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Characterization and conservation of genetic diversity in subdivided populations

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We review the available tools for analysing genetic diversity in conservation programmes of subdivided populations. Ways for establishing conservation priorities have been developed in the context of livestock populations, both from the classical population genetic analysis and from the more recent Weitzman's approach. We discuss different reasons to emphasize either within or between-population variation in conservation decisions and the methodology to establish some compromise. The comparison between neutral and quantitative variation is reviewed from both theoretical and empirical points of view, and the different procedures for the dynamic management of conserved subdivided populations are discussed.

Keywords: heterozygosity; inbreeding; coancestry; genetic differentiation; quantitative traits; genetic markers

1. INTRODUCTION

Maintenance of biodiversity is one of the most important current concerns of humankind, as wild species and domestic breeds and strains are disappearing at an alarming rate, and an increasing number of these require human intervention to guarantee their survival (Frankham *et al.* 2002). As genetic diversity is the basis of evolutionary potential of species to respond to environmental changes, this becomes an essential pillar in conservation genetics. Most populations of endangered species are commonly subdivided in different breeding groups, either in different fragments of habitats, natural reserves, arboreta or zoos, or in different breeds or strains in the case of domestic plants and animals, which are, in turn, subdivided into smaller reproductive units more or less interconnected. Thus, characterization and management of genetic diversity has to be made considering idiosyncratic population structures. In what follows, we use the term 'metapopulation', widely used in ecology, population genetics and conservation biology, to designate a group of populations with some possible gene flow among them (Hanski & Gilpin 1997). In this paper, we review the tools for measuring genetic diversity in structured populations and their application for establishing conservation priorities, particularly in the context of livestock breeds, as much work has been developed in this area. We also review the comparison between usual characterisations with molecular markers and those from quantitative variation. Finally, we discuss dynamic procedures to manage genetic diversity in subdivided populations.

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One contribution of 16 to a Theme Issue 'Population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill'.

2. GENETIC DIVERSITY: DEFINITION, TYPES AND MEASURES

Genetic diversity has been defined as the variety of alleles and genotypes present in a population and this is reflected in morphological, physiological and behavioural differences between individuals and populations (Frankham *et al.* 2002). From a functional point of view, genetic diversity can be classified as neutral, deleterious or adaptive (Hedrick 2001). Generally, neutral variants are used for conservation applications, but deleterious and adaptive variation are also important in the contexts of population survival and economically important traits in domestic plants and animals.

From a descriptive point of view, genetic information can refer to DNA sequences, individual genes, chromosomes or quantitative genetic variation. Since the beginning of the 1990s, the development of appropriate tools has resulted in a leading role for molecular markers in the characterization of genetic diversity. At this level, genetic diversity is usually measured by the frequencies of genotypes and alleles, the proportion of polymorphic loci, the observed and expected heterozygosity or the allelic diversity. In the context of structured populations, molecular measures of differentiation are based on genetic distances in allele frequencies among populations (Nei 1987; Laval *et al.* 2002), as well as on the popular Wright's (1969) fixation index, F_{ST}.

The most widely used parameter to measure diversity within populations is the expected heterozygosity, or gene diversity, defined by Nei (1973) as the probability that two alleles chosen at random from the population are different. With pedigrees, the usual way to estimate diversity is to calculate $1-F$ and $1-f$, where F (inbreeding) and f (coancestry) are the probabilities that two genes taken at random from

the same or different individuals are identical by descent (Malécot 1948), but they correspond to the observed and expected heterozygosity in a model where all the alleles in the base or reference population are assumed to be different. With markers, the usual estimated parameters are the observed and expected heterozygosity, but we would obtain the same results by applying the Malécot (1948) definition and substituting identity-by-descent by identity-in-state (Caballero & Toro 2002). In monitoring conservation programmes, a key parameter is the rate of change in gene diversity or inbreeding, the effective population size being inversely related to these.

Allelic diversity is an alternative criterion to measure genetic diversity, and some authors (Petit *et al.* 1998; Barker 2001) consider that this parameter is the most relevant in conservation programmes, as a high number of alleles imply a source of single-locus variation for important traits such as the major histocompatibility complex, which is responsible for the recognition of pathogens. It is also important from a long-term perspective, because the limit of selection response is determined by the initial number of alleles (Hill & Rasbash 1986) and, because it is more sensitive to bottlenecks than expected heterozygosity, it reflects better past fluctuations in population size. However, because 'the effective number of alleles' is, by definition, the inverse of the mean coancestry (Crow & Kimura 1970, p. 324), with respect to the genetic management of a population, the strategy of maximizing gene diversity keeps levels of allelic diversity as high as strategies maximizing allelic diversity itself, but with a better control of inbreeding (Fernández *et al.* 2004).

Quantitative genetic variation is the basis of productive and reproductive traits and therefore of greatest concern in conservation biology. Analysis of data from families allows estimates of the amount of additive genetic variance or heritability for polygenic traits to be obtained (Falconer & Mackay 1996). The relationship between the degree of divergence in neutral markers and the degree of divergence for quantitative traits can be addressed by the comparison between the fixation index F_{ST} and its analogue for quantitative traits, termed Q_{ST} by Spitze (1993). This is a dimensionless measure of the quantitative genetic variance among populations and is defined as $Q_{ST}=V_B/(V_B+2V_W)$, where V_W and V_B are, respectively, the additive within- and between-population components of the genetic variance for the trait considered.

