

Effective size in management and conservation of subdivided populations

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Abstract

A numerical method for computing the eigenvalue variance effective size of a subdivided population connected by any fixed pattern of migration is described. Using specific examples it is shown that total effective size of a subdivided population can become less than the sum of the subpopulation sizes as a result of directionalities in the pattern of migration. For an extension of the model with threshold harvesting and local deterministic logistic population dynamic we consider the problem of maximizing the total harvesting yield with constraints on the total effective size. For some simple source-sink systems and more complicated population structures where subpopulations differ in their degree of isolation, it is shown to be optimal, for a given total effective size, to raise the harvesting thresholds relatively more in small and in isolated populations. Finally, we show how the method applies to populations which are supplemented, either intentionally or unintentionally. It is shown that the total effective size can be reduced by several orders of magnitude if the captive component of a population is much smaller than the wild component, even with symmetric backward migration.

Introduction

Populations need genetic variation to adapt to changing environmental conditions. Without sufficient genetic variation, populations will lag behind the environment and suffer an environmental load which ultimately may lead to extinction (Lande & Shannon 1996).

Theoretical models predict that the amount of genetic variation in a population is determined by a balance between genetic drift (leading to random loss of genetic variability), stabilizing selection (causing disruptive selection at individual loci), and mutation (introducing new variability) (e.g. Bulmer 1989). Therefore, an important conservation goal is to maximize the effective size, in particular for relatively small populations (Schonewald-Cox *et al.* 1983; Ryman & Utter 1987; Ballou *et al.* 1995). Lande & Barrowclough (1987) argue that an effective size around 5000 individuals is necessary for long term preservation of typical level of genetic variability in quantitative characters.

Most populations are subdivided and heterogeneous, that is, different subpopulations are of different size. Also, most populations are interconnected by migration typically varying with distance, local population size, and sometimes being directional either as a result of e.g. prevailing winds (Persson & Ståhl 1990) or, for source sink systems, as a result of habitat heterogeneity creating variation in local population densities. While the effective size of subdivided populations has received some theoretical attention (Whitlock & Barton 1997), little work has been done on non-idealized migrations patterns and real world examples. One reason for this may be that computation of

effective size of subdivided populations in general, for large population systems, involves numerical computations requiring specially written computer code.

Here we present some numerical examples for a number of simple migration patterns using computer code freely available on the Internet, based on previous work on inference of migration patterns from genetic data (Tufto *et al.* 1996, 1998). Next, we develop a scenario with a composite management goal involving maximization of both effective population size and harvesting yield for a model with local population dynamics following a simple deterministic Lotka-Volterra model. The decision variables are local harvesting thresholds. The model thus predicts how to prioritize between different subpopulations varying in size and degree of isolation in order to conserve genetic variation and maximize the harvesting yield.

Finally, we apply our model to populations subdivided into a captive and a wild component, where the captive component is used to supplement the wild component, either intentionally or unintentionally. Such populations sometimes involve extreme asymmetries which can lead to surprisingly low overall effective size.

Model

In general we consider a subdivided population consisting of n subpopulations. Let the column vector $\mathbf{p}_t = (p_{1t}, p_{2t}, \dots, p_{nt})$ denote the allele frequencies in generation t . The allele frequencies in the next generation are then

given by

$$\mathbf{p}_{t+1} = \mathbf{M}\mathbf{p}_t + \mathbf{e}_t, \quad (1)$$

where element m_{ij} of the (backward) migration matrix $\mathbf{M}$ denote the probability that a individual originates from subpopulation j conditional on that it has migrated to subpopulation i , the elements e_{it} of $\mathbf{e}$ are binomial variates representing genetic drift scaled to have means equal to zero and variance equal to $p_{it}(1 - p_{it})/(2N_i)$, and N_i is the effective size of subpopulation i . The corresponding recurrence equation for the variance-covariance matrix of the allele frequencies is given by

$$\mathbf{C}_{t+1} = \mathbf{M}\mathbf{C}_t\mathbf{M}^T + \mathbf{E}, \quad (2)$$

where $\mathbf{E}$ is a diagonal matrix with elements $e_{ii} = [q(1 - q) - c_{ii,t}]/[2N_i]$ and q is the initial gene frequency in all subpopulations as shown by Felsenstein (1982). Note that (2) can be decomposed into n^2 linear equations for all $c_{ij,t}$ out of which only $n(n+1)/2$ are unique due to the symmetry of the covariance matrices in (2). This means that (2) can be rewritten as a inhomogeneous matrix difference equation on the form

