}/N_t$  assumed to be = 1) applied to  $\sigma_n$  estimates from 44 animal populations (assumed to be ideal except for fluctuations in size; Vucetich *et al.*, 1997); [■], eqn (8) applied to the same data (i.e. influence of sex ratio, variance in fecundity and generation overlap assumed to depress  $N_{e,t}$  to  $N/2$ ); [▲], estimates for an independent set of 37 animal populations where all factors known to affect  $N_e$  were accounted for explicitly (data from Frankham, 1995b). Dotted lines correspond to the recently suggested rule of thumb of 1-to-10 migrants per generation (Mills & Allendorf, 1996).

This equation is a convenient expression for  $\overline{Nm}$  because it depends only on  $\sigma_n$ , a standard measure whose properties are well studied (Pimm, 1991). In real populations,  $\sigma_n$  is commonly  $<0.25$  and rarely  $>1.0$  (Fig. 1). We emphasize that eqn (8) applies only to cases where  $N_{e,t}/N_t = 0.5$  represents a reasonable assumption. For example, adjusting  $N_{e,t}/N_t$  downward would result in an inversely proportional increase in the required number of migrants (relative to that predicted by eqn (8)).

Sensitivity analyses of the effect of naturally-occurring levels of  $\sigma_n$  (using eqn (8)) reveal that OMPG would maintain  $F_{ST}$  between 0.35 and 0.4 in populations with typical levels of  $\sigma_n$  (i.e.  $<0.25$ ) (Fig. 3). If  $F_{ST}$  is to be maintained at  $\sim 0.2$ , then two to three migrants per generation will be required for populations with  $\sigma_n < 0.25$ . Based on the estimates of  $\sigma_n$  for 44 animal populations (Vucetich *et al.*, 1997), approximately three-quarters of animal populations may require  $>3$  migrants per generation, and one-quarter may require  $>20$  migrants per generation (Fig. 2). Populations with large values of  $\sigma_n$  (i.e.  $>1.0$ ) that receive only OMPG may have  $F_{ST}$  values exceeding 0.85 (Fig. 3).

The appropriateness of eqn (8) is supported by a recent coalescent analysis demonstrating that eqn (4a) applies to fluctuating populations when  $N_e$  represents the long-term effective population size (Hudson, 1998; see also Rannala, 1996). We further evaluated the appropriateness of eqn (8) by conducting a simulation analysis (written in Borland C++ Builder™ version 3). We simulated a metapopulation with fluctuating subpopulations, but with characteristics otherwise conforming to the standard assumptions of the island model. These simulations represent an extension of analyses where population size was constant (Allendorf & Phelps, 1981). Here, each subpopulation fluctuated according to the following model (Murdoch, 1994):

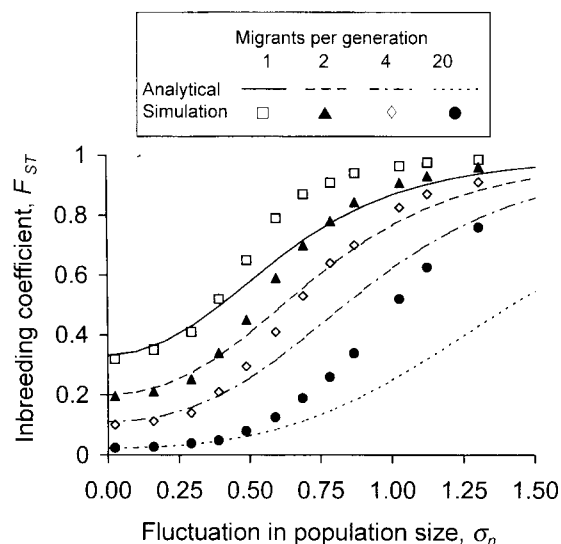
$$\ln(N_{t,i}) = \overline{N} + \alpha (\ln(N_{t-1,i}) - \overline{N}) + r_{t,i} \quad (9)$$