3. TOOLS FOR ESTABLISHING CONSERVATION PRIORITIES IN SUBDIVIDED POPULATIONS

(a) *Partition of gene diversity in a subdivided population*

In a metapopulation, gene diversity is partitioned into components between and within populations. Here, we follow closely the development of Caballero & Toro (2002), who expressed the average global coancestry as

$$\bar{f}=\tilde{f}-\bar{D},$$

or

$$\frac{\sum_{i=1}^{n}\sum_{j=1}^{n}f_{ij}}{n^2}=\frac{\sum_{i=1}^{n}f_{ii}}{n}-\bar{D}=\sum_{i=1}^{n}\frac{1}{n}\left[f_{ii}-\frac{\sum_{j=1}^{n}D_{ij}}{n}\right],$$

where n is the number of populations, f_{ij} is the average coancestry between populations i and j, $\bar{f}$ is the average global coancestry and D_{ij} is Nei's minimum distance between populations i and j. The above equation shows how the average global coancestry $\bar{f}$ depends on the within-population coancestry (first term in the brackets) and the average distance among populations (second term in the brackets). Another way of expressing this is

$$(1-\bar{f})=(1-\tilde{f})+\bar{D}$$

(Nei 1987, p. 189), which represents the partition of the total gene diversity, $GD_T=1-\bar{f}$, into a within-population component, $GD_W=1-\tilde{f}$, and a between-population component, $GD_B=(\tilde{f}-\bar{f})$. Wright's (1969) fixation index can be written as $F_{ST}=GD_B/GD_T$ or $F_{ST}=(\tilde{f}-\bar{f})/(1-\bar{f})=\bar{D}/(1-\bar{f})$ (Cockerham 1969).

Let us consider an illustrative example using data from 36 microsatellites of five strains of the Iberian pig breed (Fabuel *et al.* 2004). The relative contribution of each strain to the coancestry of the breed is given in table 1. Note that the Guadyerbas strain has the largest contribution to the within-strain coancestry and, therefore, contributes the least to the within-population component of diversity $(1-\tilde{f})$. However, because it shows the highest genetic distance to the other strains, it contributes the most to the between-population diversity $(\bar{D})$.

One way of studying the relevance of the different Iberian strains to the breed diversity as a tool for establishing conservation priorities is, following Petit *et al.* (1998), to calculate the loss or gain of diversity if one or several groups are removed, and recalculating the global average coancestry (table 2). The removal of the Lampiño variety will cause the most damaging impact, decreasing the total genetic diversity, although it will increase the average genetic distance. The removal of the Guadyerbas strain will increase the total genetic diversity of the breed. This result may seem paradoxical although it arises from a standard population genetics analysis (Caballero & Toro 2002). We must realize that we are considering a theoretical model in which populations contribute to an infinite pool of genes. If, owing to the removal of one population, gene frequencies become more equalized, then this will increase the expected heterozygosity. A similar argument explains that the variability of a metapopulation will increase if a group of the most related individuals (a group of clones, for example) is eliminated and substituted by randomly chosen individuals. When two populations are simultaneously removed, the results agree with the previous ones. The removal of Torbiscal and Guadyerbas will hardly affect to the total diversity, whereas that of Retinto and Entrepelado will produce the maximum depletion of diversity.

Caballero & Toro (2002) also considered the following question: if we had to pool the different

Table 1. Relative contribution of different strains to the global coancestry of the Iberian pig breed.

strain	contribution to		
	within-strain coancestry	distance to other strains	global coancestry
Torbiscal	0.074	0.017	0.058
Guadyerbas	0.103	0.026	0.077
Retinto	0.099	0.019	0.080
Entrepelado	0.057	0.012	0.045
Lampiño	0.056	0.012	0.043
	$\tilde{f} = 0.393$	$\bar{D} = 0.089$	$\bar{f} = 0.304$

Table 2. Loss (−) or gain (+) of diversity (and their within and between-strain components) when one or two Iberian pig strains are removed.

strain removed	within-strain diversity	between-strain diversity	total genetic diversity	optimal contributions
no removal	0.6067	0.0895	0.6962	
Torbiscal (T)	+0.0054	−0.0073	−0.0019	0.128
Guadyerbas (G)	+0.0408	−0.0348	+0.0060	0.044
Retinto (R)	−0.0126	+0.0044	−0.0082	0.113
Entrepelado (E)	−0.0157	+0.0048	−0.0109	0.302
Lampiño (L)	−0.0178	+0.0050	−0.0128	0.413
T+G	+0.0616	−0.0584	+0.0032	
E+L	−0.0447	+0.0098	−0.0349	
R+E	−0.0377	+0.0025	−0.1315	
G+R	+0.0376	−0.0333	+0.0042	

populations to produce a single one (a synthetic population or a germplasm bank), what would be the contribution of each population to the pool that would maximize its genetic diversity? If the different populations were imposed to give different contributions (c_i) to the next generation, then the genetic diversity could be obtained as

$$GD_{\mathrm{T}} = 1 - \bar{f} = 1 - \sum_{i,j=1}^{n} f_{ij} c_i c_j$$

$$= 1 - \sum_{i=1}^{n} c_i \left[f_{ii} - \sum_{j=1}^{n} D_{ij} c_j \right].$$

This question can be answered by obtaining the values of c_i in the above equation that maximize genetic diversity, with the restrictions $c_i \geq 0$ and $\sum_{i=1}^{n} c_i = 1$. These optimal contributions are given in the last column of table 2, indicating that the strains that would contribute most are Lampiño and Entrepelado. With these optimal contributions, the genetic diversity would increase up to 0.7070.

(b) *Phylogenetic reconstruction based on genetic distances*

Genetic distances estimated from polymorphic microsatellite markers have been the most popular method of choice to assess genetic diversity among populations. The main difference between the application of genetic distances between livestock and natural populations is that the first have been domesticated and improved by humankind and, therefore, the divergence period is short and the role of mutation in creating differences will be small. Another important difference, emphasized by SanCristobal *et al.* (2003) is that, when applied to breeds, genetic distance is a measure of *distinctiveness* at a given time, without reference to any model that has generated the differences but, in contrast, in the population genetics approach, genetic distance is an estimate of parameters of the model underlying the generation of differences observed.

The behaviour of the different measures of genetic distances in the livestock context has been reviewed by Laval *et al.* (2002). They conclude that all distances strongly depend on the number of generations since the divergence and on the effective population size of the breeds and, therefore, no phylogeny can be inferred from the tree in the case of closely related breeds exhibiting different effective sizes. For this reason, it is generally assumed that in dealing with breeds of farm animals, the interpretation of trees in terms of phylogeny can be misleading (Felsenstein 1982). However, some authors (e.g. Barker 1999) have argued that phylogenetic diversity provides the best objective criterion for making conservation decisions (i.e. breeds that are taxonomically distinct should be favoured for conservation). However, this approach presents several problems. First, genetic variation within populations is completely ignored. Second, construction of trees using admixed populations, as often happens in livestock, contradicts the principles of phylogeny reconstruction (Felsenstein 1982). Third, it fails to acknowledge the fact that genetic distances vary greatly according to the marker used and the recent demographic history of the breed (e.g. whether it has passed through a population bottleneck).