$$\mathbf{c}_{t+1} = \mathbf{A}\mathbf{c}_t + \mathbf{b}, \quad (3)$$

where $\mathbf{c}_t$ and $\mathbf{b}$ are column vectors of length $n(n+1)/2$, and $\mathbf{c}_t$ contains the elements of $\mathbf{C}_t$, and $\mathbf{A}$ is a $n(n+1)/2 \times n(n+1)/2$ matrix. The elements of $\mathbf{A}$ and $\mathbf{b}$ are functions of the migration matrix $\mathbf{M}$ and the vector of local effective subpopulation size $\mathbf{N} = (N_1, N_2, \dots, N_n)$. Formulas for these functions are given in Appendix A.

The asymptotic rate of convergence of the variances and covariances is determined by the dominant eigenvalue λ_1 of $\mathbf{A}$. This rate of convergence determines how fast individual alleles are fixed in the total population as a whole. Setting this equal to the rate at which the variance of an allele frequency of an idealized population of size N_e converges, $1 - 1/(2N_e)$, the effective size becomes

$$N_e = \frac{1}{2 - 2\lambda_1}. \quad (4)$$

Note that we assume that no set of subpopulations is completely isolated from rest of the population.

Because the definition is based on the variance effective sizes of each the subpopulations from which we derive the asymptotic rate of convergence based on the dominant eigenvalue of $\mathbf{A}$, we call this the eigenvalue variance effective size of the subdivided population. Whitlock & Barton (1997) present a similar treatment of inbreeding effective size. For a discussion of variance versus inbreeding effective size, see Waples (2002).

In many conservation contexts, where the objective is to evaluate the sustainability or long term consequences of alternative management strategies, the above measure is arguably the parameter of interest. Of some interest is also the time needed before this asymptotic size is attained. This is determined by the second largest dominant eigenvalue of $\mathbf{A}$, λ_2 . Provided that $\mathbf{A}$ is primitive, it follows that deviations from the asymptotic rate of convergence are reduced by a proportion $1 - \lambda_2/\lambda_1$ each generation (see e.g. Caswell 2001, p. 86 for an analogous treatment of convergence towards stable

age structure). The inverse of this,

$$t_e = \frac{1}{1 - \lambda_2/\lambda_1}, \quad (5)$$

is therefore a measure of the time scale needed for the variance-covariance matrix and hence the effective size to reach its asymptotic rate of convergence.

Numerical examples

The main difficulty in this approach is to rewrite (2) into (3). An algorithm implementing this and calculating the corresponding effective size which can be run using the free software R is available at <http://www.math.ntnu.no/~jarlet/migration>. Here we first present some numerical examples.

For simple situations with symmetric migration, numerical analysis verified well known previous results (e.g. Wang & Caballero 1999, eq. (1)), showing that the effective size becomes either equal to or greater than the sum of the subpopulation sizes, depending on the rate of migration and amount of differentiation between populations.

In situations with asymmetric migration, however, the effective size can become greatly reduced. Considering an asymmetric pattern of migration with migration matrix and local effective population size

$$\mathbf{M} = \begin{bmatrix} 0.9 & 0.1 \\ 0.01 & 0.99 \end{bmatrix}, \quad \mathbf{N} = \begin{bmatrix} 10 \\ 10 \end{bmatrix}, \quad (6)$$

so that subpopulation 1 receives 10% migration from subpopulation 2 and subpopulation 2 1% from subpopulation 1, the total effective size becomes $N_e = 13.16$, that is, smaller than the sum of the subpopulation sizes. This

result is similar to results in Whitlock & Barton (1997). These authors derived an expression for the effective size of a metapopulation allowing variable contributions from different subpopulations and concluded that the effective size can become less than the sum of local population sizes, provided that the variance in fitness among subpopulations is sufficiently large. Because an asymmetric pattern of migration in effect means that the contributions of different subpopulations vary, this results is consistent with previous findings.

That asymmetric migration should lead to a reduction in effective size can also be understood by considering the extreme case of complete one-way migration. The ultimate fate of a two-population system and hence the asymptotic rate of convergence of the covariances will be completely governed by the size of the subpopulation emitting migrants. The same effect occur in case (6), only to a smaller extent.