where  $N_{t,i}$  is the size of subpopulation  $i$  in generation  $t$ ,  $\alpha$  is the autocorrelation in log-transformed population sizes, and  $r_{t,i}$  is the log-transformed growth rate, a normally and independently distributed random variable with a mean of zero and a variance of  $\sigma^2$ . Because animal populations typically exhibit dynamics that are intermediate between white noise ( $\alpha = 0$ ) and Brownian motion ( $\alpha = 1$ ) (Ariño & Pimm, 1995), all simulations were conducted with  $\alpha$  fixed at 0.5. Populations were not permitted to go extinct (see Hedrick & Gilpin, 1997 for the genetic consequences of extinction). Each subpopulation was also characterized by a single locus with two alleles (denoted  $A$  and  $a$ ). The initial frequency of each allele for each subpopulation ( $p_{o,i}$ ) was 0.5. The most straightforward way to simulate genetic processes within subpopulation  $i$  would be to draw  $2N_{t,i}$  alleles, independently and randomly. However, to provide an appropriate comparison with eqn (8), which assumes  $N_{e,t}/N_t = 0.5$ , we selected  $2N_{e,t,i}$  ( $= (2N_{t,i})/2$ ) alleles. Each allele was selected from the gene pool of subpopulation  $i$  with probability  $(1-m)$  and subpopulation  $j$  (where  $j$  is

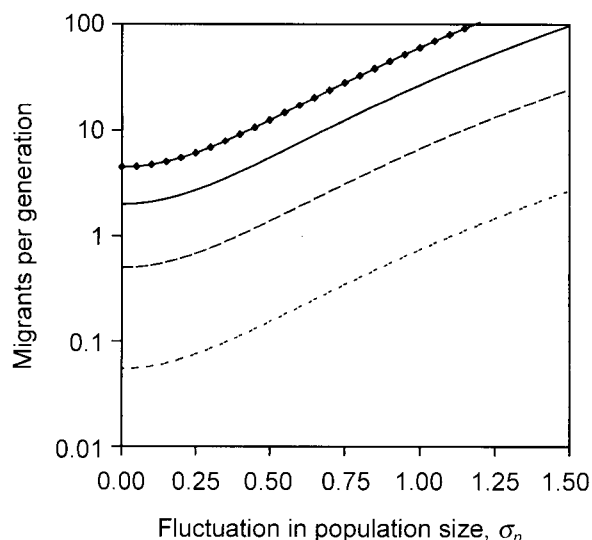
randomly selected and  $j \neq i$ ) with probability  $m$ . Then allele  $A$  was selected with probability  $p_{t,i}$  for resident parents and  $p_{t,j}$  for immigrant parents. Selection and mutation were not modelled in these simulations. For each of the 40 subpopulations comprising the metapopulation, the average inbreeding coefficient in generation  $t$  (which is denoted  $F_{ST(t)}$ ) was calculated as  $F_{ST(t,i)} = 1 - (H_{S(t,i)}/H_{T(t)})$ , where  $H_{T(t)}$  and  $H_{S(t,i)}$  are the heterozygosities of the total population and each subpopulation, respectively, and are based on  $p_{t,i}$  and the Hardy-Weinberg theorem. To analyze this model we estimated the equilibrium inbreeding coefficient ( $F_{ST}$ , obtained by averaging  $F_{ST(t)}$  for  $t \in (500, 2000)$ ) for various values of  $\overline{Nm}$  and  $\sigma_n$  (manipulated by varying  $\sigma^2$  and observing  $\sigma_n$  in the simulated subpopulations).

Simulation results suggest that eqn (8) is a useful approximation when  $\sigma_n < 0.50$  (Fig. 3), which is typical for most animal populations (Fig. 1). Equation (8) also performs well when as many as 20 migrants are received per generation. However, eqn (8) significantly underestimates the effect of FPS on  $F_{ST}$  for given values of  $\overline{Nm}$  for populations with high levels of  $\sigma_n$  (i.e.  $>0.50$ ) (Fig. 3). Consistent with eqns (3)–(4) and (7)–(8) the simulation results are independent of  $\overline{N}$  (result not shown), except that  $\overline{N}$  must be sufficiently high (or  $\sigma_n$  sufficiently low) so that significant drift does not occur at the metapopulation level. For example, when  $\sigma_n > 1.0$ ,  $\overline{N}$  must exceed 400 to avoid significant drift in the metapopulation. However, for  $\sigma_n < 0.5$ ,  $\overline{N}$  can be less than 100 without leading to significant drift in the metapopulation. Complete characterization of the interactions among migration, fluctuation in population size, and  $F_{ST}$  when drift occurs in the metapopulation is beyond the scope of this paper (see Barton & Whitlock, 1997; Hedrick & Gilpin, 1997). When drift in the metapopulation is significant, conclusions about gene flow should be based on specifically tailored simulations.