(c) *Multivariate consensus representation of genetic relationship among populations and clustering analysis*

Among the many multivariate analysis methods, principal component analysis is a simple and powerful one that has been advocated by Moazami-Goudarzy & Laloe (2002). The advantages of this method are that it is less sensitive to data where admixtures are known to have occurred, it is independent from the mutation model assumed and it can be applied to various types of markers (microsatellites, AFLPs, proteins, blood groups, phenotypical traits, etc.).

Recently, a clustering method has been proposed (Pritchard *et al.* 2000; Dawson & Belkhir 2001; Corander *et al.* 2003; see Rosenberg *et al.* 2001 for an application to 20 chicken breeds) that constructs genetic clusters from a set of individual multilocus genotypes estimating, for each individual, the fraction of its genome that belongs to each cluster without any prior information on the structure of the population. Thus, the individuals are assigned (probabilistically) to populations, or jointly to two or more populations if their genotypes indicate that they are admixed. The algorithm is solved adopting a Bayesian approach computed using Markov Chain Monte Carlo methods and constitutes a flexible alternative to cluster methods based on genetic distances. As an example,

Table 3. Proportion of membership of each predefined population in each of either two or five possible clusters.

	two clusters assumed		five clusters assumed				
population	1	2	1	2	3	4	5
Torbiscal	0.001	0.999	0.004	0.003	0.002	0.985	0.006
Guadyerbas	0.001	0.999	0.001	0.001	0.001	0.002	0.995
Retinto	0.011	0.989	0.449	0.451	0.009	0.084	0.007
Entrepelado	0.050	0.950	0.527	0.419	0.008	0.030	0.016
Lampiño	0.010	0.990	0.321	0.223	0.351	0.024	0.081
Duroc	0.997	0.003	—	—	—	—	—

table 3 shows results from the five strains of the Iberian breed considered in previous examples and one population of Duroc breed (Fabuel *et al.* 2004). The strains are classified in two clusters by the STRUCTURE algorithm of Pritchard *et al.* (2000), with all the Iberian strains falling into the same cluster, and the Duroc breed constituting the other. Torbiscal and Guadyerbas strains are the populations whose genomes are differentiated the most unambiguously from Duroc. In addition, when the algorithm is applied to the Iberian breed assuming the same number of clusters as populations (five), we obtain the results presented in the right-hand side of the table. On average, 98.5% of the Torbiscal genomes and 99.5% of the Guadyerbas genomes are classified as two separate clusters. However, the results are less clear for the other populations, whose genomes are attributed to diverse clusters. This again emphasizes that the first two strains constitute more defined populations than the others.

Rosenberg *et al.* (2001) have argued that genetically distinctive populations can be identified based on how difficult is to separate them from others. That is, if some populations were easier to separate into clusters than others with only a small number of markers, then this could indicate the presence of distinctive multilocus genetic combinations in those populations that were easier to separate. Therefore, they suggest that the relative number of loci required for the correct clustering of several populations can be used as a way of identifying those that are genetically distinctive with respect to a collection.

(d) *The Weitzman approach*

Thaon d'Arnoldi *et al.* (1998) proposed to set conservation priorities for livestock breeds through the analysis of genetic distances by the Weitzman (1992) approach to measure the global diversity and the marginal loss of diversity attached to each population. From a genetic distance matrix, Weitzman (1992) proposed a computationally intensive method to construct hierarchical trees based on a form of maximum-likelihood phylogeny conditional on the model. Thus, the contribution of an element to group diversity is proportional to the reduction in tree length caused by the removal of the element from the group. Laval *et al.* (2000) applied this method to analyse the genetic diversity of 11 pig breeds from six European countries, Cañón *et al.* (2001) to 18 European beef cattle breeds, Aranguren-Méndez *et al.* (2002) to 5 endangered Spanish donkey breeds and Reist-Marti *et al.* (2003) to 49 African cattle breeds.

Table 4. Reanalysis of genetic diversity with the data of Laval *et al.* (2000).

Breed	Weitzman	loss/gain GDT
BEPI	−3.8	−0.80+1.01=+0.21
DKSO	−10.6	−0.23−0.22=−0.45
FRBA	−15.2	+2.62−1.95=+0.67
FRGA	−7.9	+0.48+0.12=+0.60
FRLI	−10.8	+1.34−0.66=+0.68
FRNO	−9.5	+0.48−0.05=+0.43
DELR	−11.6	−1.23−1.30=−2.53
DESH	−5.2	−1.80−0.14=−1.94[a]
NLLW	−12.1	+0.48−0.58=−0.10
SELR	−4.4	−0.52+1.16=+0.64
SEWP	−9.4	−0.80−0.02=−0.82

[a] This corrects a mistake in Caballero & Toro (2002).

Several authors have criticized the application of the Weitzman approach in the context of within-species diversity (Caballero & Toro 2002; Eding *et al.* 2002), because the method does not have a clear interpretation in terms of the most widely accepted measure of genetic variability; Nei's (1973) expected heterozygosity. The method has properties such as that the removal of an element always decreases the variability or the calculation of marginal diversity that are inconsistent with classical population genetics ideas. Moreover, it does not have a way of including the population size, if desired, and most important of all, it ignores within-population variability, which is a crucial component of global diversity. Ignoring the within-group variability is a characteristic not only of the Weitzman method, but also of all methods based only on genetic distances. In fact, one of the properties of the method (monotonocity in distance) is that the diversity in a set of populations should increase if the distance between populations increases. Thus, it will favour inbred populations with extreme allele frequencies, whereas the coancestry approach would favour non-inbred populations with an even distribution of gene frequencies. It should be noted, however, that small inbred populations can be useful if they harbour unusual alleles.