Effective size for any pattern of migration can be computed, for example, for a 4-subpopulation stepping stone-like migration pattern with

$$\mathbf{M} = \begin{bmatrix} 0.95 & 0.05 & 0 & 0 \\ 0.05 & 0.9 & 0.05 & 0 \\ 0 & 0.05 & 0.9 & 0.05 \\ 0 & 0 & 0.05 & 0.95 \end{bmatrix}, \quad \mathbf{N} = \begin{bmatrix} 10 \\ 10 \\ 10 \\ 10 \end{bmatrix},$$

the effective size corresponding to the dominant eigenvalue of the 10×10 matrix $\mathbf{A}$ becomes $N_e = 54.10$.

Harvesting and effective size

Typically, real world conservation plans involve a number of different and often conflicting management goals. For example, for Atlantic salmon (*Salmo salar*), some subpopulations are considered healthy and are harvested while other subpopulations are considered threatened by small population size possibly leading to loss of genetic variation (World Wildlife Fund 2001). Here we propose a unified approach to how these two conflicting goals can be reconciled at the level of each subpopulation.

We extend model (1) by introducing a simple deterministic population dynamic model where the change in population size in subpopulation i is given by

$$\Delta N_i = r_i N_i \left(1 - \frac{N_i}{K_i}\right) - Y_i(N_i) - N_i + \sum_{j=1}^n \tilde{m}_{ij} N_j. \quad (7)$$

For brevity and without any loss in generality we assume that local population sizes equal the local effective size.

The first term on the right hand side is the standard Lotka-Volterra logistic growth model. The second term represents the rate Y_i at which the population is harvested as a function of local population size N_i , and the last two terms represent emigration and immigration. Note that $\tilde{m}_{ij}$ now represent forward migration probabilities, that is, $\tilde{m}_{ij}$ is the probability that an individual migrates to subpopulation i conditional on that it originates from subpopulation j . Also note that $\tilde{m}_{ii}$ is the probability of staying resident so that a population makes a contribution $-(1 - \tilde{m}_{ii})N_i$ to change in its own size.

We only consider a simple deterministic scenario where all subpopulations are kept at chosen thresholds N_i^* by harvesting. At this equilibrium all rates of change in local population sizes are zero. Hence, setting the left hand side of (7) equal to zero, solving for $Y_i(N_i)$ for each i , and summing over i we find that the total harvesting yield becomes

$$Y = \sum_{i=1}^n Y_i(N_i) = \sum_{i=1}^n \left(r_i N_i \left(1 - \frac{N_i}{K_i} \right) - N_i + \sum_{j=1}^n \tilde{m}_{ij} N_j \right). \quad (8)$$

Also noting that migration inside a completely closed population system does not influence the total yield, because the two last terms of the sum in (8) cancel each other, we see that (8) simplifies to

$$Y(N_1, N_2, \dots, N_n) = \sum_{i=1}^n r_i N_i \left(1 - \frac{N_i}{K_i} \right). \quad (9)$$

Thus, regardless of the pattern of migration, if our goal is to maximize $Y(N_1, N_2, \dots, N_n)$ only, the trivial solution for the optimal choice of harvesting thresholds becomes

$$N_i^* = \frac{K_i}{2}, \quad (10)$$

the classical maximum sustainable yield solution applied to each subpopulation.

Our interest here, however, is in the optimal solution with constraints on the total effective size. We want to maximize (9) subject to the constraint

$$N_e(N_1, N_2, \dots, N_n) - N_e^* = 0, \quad (11)$$

where N_e^* is the chosen required total effective size.

This problem can be solved using the method of Lagrange multipliers (e.g. Edwards & Penney 1986, p. 809). It follows that the solution satisfies

$$\frac{\partial Y}{\partial N_i} = \gamma \frac{\partial N_e}{\partial N_i}, \quad (12)$$

for all $i = 1, 2, \dots, n$. The left hand side of (12) is not available analytically and solution of (12) must therefore be determined by numerical methods.

For numerical efficiency we used a slight variation of the numerical analog to the method outlined above given in Appendix B. Note that N_e is a function of the backward migration matrix $\mathbf{M}$ which in turn is a function of the forward migration matrix $\tilde{\mathbf{M}}$ and the equilibrium population sizes, through the relation

$$m_{ij} = \frac{\tilde{m}_{ij} N_j}{\sum_{k=1}^n \tilde{m}_{ik} N_k}. \quad (13)$$

In the following examples, the forward matrix, that is, probabilities of migrating to subpopulation i given migration from subpopulation j , are kept constant.