To maintain  $F_{ST}$  at a particular value,  $\overline{Nm}$  increases exponentially with increases in  $\sigma_n$  (Fig. 4). At least two migrants per generation are required to maintain  $F_{ST}$  at 0.2 for any level of  $\sigma_n$ . For some populations, fitness may not be maintained unless  $F_{ST} \leq 0.2$ . For example, maintaining  $F_{ST}$  at 0.1 may require as many as 10 migrants per generation for populations with commonly observed values of  $\sigma_n$  (i.e.  $\sigma_n < 0.5$ ). Alternatively, the viability of some population may be maintained for  $F_{ST} > 0.2$  (see Frankham, 1995b). In such populations, fewer migrants may be required to avoid inbreeding depression. For example, if fitness is maintained at  $F_{ST}$  values as high as 0.5, then less than OMPG may be required (Fig. 4). In extreme cases, where a population's fitness might be maintained at  $F_{ST}$  values as high as 0.95 (see Frankham, 1995b), perhaps only one migrant every 50 generations would be required for populations with typical levels of FPS (i.e.  $\sigma_n < 0.25$ ). At the other extreme, however,  $>10$  and perhaps as many as 100 migrants per generation may be required to maintain  $F_{ST}$  at 0.2 in populations with high levels of FPS (i.e.  $\sigma_n > 0.75$ ). The patterns of underestimation in eqn (8) (see Fig. 3) suggest



**Fig. 3.** Equilibrium inbreeding coefficient ( $F$ ) for hypothetical populations experiencing various levels of temporal fluctuation in size (measured as  $\sigma_n$ ) and receiving various numbers of migrants per generation. Curves generated from eqn (8). Symbols represent the results of simulations described in the main text.



**Fig. 4.** Influence of temporal fluctuation in population size ( $\sigma_n$ ) on the number of migrants per generation ( $Nm$ ) required to maintain the equilibrium inbreeding coefficient ( $F$ ) at various values. Curves generated from eqn (8).  $F$  (inbreeding coefficient) values are: [◆], 0.1; —, 0.2; ---, 0.5; -.-, 0.9.

that the results of Fig. 4 also underestimate the number of migrants required for  $\sigma_n > 0.5$ .

Correlates of  $\sigma_n$  (Pimm, 1991) may give rise to corresponding patterns in  $Nm$ . Invertebrate populations are often characterized by higher values of  $\sigma_n$  than are vertebrate populations, and thus may typically require more migrants per generation. In a sample of 16 invertebrate populations (Vucetich *et al.*, 1997), the median  $\sigma_n$  was 0.72. For this value, without even considering other fac-

tors that also tend to inflate the required number of migrants, >11 migrants per generation are required to maintain  $F_{ST}$  at 0.2 (OMPG would maintain  $F$  at 0.74). By contrast, in a sample of 28 vertebrate populations (Vucetich *et al.*, 1997), the median  $\sigma_n$  was 0.27. For this value, roughly three migrants per generation are required to maintain  $F_{ST}$  at 0.2 (OMPG would maintain  $F_{ST}$  at 0.41). Future analysis may reveal finer-scale taxonomic patterns in FPS and hence  $Nm$ .

## CONCLUSIONS

We have evaluated the possibility that more than one migrant per generation may be required for the genetic management of conserved, isolated populations. By relaxing just a single ideal assumption (i.e. by recognizing that real populations fluctuate in size), our analysis reveals that 3–10 migrants may often be required to maintain a particular level of inbreeding (Fig. 2, see curve corresponding to eqn (7)). These results, significantly, were clearly anticipated by results of an independent modelling approach based on joining diffusion processes that represent population demography and genetic drift (see Figure 5 in Vucetich & Waite, 1999). We also emphasize that the application of our conclusions extend beyond populations that exhibit severe, discrete bottlenecks. Rather, our conclusions apply to fluctuations that include the cumulative effect of smaller, continuous variations in size (as well as severe, discrete bottlenecks) and any excursion above or below the mean population size. Moreover, because additional assumptions of the OMPG rule are routinely violated (Mills & Allendorf, 1996; see also Lacy, 1987), this recommendation is overly optimistic. Our analysis thus suggests that >10 migrants per generation are required to conserve the genetic diversity of many animal populations (Fig. 2).

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