As an example, consider the analysis of genetic diversity carried out by Laval *et al.* (2000) for 11 European pig breeds using 18 microsatellites. Column 2 of table 4 shows the marginal losses of diversity calculated by Laval *et al.* (2000) with the Weitzman method, when each of the eleven breeds is removed from the set. Column 3 of table 4 gives the loss/gain of global genetic diversity when each of the breeds is

Table 5. Optimal contributions to a synthetic line or to a germplasm bank for different weights of the within- and between-population components of global diversity $\lambda(1-\tilde{f})+\bar{D}$.

population	$\lambda=0$	$\lambda=0.2$	$\lambda=1$	$\lambda=2$	$\lambda^*=2$
Torbiscal	0.228	0.208	0.128	0.000	0.020
Guadyerbas	0.406	0.333	0.044	0.000	0.020
Retinto	0.173	0.161	0.113	0.012	0.020
Entrepelado	0.162	0.190	0.302	0.412	0.392
Lampiño	0.031	0.107	0.413	0.576	0.548
$\tilde{f}$	0.443	0.424	0.349	0.326	0.332
$\bar{D}$	0.103	0.101	0.056	0.027	0.036
$\bar{f}$	0.340	0.323	0.293	0.298	0.297

removed, calculated as in the example of table 2. Again, the first term of the sum refers to the loss/gain of diversity due to the average coancestry of the population, whereas the second term refers to the loss/gain of diversity due to its average distance from all the others. That the Weitzman method only gives weight to the distance among populations becomes evident from the correlation between the Weitzman values (column 2) and the second term in column 3. This correlation is 0.90 (L. Ollivier, personal communication). In addition, the correlation between the Weitzman values and the first term in column 3 is negative (-0.66), producing an overall null correlation (-0.02) between the Weitzman values and the total loss/gain of gene diversity in column 3.

According to the Weitzman approach, the highest and lowest losses of diversity are incurred with the removal of the French Basque (FRBA) and the Piétrain (BEPI) breeds, respectively. In addition, the four French local breeds (FRBA, FRGA, FRLI and FRNO) altogether account for half of the total diversity, supporting the potential value of preserving local endangered breeds in the maintenance of species diversity. However, the analysis of genetic diversity using the global coancestry when each breed is removed (column 3 of table 4) gives quite different results (Caballero & Toro 2002). Removal of the FRBA breed will produce one of the largest increases in diversity across the remaining pool, while removal of the BEPI breed will produce a slight increase in diversity. In addition, removal of the four French breeds would produce a substantial increase in diversity ($+3.21\%$) instead of a large decrease. Therefore, the conclusions that one can draw from the two analyses are very different and, in fact, can be opposite.

(e) *How important is within- versus between-population genetic diversity?*

The important point that arises above is that the results obtained either using between-population diversity or total diversity will produce different and sometimes opposite conservation priorities. An over-emphasis on between-population variation may result in ignoring most of the global diversity, but an over-emphasis on within-population variation will favour the largest breeds, of current commercial value, and therefore the less endangered ones. In addition, in the context of animal breeding, between-breed diversity plays an essential role in the benefits derived from heterosis and complementarity (Ollivier & Foulley 2002). Therefore, some compromise should be attempted. In the framework of the classical partition of gene diversity, the simplest way to act is to carry out the analysis of gene diversity considering a weighted combination of the within-population gene diversity and the average genetic distance,

$$\lambda(1-\tilde{f})+\bar{D}.$$

Table 5 presents an application to the calculation of the optimal contributions of the five strains of Iberian pigs to a possible synthetic line or germplasm bank (Fabuel *et al.* 2004). For maximizing global genetic diversity ($\lambda=1$), the strains that should contribute more are the Entrepelado and Lampiño, whereas if the objective were to maximize the genetic distance ($\lambda=0$), the Guadyerbas and Torbiscal strains should be prioritized. For $\lambda=2$, two of the populations would have a null contribution. If, for whatever reason, we wanted to set up a minimum for the contribution of any strain or variety, then we can include a restriction in the quadratic programming solver and we would obtain the appropriate solutions ($\lambda^*=2$, minimum contribution equal to 0.02).

Other alternatives have been proposed. Eding *et al.* (2002) suggested always working with optimal contributions. Their strategy is to calculate the gene diversity of a safe core set formed by commercial lines together with their optimal contributions. Then, the gain in gene diversity is calculated when one extra breed is added to the safe core. They illustrate the method by an example involving 45 Dutch poultry breeds.

Ollivier & Foulley (2002) proposed an aggregate diversity (linear combination of within and between-population diversity weighted appropriately),

$$F_{ST}V+(1-F_{ST})[1-H(S/k)/H(S)],$$

where V is the Weitzman measure of loss of diversity, $H(S)$ is the average within-population heterozygosity and $H(S/k)$ is the average heterozygosity deleting breed k. The expression is intuitively appealing, and gives results for the data of Laval *et al.* (2000) highly correlated to the classical measures of genetic diversity (third column in table 4; see Ollivier & Foulley 2002).

Piyasatian & Kinghorn (2003) argued that the weights to be given to within- versus between-breed genetic diversity depend on the scenario imagined for the medium term use of the genetic diversity. They suggest giving five times more weight to the variation between populations than to that within populations.

The reason is that variation between populations may be more desirable because genetic effects are 'packed' in a more accessible way. Quantitative trait loci (QTL) would be easier to access at extreme frequencies if we are looking towards a greater adaptation to a changing or novel environment. The five value is supposed to reflect the speed by which genetic change can be made across populations compared with selection within one large mixed population.

Reist-Marti *et al.* (2003) also considered between-breed variation as much more important because the most valuable characteristics are probably those for which genes are fixed or at high frequencies within the population displaying these characteristics. Between-population diversity can also be more valuable if the plan is to use it as part of crossbreeding or introgression programmes. However, for the future creation of a new purebred population able to cope with a challenging environment or with diversified production conditions, within-population diversity should be more relevant (Notter 1999).