Source-sink example, low rate of migration

The optimal harvesting thresholds and corresponding local and global yields as function of different choices of N_e for a simple two-population source-sink system is shown in Fig. 1, first column. It should first be noted that the left-most points on the curves correspond to the simple classical unconstrained maximum sustainable yield solution (10), that is, harvesting thresholds at half the carrying capacities at 25 and 50 individuals for subpopulation 1 and 2, respectively. When we require a higher total effective size N_e , the thresholds have to be raised. It turns out to be optimal, in terms of maximizing the

total yield, to first raise the threshold in smallest subpopulation, while keeping the threshold in the largest population around 50. This leads to some reduction in the local harvesting yield in subpopulation 2 but a relatively small reduction in the total yield (solid line in upper panel). We see that an increase in effective size N_e from 90 to 130 can be achieved with almost no reduction in total yield.

Note that when the effective size exceeds 130 the harvesting yield in subpopulation 1 drops to zero and any extra increase in effective population size can be achieved only by raising the threshold and reducing the yield in subpopulation 2.

Much of the increase in effective size is gained by taking into account population subdivision structure. This can be seen by comparing the constrained maximum yield solution with two more naive strategies (Fig. 1, second and third columns). The first alternative strategy we consider is based on raising the thresholds proportionally relative to local carrying capacities in all subpopulations letting

$$N_i = aK_i. \quad (14)$$

This strategy thus includes (10) as a special case when the decision variable $a = 1/2$.

A second alternative strategy is to harvest with a uniform effort everywhere. This can be modeled by letting

$$Y_i(N_i) = bN_i, \quad (15)$$

in all subpopulations i . This would correspond to certain types of migratory

organisms, for examples, anadromous salmonid species subdivided into distinct subpopulations only in the freshwater phase of the lifecycle, and with all harvesting occurring indiscriminately in the ocean phase.

These two alternative strategies are shown in the middle and rightmost columns of Fig. 1. Compared to the optimal solution, the total yields under proportional threshold and uniform effort harvesting are reduced by almost a factor of two when the effective size is raised from 90 to 130.

Source-sink example, high rate of migration

A second example with parameters identical to that in Fig. 1 but with a higher rate of migration is shown in Fig. 2. In this case the thresholds under the optimal strategy become quite similar to the equilibrium population sizes under uniform effort harvesting, essentially because individuals accumulate in the smaller population as a result of the high rate of migration. The side effect of this is that the degree of directionality in the migration pattern is reduced which helps increase the total effective size. Therefore, less is gained by optimizing all thresholds independently.

Under proportional threshold harvesting, in contrast, we do not get this effect because the thresholds are set in proportion to local carrying capacities. This strategy therefore performs considerably worse for this population system.

Effect of isolation

Any arbitrary populations structure can be analyzed. The final example demonstrates how the harvesting thresholds should be adjusted when differ-

ent subpopulations vary in their degree of isolation. We consider a population consisting of four subpopulations with identical local population dynamic, exchanging migrants at rates 0.1, 0.05, 0.02, and 0.01 through a common migrant pool (in which migrants are mixed randomly). This corresponds to a migration matrix

$$\tilde{\mathbf{M}} = \begin{bmatrix} 0.955 & 0.027 & 0.011 & 0.005 \\ 0.027 & 0.963 & 0.005 & 0.002 \\ 0.011 & 0.005 & 0.982 & 0.001 \\ 0.005 & 0.002 & 0.001 & 0.990 \end{bmatrix}. \quad (16)$$

The optimal total yields and local harvesting thresholds for this population setup are shown in Fig. 3. The main result is that, rather than raising all thresholds jointly, it pays off to harvest relatively less in isolated populations because these contribute more to the total effective size.

Supplementation and effective size

Many threatened species are sought being maintained by supplementation or restocking in the nomenclature of World Conservation Union (1987), that is, by intentionally releasing individuals held in captivity or taken from other more healthy populations. An increasing number of species are also used in cultivation. In some cases large numbers of cultivated individuals escape accidentally from closed culture operations or are released intentionally in the context of sea ranching (Hindar *et al.* 1991). This can be regarded as a form of unintentional supplementation.

Here we consider one extreme example of unintentional supplementation. In Norway, Atlantic salmon is used extensively in marine aquaculture and the harvest from wild populations is now outnumbered by the production of farmed fish by a factor of over 300 (World Wildlife Fund 2001). Thus, despite relatively low escape rates from marine cages, the rate of immigration into wild populations is very high. It has been estimated to around 7-8% in an average river when adjusting for differences in lifetime reproductive success (Mork *et al.* 1999; Fleming *et al.* 2000).

