

METAPOPOP—A software for the management and analysis of subdivided populations in conservation programs

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Abstract We introduce a computer program for the dynamic and flexible management of conserved subdivided populations. Using molecular marker data or pedigree information, the software determines the optimal contributions (i.e., number of offspring) of each individual, the number of migrants, and the particular subpopulations involved in the exchange of individuals in order to maintain the largest level of gene diversity in the whole population with a desired control in the rate of inbreeding. Restrictions can be introduced for the total number of migrants, and the mating of particular pairs and their contribution. A full genetic diversity analysis of the population is carried out. The optimal contribution from each subpopulation to a pool of maximal gene diversity is also provided by the program.

Keywords Inbreeding · Genetic drift · Migration · Population differentiation

Introduction

From a genetic point of view, conservation programs are aimed to reduce the increase in inbreeding and to maintain the highest levels of genetic variability for the

population to be able to face future environmental changes (Allendorf and Luikart 2007). In the context of ex situ conservation programs, a scenario of population subdivision is frequent (e.g., zoos, natural reserves, etc.), implying the necessity for maintaining the global gene diversity, which is known to be maximal for isolated subpopulations, and avoiding the local inbreeding in each subpopulation. A commonly accepted rule of thumb establishes that the minimum migration rate to avoid an excessive increase in inbreeding is to allow for one migrant per generation (OMPG) and subpopulation (see, e.g., Wang 2004) yielding a considerable differentiation between subpopulations if this is required, but not accounting explicitly for the levels of genetic diversity. However, more effective strategies have been developed recently (Wang 2005; Fernández et al. 2008). When individual pedigrees are known or molecular data are available to infer them, an effective method can be used which allows for optimizing the individuals' contribution by minimizing the whole population coancestry (Fernández et al. 2008). The method takes account of both the within- and between-subpopulation components of coancestry (with variable weights depending on the importance desired for each one) and, at the same time, provides the optimum scheme of migrations, being able to control the total number of movements if required. In this note we present a user-friendly computer program (freely available at <http://webs.uvigo.es/anpefi/metapop/>) which implements this dynamic procedure for the management of conserved subdivided populations. As an alternative to the dynamic method, the one-migrant-per-generation (OMPG) strategy or an option of isolated subpopulations can also be performed. The software also implements a full analysis of population diversity following Caballero and Toro (2002).

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Principles of the dynamic management method

In the context of a structured population (a population with n subpopulations with the possibility of gene flow between them), the objective function to be minimized can be a compound of the within-subpopulation (W) and between-subpopulation (B) terms of global population coancestry, with a factor λ balancing the relative importance of the

$$\text{terms, } B + \lambda \cdot W, \text{ where } W = \sum_{k=1}^n \frac{1}{4} \left(\sum_{s=1}^2 \sum_{s'=1}^2 \sum_{i=1}^N \sum_{j=1}^N \frac{f_{ij} c_{isk} c_{js'k}}{N_{sk} N_{s'k}} \right)$$

$$\text{and } B = \sum_{k=1}^n \sum_{l \neq k}^n \frac{1}{4} \left(\sum_{s=1}^2 \sum_{s'=1}^2 \sum_{i=1}^N \sum_{j=1}^N \frac{f_{ij} c_{isk} c_{js'l}}{N_{sk} N_{s'l}} \right)$$

(Fernández et al. 2008), s and s' being the sex of the offspring to be generated, N_{sk} the number of individuals of sex s in subpopulation k , and c_{isk} the number of offspring of sex s to be contributed by individual i to subpopulation k . Under random mating, higher values of λ would lead to solutions with lower average inbreeding levels, as more weight is given to the within-subpopulation coancestry generated. Because the value of λ to be used is arbitrary, an alternative offered by the program is to make a constraint in the maximum per-generation rate of inbreeding allowed in the population. The formulation also permits controlling the maximum number of migrants per generation allowed to move each generation. Finally, the program can also deal with a single undivided population if the number of subpopulations is set at $n = 1$.

Implementation of the method

Optimal solutions for contributions are obtained using a *simulated annealing* algorithm (Kirkpatrick et al. 1983),

whose default parameters can be changed by the user. Mating is first arranged randomly between males and females so that all females are allowed to mate once but males can mate more than once, in a polygamous system. This tries to represent a typical situation encountered in animal species. Alternatively, monogamous mating can also be forced, if desired. Afterwards, contributions are randomly assigned to each couple. Then, the recursive optimization procedure acts by changing the contributions from couples to the progeny and also interchanging males with replacement (polygamous mating) or without replacement (monogamous mating) when contributions of a given couple are null (see Fig. 1).

The program allows for specific mating pairs to be forced and the maximum number of contributed progeny from each pair to be set up. This is useful, for example, when the initial optimization has produced a set of mating pairs and contributions, but one or more of them have actually failed or the required number of progeny have not been generated. Thus, a second run of the program can be carried out including these restrictions, so that the optimization is made under the given constraints. In addition, the program allows for the restriction of specific pairs. This is useful, for e.g., when some pairs between close relatives are desired to be avoided. Another feature of the program is that the number of progeny is not necessarily the same as the number of parents. Thus, the desired number of males and females in the following generation can be set up freely, for e.g., to increase subpopulation numbers or to balance the sex ratio.

Finally, the program output gives the coancestry matrix among the expected progeny. This matrix can be directly included in the input window in order to run again the program and find the contributions of individuals and

Fig. 1 Window of the metapop program showing an example of the output matrix with optimized mating pairs and their contributions to each subpopulation

*** Dynamic method ***

5. Mating matrix

Subpopulation	Family	female	male	females to Sub1	males to Sub1	females to Sub2	males to Sub2	females to Sub3	males to Sub3	females to Sub4	males to Sub4
Sub1	1	A	D	3	2	3	0	0	0	0	0
Sub1	2	B	E	0	1	0	0	0	0	0	0
Sub1	3	C	E	0	0	0	1	0	0	0	0
Sub2	4	G	I	0	0	0	2	0	0	0	0
Sub3	5	K	N	0	0	0	0	1	2	0	0
Sub3	6	L	M	0	0	0	0	2	1	0	0
Sub4	7	O	Q	0	0	0	0	0	0	1	1
Sub4	8	P	R	0	0	0	0	0	0	2	2

Energy = 35.7240

6. Input for the next Generation.

n 4
nloci 0
Sub1
N 6
1 [1] 0

migrations expected in a further generation. This is useful, for e.g., to compare different alternative methods or different parameters and restrictions (migration rates, restrictions on inbreeding, etc.), what can be extremely useful for the manager in order to take the current decisions on the population.

Population analysis and other features of the program

From genotypic data on autosomic codominant molecular markers the coancestry between all pairs of individuals is obtained from the information on the frequencies of the markers, as made explicit by Caballero and Toro (2002). Alternatively, a pedigree coancestry matrix can be used as input for the program. The software makes a number of calculations (per locus and over loci) regarding coancestry, inbreeding and genetic distances within and between subpopulations with bootstrapping confidence intervals.

The loss/gain of diversity if one of the subpopulations is removed from the pool is given by disregarding that subpopulation and recalculating the global average coancestry and its components from the remaining pool. Relative contributions from each subpopulation can also be obtained if they should contribute to produce a single pool

(a synthetic population or a germplasm bank), with a given weighting factor balancing the relative importance of the within and between components of gene diversity.

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