The above methods deal mainly with the use of genetic information, but this is only one of the criteria to consider in the final decision of setting priorities in livestock conservation (Oldenbroek 1999; Ruane 1999). In recent years, there have been several attempts to include different additional sources of information. Piyasatian & Kinghorn (2003) suggested a method for balancing genetic diversity, population viability and genetic merit of the breed as an objective function. Simianer *et al.* (2003), following a suggestion of Weitzman (1993), extended the approach to include extinction probabilities over a chosen time period. A simple way of setting the extinction probabilities is to assume that they are directly proportional to $\Delta F = 1/2N_e$, but it could be done in a more elaborate way. For example, in the analysis of 49 African cattle breeds, Reist-Marti *et al.* (2003) calculated extinction probabilities using four variables related to the population (population size, change over time, distribution of the breed and risk of indiscriminate crossing), four related to the environment (organization among the farmers, existence of a conservation scheme, political situation and reliability of the information) and two related to the value of the breed (presence of special traits and cultural value). Note, however, that including extinction probabilities in the Weitzman method will give an even higher weight to the inbred populations, thereby exacerbating its problems (Eding *et al.* 2002).

4. RELATIONSHIP BETWEEN MOLECULAR AND QUANTITATIVE MEASURES OF GENETIC DIVERSITY

Estimates of gene diversity (expected heterozygosity, H) and allele frequency differentiation (F_{ST}) are usually intended as indirect ways to measure variation for adaptive polygenic traits (additive genetic variance, V_A, or heritability, h^2, and population differentiation, Q_{ST}, respectively). However, monitoring quantitative genetic variation may reveal variation more closely related to fitness and hence, it may yield more interesting information on the effect of genetic and environmental changes to genetic diversity (Lynch 1996; Storfer 1996; McKay & Latta 2002; Bekessy *et al.* 2003). In fact, although the establishment of evolutionary significant units and management units for conservation have been basically defined in terms of phylogenetic distances and molecular markers (Krajewski 1994; Moritz 1995; Barker 1999), more emphasis has been recently given to a combination of ecological and genetic criteria (Crandall *et al.* 2000). Locally adaptive genetic diversity within units is probably of greater importance when choosing populations that are most suitable as translocations or restoration resources (McKay & Latta 2002). In addition, quantitative genetic variation can be a useful tool to detect some human-induced impacts on genetic diversity that cannot be detected with molecular neutral variation (Carvajal-Rodríguez *et al.* 2005). This is particularly the case for those anthropogenic effects prone to cause changes in quantitative traits, such as the increases in environmental variance or the shifts in adaptation to local optimal conditions caused by environmental contaminants.

The main problem with monitoring quantitative variation is that estimates of additive genetic components cannot be easily obtained and, even so, the results may be complicated by variation from environmental and non-additive genetic sources (Falconer & Mackay 1996). However, this is most likely to be the case for life-history traits (Crnokrak & Roff 1995; DeRose & Roff 1999), and not so much for many morphological traits, which usually show low levels of non-additive genetic variation, are less prone to variation from environmental sources but still can show some adaptation to environmental conditions. Thus, morphological variation could be a quite attractive tool for screening overall adaptive genetic diversity.

(a) *Theoretical expectations*

A comparison between molecular and quantitative estimates of genetic variation can shed light on the selective forces acting on the populations. For genes that are neutral for fitness, with additive action between and within loci for some trait, heterozygosity and additive variance behave in parallel. Accordingly, it is expected that $F_{ST} = Q_{ST}$, and this result holds quite generally, regardless of the model of population structure (Whitlock 1999). For traits under divergent selection pressure between populations, Q_{ST} is expected to be greater than F_{ST} whereas $Q_{ST} < F_{ST}$ would indicate that selection acts on the trait towards the same optimal phenotype.

Using computer simulations, Le Corre & Kremer (2003) compared genetic diversity for an additive quantitative trait with estimates, using unlinked neutral molecular markers or using the loci controlling the quantitative trait. The setting consisted of an island model metapopulation under a range of situations involving differential gene flow among populations, variable strength of stabilizing selection within populations, and diversifying selection expressed as variation in the local optima among populations. They showed that F_{ST} and Q_{ST} can also be equal under selection when disequilibrium among loci is of the same order within and

Table 6. Relationships between heritability (h^2) and quantitative differentiation (Q_{ST}) for a quantitative trait, heterozygosity (H) and genetic differentiation (F_{ST}) for quantitative trait loci (subscript QTL) or neutral molecular markers (subscript M). (Quantitative trait variation was controlled by 10 unlinked additive loci with effects extracted from a normal distribution and subject to stabilizing selection towards a local optimum, with possible variation among local optima; diversifying selection. Extracted from figs 5 and 6 of Le Corre & Kremer 2003.)
(Gene flow: low ($Nm=0.1$), high ($Nm=10$). Stabilizing selection: weak ($V_s=100$); strong ($V_s=10$), where V_s is the width of the fitness curve. Diversifying selection: no (equal phenotypic optima across populations); yes (variance among phenotypic optima across populations equal to 10).)

diversifying selection	stabilizing selection	gene flow	diversity estimates
no	strong	low	$H_M > H_{QTL} \approx h^2$ $F_{ST(QTL)} > F_{ST(M)} \gg Q_{ST}$
		high	$H_M \gg H_{QTL} \approx h^2$ $F_{ST(QTL)} \approx F_{ST(M)} \approx Q_{ST} \approx 0$
yes	weak	low	$h^2 > H_M > H_{QTL}$ $Q_{ST} > F_{ST(QTL)} > F_{ST(M)}$
		high	$h^2 \gg H_M > H_{QTL}$ $Q_{ST} \gg F_{ST(QTL)} > F_{ST(M)}$

between populations, but this is an unlikely situation. Table 6 shows a summary of some of their main findings. Under strong stabilizing selection within populations but no diversifying selection among them, heterozygosity for neutral markers (H_M) can be much larger than that for QTLs (H_{QTL}) or heritability (h^2), depending on the gene flow, whereas $F_{ST} \gg Q_{ST}$ under low gene flow. For strong diversifying selection among populations, h^2 and Q_{ST} can be much higher than those estimates based on QTL or neutral markers, particularly for high gene flow. Note that, contrary to what might may be expected *a priori*, estimates of variation obtained by directly studying the loci controlling the QTL, are not necessarily closer to direct estimates obtained from the quantitative measures than those from neutral variation (see also Latta 1998; McKay & Latta 2002). This is a consequence of the multilocus nature of quantitative traits *versus* single locus estimates from neutral markers or QTL. Thus, for example, covariances of allelic effects generated by linkage disequilibrium among selected loci and contributing to differentiation for the quantitative trait are not expressed in single locus estimates. In addition, under strong diversifying selection and substantial gene flow, most of the loci contributing to the trait will have F_{ST} values similar to those of the neutral markers, whereas only a few would exhibit important allelic differentiation and important contribution to the between-population variance of the trait (Le Corre & Kremer 2003). This implies that differentiation of many QTL might not be more informative than differentiation on neutral markers.