The main Norwegian breeding program which was started in the early 1970s is based on four separate breeding lines corresponding to four different cohorts. The average effective size of each of these breeding lines has been estimated to about 80 individuals (Mork *et al.* 1999). Ignoring differentiation between each of the breeding lines, the total effective size of the captive subpopulation is thus roughly 320 individuals. The effective size of the total Norwegian population of Atlantic salmon (the wild component) is not known but it is probably on the order of 10^4 or 10^5 per generation (cf. Altukhov & Salmenkova 1994; Ryman 1997) as around 100000 spawners are found in Norwegian rivers each year (Ståhl & Hindar 1988) and the generation time (mean reproductive age) is about 5.7 years (Hutchings & Jones 1998).

There is, however, no migration from the wild component into the breeding line. Under this form of perfect one-way migration, that is,

$$\mathbf{M} = \begin{bmatrix} 1 & 0 \\ 0.075 & 0.925 \end{bmatrix} \quad (17)$$

it follows that the effective size of the total system is simply $N_e = 320$ indi-

viduals. Applying (5), we find that the time needed before this asymptotic effective size is attained is of the order of $t_e = 13.7$ generations.

In order to counteract the loss of genetic variation in captive populations, conservation biologist have proposed that a certain number of wild individuals should continually be reintroduced back into captivity to reduce the potential loss of genetic variation (Schonewald-Cox *et al.* 1983; Ballou *et al.* 1995). The same logic could be applied for preserving genetic variation in the population of captive and wild Atlantic salmon. However, even allowing 5% migration from the wild population back into the breeding lines so that we have

$$\mathbf{M} = \begin{bmatrix} 0.95 & 0.05 \\ 0.075 & 0.925 \end{bmatrix} \quad (18)$$

and setting the effective size of the wild component equal to 10^4 would raise only the effective size to $N_e = 882$ (and lower t_e to 8 generations). Thus even with approximately symmetric migration, the asymmetry in subpopulation sizes still creates a dramatic effect on the total effective size. A total effective size this low will probably not be sufficient for long-term preservation of typical levels of genetic variability (Lande & Barrowclough 1987).

Discussion

For a model with constant subpopulation sizes and a fixed but arbitrary pattern of migration we have shown in detail how effective population of a subdivided population can be computed using numerical methods. Our method differs from the approach used by Whitlock & Barton (1997) in

that we compute the effective size as a direct function of the primary parameters of the model, the migration matrix and local effective population sizes, whereas Whitlock & Barton's (1997) expression for the effective size involves correlations in allele frequencies within and among demes ρ_{ij} which implicitly depends on the migration matrix. These correlations need to be estimated from data sampled from a population in stochastic equilibrium. In situations where such data is not available, for example at times when a new management regime is introduced, it is in general not possible to predict the asymptotic rate of convergence (or the asymptotic values of the correlations in Whitlock & Barton's (1997) formula) without resorting to some approach based on the eigenvalues and eigenvectors of the transition matrix for variances and covariance or for probabilities of identity by descent. The two approaches are thus valuable in different situations depending on what information is available.

In cases with moderate or strong directionalities in the migration pattern we have shown that the total effective size can become less than the sum of the subpopulation sizes. As already noted, because asymmetries in the pattern of migration implies that different subpopulations contribute differently, this result is consistent with similar previous results (Whitlock & Barton 1997) for the effective size of a metapopulation.

Not only asymmetric migration can create a reduction in total effective size. As shown by the example of unintentional supplementation, strong asymmetries in subpopulation sizes can make one population dominate the other such that total eigenvalue effective size is dramatically reduced, even

when there is no directionality in the migration pattern. Again, this result can be understood through Whitlock & Barton's (1997) approach based on each subpopulations contribution to the next generation. The quantitative conclusions in the case of Atlantic salmon must be regarded as preliminary, however, because complications of age-structure and geographic structure within the captive and wild component of the population is not analyzed. It does show, however, that long-term effects of supplementation on genetic variability are likely to occur and may be of great importance in addition to other effects of more immediate concern (e.g. Tufto 2001, 2000).

Supplementation, as defined here, should not be confused with so called supportive breeding programs (Nomura 1999; Ryman *et al.* 1995) in which a population is only separated into a captive and wild component during the mating phase of the life cycle. Intentional and unintentional supplementation, in contrast, is more appropriately modeled as a population completely subdivided into captive and wild components with strong directional migration from the captive to the wild subpopulation. The formulas presented by e.g. Ryman *et al.* (1995) are therefore not applicable in the simple two-population scenarios presented here.