The above predictions are based exclusively on additive gene action for the quantitative trait and Hardy–Weinberg equilibrium. Deviations from Hardy–Weinberg equilibrium can cause estimates of Q_{ST} to depart from the neutral expectation (Yang *et al.* 1996). In addition, non-additive genetic components and uncontrolled maternal and common environmental effects can potentially modify the expectations (Lynch *et al.* 1999; Whitlock 1999; Hendry 2002; López-Fanjul *et al.* 2003). Whitlock (1999) showed that under additive-by-additive epistasis it is generally expected that $Q_{ST} < F_{ST}$. López-Fanjul *et al.* (2003) carried out a more detailed study on the theoretical relationship between Q_{ST} and F_{ST} after consecutive bottlenecks. They showed that under dominance, $Q_{ST} < F_{ST}$ for low to moderate frequencies of the recessive alleles, otherwise $Q_{ST} > F_{ST}$. With reinforcing epistasis, the condition $Q_{ST} < F_{ST}$ is extended to a broader range of frequencies, becoming a quite general outcome. Thus, under non-additive gene action, the comparison between Q_{ST} and F_{ST} largely depends on the frequencies of single loci. However, the most probable consequence of dominance and epistasis is that $Q_{ST} < F_{ST}$.

(b) *Experimental results*

The empirical relationship between molecular variability and morphological, behavioural or life-history variability seems to be generally low (Butlin & Tregenza 1998; Pfrender *et al.* 2000; Reed & Frankham 2001; Merilä & Crnokrak 2001; McKay & Latta 2002). For example, Reed & Frankham (2001) carried out a meta-analysis based on 71 datasets (60 of allozymes) of molecular heterozygosities and genetic distances and quantitative measures of genetic variation. The mean correlation between molecular and quantitative estimates was weak (0.217 ± 0.05), indicating that molecular measures only explain 4% of the variation in quantitative traits. Furthermore, the correlation did not differ significantly from zero for life-history traits (-0.110) but was higher and significant for morphological traits (0.311 ± 0.052). Finally, there was no significant relationship with heritability (-0.08), considered the best indicator of adaptive potential. Alternative explanations for the discrepancy between molecular and quantitative measures are discussed by Reed & Frankham (2001).

Although the errors in the estimation of F_{ST} and Q_{ST} are usually large, meta-analyses carried out by Merilä & Crnokrak (2001) and McKay & Latta (2002) involving studies on a variety of plant and animal species indicated that Q_{ST} was generally larger than F_{ST},

Table 7. Estimates of diversity and their precisions (given as the standard deviation, s.d., of estimates among 50 simulated replicates ± standard error) from a single molecular marker, and a single quantitative trait controlled by an infinitesimal model of gene effects. (Metapopulation with five populations of 500 individuals each, migration rate m among adjacent populations and intensity of stabilizing selection V_s for the quantitative trait. The average number of alleles segregating for the molecular marker at the time of the analysis is indicated. Results from Carvajal-Rodríguez *et al.* 2005.)

	alleles	H (s.d.(H) ± s.e.)	V_A (s.d.(V_A) ± s.e.)	F_{ST} (s.d.(F_{ST}) ± s.e.)	Q_{ST} (s.d.(Q_{ST}) ± s.e.)
$V_s=\infty$					
$m=0$	2.3 ± 0.0	0.37 (0.214 ± 0.004)	0.34 (0.033 ± 0.001)	0.60 (0.104 ± 0.002)	0.59 (0.182 ± 0.006)
$m=0.001$	4.9 ± 0.1	0.59 (0.142 ± 0.007)	0.60 (0.043 ± 0.003)	0.35 (0.063 ± 0.002)	0.42 (0.171 ± 0.004)
$m=0.01$	9.4 ± 0.2	0.80 (0.053 ± 0.002)	0.80 (0.057 ± 0.002)	0.08 (0.024 ± 0.001)	0.11 (0.085 ± 0.005)
$V_s=20$					
$m=0$	2.4 ± 0.0	0.47 (0.165 ± 0.011)	0.46 (0.034 ± 0.001)	0.47 (0.080 ± 0.005)	0.50 (0.042 ± 0.002)
$m=0.001$	4.1 ± 0.1	0.59 (0.143 ± 0.005)	0.57 (0.046 ± 0.001)	0.35 (0.060 ± 0.002)	0.37 (0.038 ± 0.002)
$m=0.01$	9.3 ± 0.2	0.80 (0.053 ± 0.004)	0.75 (0.052 ± 0.001)	0.08 (0.023 ± 0.001)	0.07 (0.024 ± 0.001)

and it was thus concluded that a considerable part of the observed population divergence for quantitative traits should be attributed to differential selection pressures imposed by local environmental conditions. Dominance and epistasis are unlikely to be the explanations for this observation because, as stated above, these particular gene actions usually imply $Q_{ST} < F_{ST}$. In addition, the difference between Q_{ST} and F_{ST} was only significant for morphological traits, those expected to show less non-additive genetic components of variance, whereas life-history traits showed similar differentiation as molecular markers (Merilä & Crnokrak 2001). Nevertheless, maternal and common environmental effects inflating estimates of Q_{ST} cannot generally be neglected.

(c) *The precision of estimates*

A final issue is that estimates obtained from molecular markers and quantitative traits can involve different precisions. A single biallelic molecular marker gives estimates of genetic distance with the same precision as a neutral polygenic quantitative trait (Rogers & Harpending 1983), but the precision of the marker increases with the number of alleles (Foulley & Hill 1999; Kalinowski 2002). Carvajal-Rodríguez *et al.* 2005 have compared the precision of diversity estimates obtained from molecular markers and quantitative traits by calculating the standard deviation among simulated replicates of the estimates of H and F_{ST} from a single molecular marker, and from V_A and Q_{ST} from a quantitative trait. An increase in the number of alleles of the molecular marker increases the precision for both H and F_{ST}, as deduced by Foulley & Hill (1999) for genetic distances. In addition, an increase in the number of loci controlling the quantitative trait substantially enhances the precision of V_A. This is attributable to the cancelling of random changes in gene frequency because of genetic drift occurring at different loci. On the contrary, the precision of estimates of Q_{ST} does not increase with the number of loci, which remains about the same as the precision of F_{ST} for a biallelic marker, as deduced by Rogers & Harpending (1983).

The precision of the estimates under a metapopulation setting allowing migration among populations and stabilizing selection acting on the quantitative trait is shown in table 7. For each migration rate and selection regime, the estimates of diversity are very similar for the molecular marker and the quantitative trait in all cases, so that the comparisons between precisions are fair. Under no selection ($V_s=\infty$) the precision of V_A is larger than that of H for low migration rates, whereas molecular differentiation (F_{ST}) has more precision than quantitative differentiation (Q_{ST}). Under a typical selection intensity ($V_s=20$) and low migration rates, the precisions of both within and between-population diversity from a quantitative trait are higher than those from a single marker. It is deduced that between 10 and 20 independent markers are necessary for the precision of H to be the same as that for V_A from a single trait, and between 2 and 4 independent markers are necessary for the precision of F_{ST} to be the same as that for Q_{ST}.

5. DYNAMIC GENETIC MANAGEMENT OF SUBDIVIDED POPULATIONS

The management of a subdivided population is not a straightforward issue, because a range of factors are involved in the decisions about whether or not a captive population should be subdivided and the level of differentiation required. Dynamic management has a key role on the maintenance of neutral diversity (e.g. Wang 2005), the elimination of deleterious mutations (e.g. Couvet 2002), and the use of resources in commercial species (e.g. Tufto & Hindar 2003). In the following discussion, we will mostly consider genetic aspects, ignoring other considerations (e.g. breeding facilities, spread of disease, cost of translocations, catastrophes, cultural aspects, etc.), perhaps sometimes more decisive than the genetic ones, and that usually point towards the subdivision of captive populations (e.g. Woodford & Rossiter 1994).

(a) *Genetic effects of subdivision*

In terms of pure genetic diversity, the arguments should focus on the effective size of the metapopulation and, for this purpose, we follow the reasoning of Wang & Caballero (1999) and Caballero & Toro (2002). Variance and inbreeding effective sizes are not always the same in a metapopulation but, if it is not completely subdivided and its size and structure are constant over generations, then they will reach an asymptotic value after a sufficient number of

generations (Wang & Caballero 1999; see also Pannell & Charlesworth 2000 for other definitions of effective size in metapopulations). Let us consider a simple expression of the metapopulation effective size assuming random mating within populations,

$$N_e \approx \frac{2Nn}{(V_W + V_B + 1)(1 - F_{ST})}$$

(Caballero & Toro 2002), where V_W and V_B are the variances of long-term contributions of individuals within- and between populations, respectively. The above expression is in agreement with others obtained by Whitlock & Barton (1997), Nunney (1999) and Wang & Caballero (1999) and, because of its simplicity, is adequate for illustrative purposes. Population subdivision may increase or decrease N_e with respect to a single population of size Nn, mainly depending on the variance of contributions among populations. If contributions from individuals within populations are random ($V_W = 1$) and populations contribute equally to the next generation ($V_B = 0$), then the expression is reduced to the classical one by Wright (1943), $N_e \approx Nn/(1 - F_{ST})$, which shows that subdivision increases the metapopulation effective size. In a conservation programme, equalization of family sizes (or minimization of variation in contributions) within populations should usually be followed ($V_W = 0$), because this gives a doubling of effective size, $N_e \approx 2Nn/(1 - F_{ST})$. However, if there is some variation of contributions among populations, then the metapopulation size decreases with subdivision. For example, if the variance of the number of offspring among populations is twice the accumulated Poisson variance, $V_B \approx 4F_{ST}/(1 - F_{ST})$ and $N_e = Nn/(1 + F_{ST})$, then differentiation decreases the effective size (Wang & Caballero 1999). This implies that subdivision, even in captive controlled conditions, is much more likely to result in a decrease than an increase in N_e. In natural populations (and perhaps also in some captive ones), extinction of some populations is destined to occur, substantially amplifying the reproductive variance among subpopulations and thus decreasing N_e enormously (Gilpin 1991; Lande 1992; Hedrick & Gilpin 1997; Whitlock & Barton 1997).

Thus, at the planning stage of a conservation programme, the question of whether a population should be subdivided or not depends on the level of management of population contributions. If the reproduction and migration of the population and the demographic factors can be intensively managed, then subdivision and low gene flow may be beneficial for conserving the genetic variation for a given total population size. However, in situations where to practise intensive management is difficult, it would generally be safer to maintain a single large population rather than a number of subpopulations. Nevertheless, other genetic aspects should also be considered along these lines. The beneficial effects of subdivision may be realized only after many generations (recall that we are discussing the asymptotic effective size) during which the inbreeding rate might be increased compared with panmixia. The subdivision of the population implies a constraint in the mating system and, thus, follows the same principles as those applicable to non-random mating in a single population (Wang & Caballero 1999). Subdivision of the population, such as mating between relatives, decreases the long-term rate of inbreeding but increases that in the short-term. A higher probability of extinction because of inbreeding depression (Saccheri *et al.* 1998), as well as the more probable impact of demographic and environmental stochasticity in small populations (Lande 1988), could result in a drastic decrease in the metapopulation N_e, contrary to putative planning predictions. Thus, maintenance of isolated small populations for a long time before an extensive exchange of genetic material can be successful in experimental species (Margan *et al.* 1998), but is arguably less practical in real situations.