The extension of the model to include a more elaborate harvesting scenario shows how effective size of the total population can be taken into account explicitly when setting local harvesting thresholds or conservation limits. Our examples demonstrate that considerable gain can be made in total effective size through harvesting based on knowledge about population subdivision, either from estimates of population sizes and migration pattern or

from genetic information on population structure (e.g. Tufto *et al.* 1998).

The harvesting strategy used and the choice of a deterministic population dynamic model are in some respects very simplistic, and much more realistic approaches based on stochastic population models have been developed in the case of single populations (e.g. Lande *et al.* 1995; Sæther *et al.* 1996; Engen *et al.* 1997). However, it would seem reasonable to presuppose that harvesting threshold adjustments similar to the ones derived here would apply also to harvesting for stochastic subdivided population models.

Previous treatments have mostly dealt with this problem by considering each subpopulation independently without explicitly taking into account the population subdivision structure and total effective size. It can be argued that the total effective size of the population is a too simplistic management goal and that other factors such as local inbreeding depression (Lynch 1991) and local demographic and environmental stochasticity (Lande *et al.* 1999) need to be taken into account. In principle there are no obstacles to incorporating such processes into the framework presented here. This could essentially be done by adding more terms to equation (B.1) quantifying e.g. the genetic load associated with inbreeding depression or the probability of local extinction associated with demographic and environmental stochasticity. However, a fundamental difficulty is how to value effective size against harvesting yield or losses arising from other processes. Essentially, which point along the trade-off curve in Fig. 1 should we choose? More generally, with uncertainty in the parameters, rationality and decision theory require us to fully specify a utility function $U(Y, N_e)$ or to follow some procedure

corresponding to fully specifying a utility function (Berger 1985). Some of these value judgments could possibly be resolved by going back to the theory and empirical data on how effective size ultimately reduces the growth rate and productivity of a population through loss of genetic variation and adaptation.

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Appendix A Rewriting (2) on the form of (3)

The same approach as in Tufto *et al.* (1996) is used but some details differ because we are considering the transition from one generation to the next and not the equilibrium problem. First, let

$$\delta_{ij} = \begin{cases} 0 & \text{for } i \neq j \\ 1 & \text{for } i = j. \end{cases} \quad (\text{A.1})$$

For each element of $\mathbf{C}$, there is a corresponding linear equation which now can be written

$$c_{ij,t+1} = \sum_{k=1}^n \sum_{l=1}^n m_{ik} m_{jl} c_{kl,t} + \delta_{ij} \frac{q(1-q) - c_{ij,t}}{2N_i}. \quad (\text{A.2})$$

Following Tufto *et al.* (1996), because $c_{ij,t} = c_{ji,t}$, this can be rearranged to

$$c_{ij,t+1} = \sum_{k=1}^n \sum_{l=1}^{k-1} (m_{ik} m_{jl} + m_{il} m_{jk}) c_{kl,t} + \sum_{k=1}^n m_{ik} m_{jk} c_{kk,t} - \delta_{ij} \frac{1}{2N_i} c_{ij,t} + \delta_{ij} \frac{q(1-q)}{2N_i}. \quad (\text{A.3})$$

which is on the form of equation (3). Using r and s as indexes for the elements of $\mathbf{A}$, $\mathbf{b}$, and $\mathbf{c}$, where each value of r and s correspond to one particular combination of ij and kl , we can write the elements of $\mathbf{A}$ as

$$a_{rs} = \begin{cases} m_{ik} m_{jl} + m_{il} m_{jk} & \text{for } r \neq s \wedge k \neq l \\ m_{ik} m_{jk} & \text{for } r \neq s \wedge k = l \\ m_{ik} m_{jl} + m_{il} m_{jk} - \delta_{ij} \frac{1}{2N_i} & \text{for } r = s \wedge k \neq l \\ m_{ik} m_{jl} - \delta_{ij} \frac{1}{2N_i} & \text{for } r = s \wedge k = l. \end{cases} \quad (\text{A.4})$$

The elements of $\mathbf{b}$ in (3) are given by

$$b_r = -\delta_{ij} \frac{q(1-q)}{2N_i}, \quad (\text{A.5})$$

and the vector $\mathbf{c}$ has elements

$$c_{r,t} = c_{ij,t}. \quad (\text{A.6})$$

Appendix B Numerical maximization of the yield

Instead of solving the maximization problem (9) and (11) for different specific choices of N_e^* , we varied γ and solved for the corresponding set of harvesting thresholds $N_1^*, N_2^*, \dots, N_n^*$ for each specific choice of γ . Also, rather than solving (12) for each $i = 1, 2, \dots, n$, we instead computed the optima by maximization (using `nlm` in the statistical software package R) of the function

$$N_e(N_1, N_2, \dots, N_n) - N_e^* - \gamma Y(N_1, N_2, \dots, N_n) \quad (\text{B.1})$$

which turned out to be numerically more efficient.