(b) *Level of gene flow among populations*

Because of the practical necessity of subdividing captive populations, the question arises as to how much gene flow should be maintained between populations. A simple rule emerging from the seminal work of Wright (1931) is that one migrant individual per local population and generation (OMPG) is appropriate to maintain genetic diversity in metapopulations. Although somewhat arbitrary, the rule arises from a desired balance of preventing the loss of alleles and minimizing loss of gene diversity within populations but allowing genetic divergence to exist between them. This rule has been widely adopted in conservation, and there are a substantial number of works addressing the robustness of the rule under violation of the simplifying assumptions (e.g. Mills & Allendorf 1996 and references therein). The latest one has been carried out by Wang (2004). Most departures from the ideal model can be accounted for by using the effective number of migrants, defined as $N_e m_e$, where N_e is the effective population size and m_e is the effective migration rate—that is,the rate of migration in Wright's island model, which would result in the same F_{ST} as observed in the actual population differing from the island model in migration pattern only (Wang 2004). Most of the complexities observed within subpopulations (e.g. age and sex structure, variance in reproductive success, non-random mating) can be captured by N_e, whereas those between populations (migration pattern) can be accommodated by m_e. Wang evaluates the impact of different scenarios on the actual number of migrants, showing that it usually needs be larger than one and, with scarce relevant information, Mills & Allendorf's (1996) conservative suggestion of 1 to 10 migrants may be followed.

The OMPG rule is a practical compromise that can be used as a general guide. However, the specific migration rate and pattern in a conservation programme should depend on the particular situations. Ideally, migration among populations should also be planned according to the optimization criterion followed to maintain genetic diversity. Wang (2005) has developed a method to monitor and maintain conserved subdivided populations when information from pedigrees and molecular markers is lacking and only census numbers and migration patterns are available from previous generations. In this case, expected coancestries and

inbreeding from each population can be calculated and used to take management decisions. Optimization of selection and movement of individuals can be accomplished by minimizing some objective function. He proposes that the pattern of migration be such that the average coancestry within populations is minimized subject to a given constraint on the maximum number of migrants, as translocations can be associated to a cost in terms of risk of infectious diseases or other reasons. This procedure would tend to equalize the lineage distributions among populations within the constraint and thus reduce accidental loss of genetic variation. Wang allows for a cost of migrations but not for variation in census sizes of populations, so that these may vary freely from generation to generation, a situation that can also be costly in many instances.

6. NEW DIRECTIONS IN FUTURE STUDIES

Conserved populations of domestic species could be useful because of their better adaptation to specific environments or disease, or because of the possession of specific traits of cultural, historical or scientific value. However, the setting of priorities in conservation is a controversial issue and we have given indications about how to combine within- and between-population diversity, and emphasizing that this depends on the imagined scenario for the medium or long-term use of genetic diversity. Furthermore, Hill (2000) and Hill & Zhang (2004) have repeatedly stressed that the practical usefulness of conserved populations is far from obvious. To introduce genetic variability, either polygenic or QTL based, from a conserved population into a selected one, is a lengthy process and requires that the conserved population have at least moderate performance in order not to be too far behind the commercial population. On the other hand, if selection objectives change to target adaptation to a new physical or commercial environment, then the use of the variation present in a single current large population, by appropriate recording and selection, could be more costly. In any case, as these authors concluded, native breeds are an important part of our landscape and culture and, therefore, there is a case for maintaining them.

The dichotomy between neutral versus adaptive/deleterious variation presents contrasting interests from the conservation point of view. On the one hand, adaptive variation can provide new criteria and measurements to back up conservation decisions. Differences between populations that are functional rather than neutral can be required, either for individual loci or genome regions. On the other hand, strictly neutral variation would be of prime interest in order to carry out genetic analysis of population structure or history. Thus, selected loci are the relevant ones in the first case, whereas these should be removed from the analysis in the second. One way of approaching the problem is to use the existing type I markers (markers associated to known functional genes) to characterize the populations, as is planned in recent biodiversity projects (Blott 2003). The second is to identify loci that have been subject to selection, showing that they present deviations from neutral expectations or, in other words, identifying signatures of selection among molecular markers. Based on the seminal test of neutrality proposed by Lewontin & Krakauer (1973), more recent developments by Bowcock *et al.* (1991), Beaumont & Nichols (1996) and Vitalis *et al.* (2001) have addressed this question. The idea behind this is to compare the observed distribution of F_{ST} values from markers with that expected under the neutral hypothesis, to identify those loci that significantly deviate from neutrality. To avoid the confounding effects of population structure and history, Bowcock *et al.* (1991) proposed to simulate the expected distribution of F_{ST} values at a range of ancestral allele frequencies so as to establish confidence limits to detect selected loci. Beaumont & Nichols (1996) improved the method by considering heterozygosities rather than allele frequencies to obtain the expected distribution of F_{ST}. Finally, Vitalis *et al.* (2001) defined new population-specific parameters of population divergence and constructed sample statistics to estimate these parameters in order to use the joint distribution of these estimators to identify selected loci. It seems probable that the characterization of diversity in future works will include an increasingly high use of adaptive variation, through the analysis of specific genes or quantitative traits, in combination with neutral variation.

General flexible procedures for the management of variation in subdivided populations are still to be developed. For a single undivided population, the most effective way of maintaining diversity when pedigree data and/or molecular information is available on an individual basis, is to set the contributions of individuals to values that minimize the average coancestry of progeny (Ballou & Lacy 1995; Caballero & Toro 2000). Extending this idea to a metapopulation with n populations of constant size N, an objective function

$$\sum_{k=1}^{n}\sum_{l=1}^{n}\sum_{i=1}^{N}\sum_{j=1}^{N} c_{ik}c_{jl}f_{ij}$$

should be minimized (J. Fernández, unpublished work), where c_{ik} is the contribution of individual i of population k and f_{ij} is the coancestry between individuals i and j. This function can be partitioned into a component within populations and another between populations, so that different weights can be given to each component, according to the particular needs. This method will allow for an automatic control of contributions and migrations between populations in order to maintain the maximum genetic diversity in the metapopulation, and a restriction of the number of migrants can also be imposed to allow for its cost.

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