All local harvesting thresholds are constrained to be non-negative. In addition, all harvesting yields are constrained to be non-negative. This second set of constraints on the yields do not easily translate into a simple modified set of constraints on local harvesting thresholds. Therefore, these constraints were instead implemented through an extra penalty term

$$-b \sum_{\{i: Y_i(N_i) < 0\}} |Y_i(N_i)| \quad (\text{B.2})$$

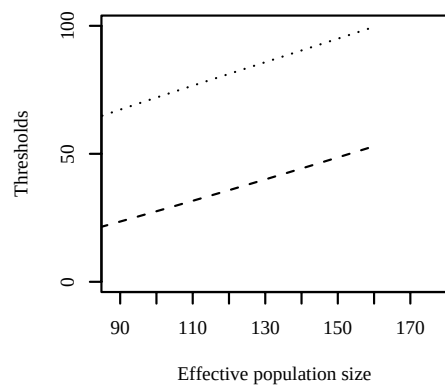
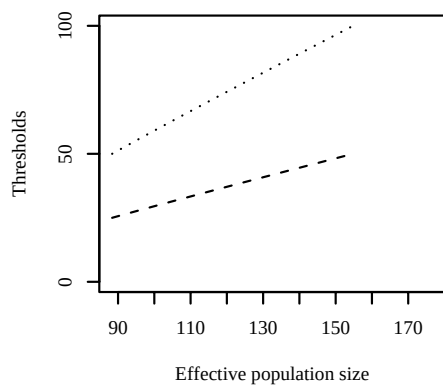
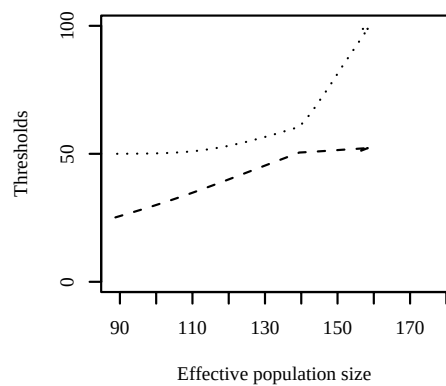
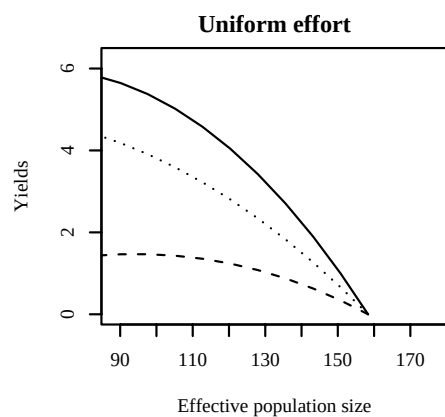
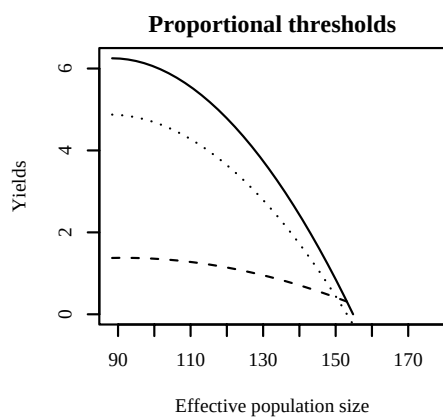
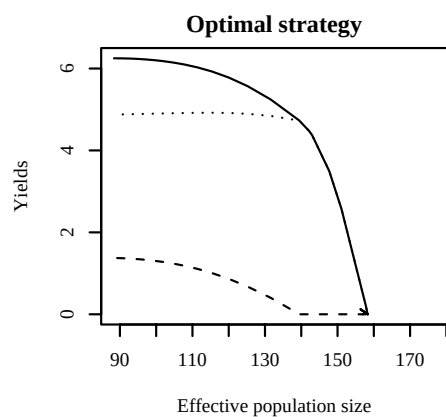
in (B.1) which as shown in Fig. 1 and 3 worked well when setting $b = 50$ (see e.g. Templeman 1982).

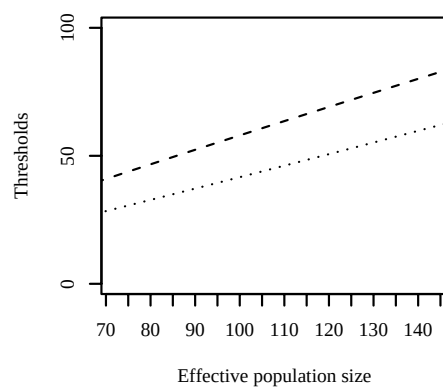
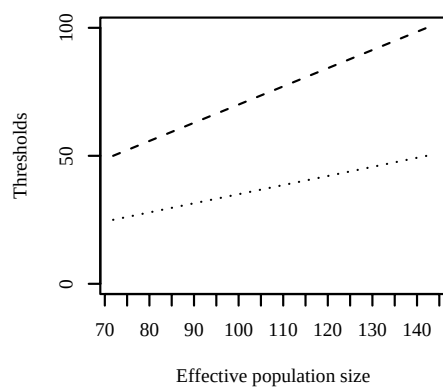
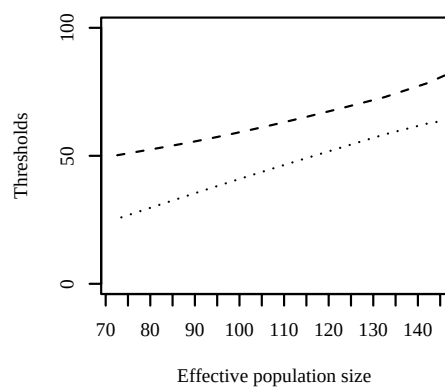
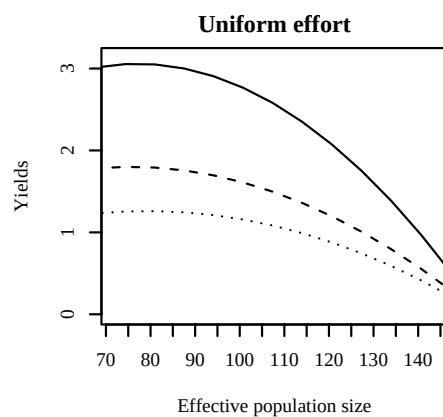
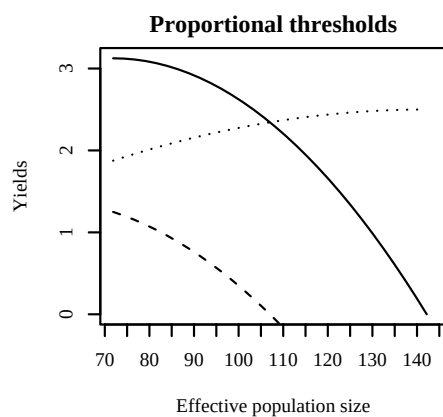
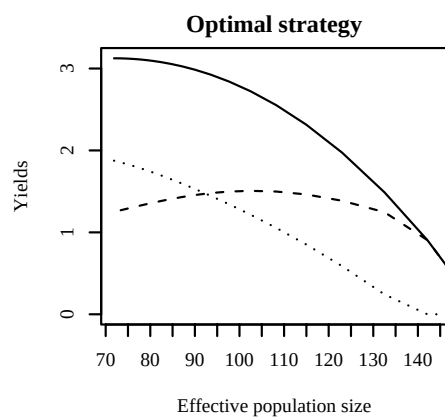
Figure captions

Figure 1: Harvesting yields (upper subplots) and harvesting thresholds (lower subplots) for subpopulation 1 (dashed line) and 2 (dotted line) under the optimal strategy (left column), the proportional threshold strategy (middle column), and the uniform effort strategy (right column). The total yields under each strategy is shown by the solid lines. The parameters used are $r_1 = 0.1$, $K_1 = 50$, $r_2 = 0.2$, $K_2 = 100$, $\tilde{m}_{12} = \tilde{m}_{21} = 0.005$.

Figure 2: Same as Fig. 1 but with $\tilde{m}_{12} = \tilde{m}_{21} = 0.05$.

Figure 3: Optimal thresholds and yields as function of effective size for a finite island model with four subpopulations with $r_i = 0.1$, $K_i = 50$ for all i . The subpopulation $i = 1, 2, \dots, 4$ exchanges migrants through a common migrant pool at rates of 0.1 (short dashes), 0.05 (dotted line), 0.02 (dashed dotted line), 0.01 (long dashes), respectively.





Optimal strategy

