

# Using Genetics to Identify Intraspecific Conservation Units: a Critique of Current Methods

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## Introduction

Genetic criteria have recently been proposed for identifying evolutionarily significant units (ESUs) and management units (MUs; Moritz 1994). Although this proposal has proved useful for focusing discussion about the intraspecific groupings of relevance to conservation, I am concerned that the criteria put forward have been accepted and applied without sufficient debate about their merit or limitations. My aim is to stimulate renewed debate on this subject by identifying some weaknesses in the proposed criteria.

Although Moritz (1994) distinguished between the biological definitions of ESUs and MUs and the genetic criteria he proposed for recognizing such groups, many papers that cite his work erroneously refer to the recognition criteria as the definitions. An ESU is a group of organisms that has been isolated from other conspecific groups for a sufficient period of time to have undergone meaningful genetic divergence from those other groups (Ryder 1986). Moritz (1994) suggested that ESUs could be identified genetically as groups whose mtDNA lineages were reciprocally monophyletic, meaning that all lineages within each group share more-recent common ancestors than any lineage from one group shares with any lineage from the other group. In contrast, an MU is a group in which local population dynamics are determined primarily by birth and death rather than immigration and emigration (Moritz et al. 1995). Moritz (1994) suggested that MUs could be identified as populations with significant differences in allele distributions. An important point regarding both of these concepts is that they apply only when the populations under study are naturally divided into groups (Moritz et al. 1995). Of

course, genetic study may also be of value in situations where populations are continuously distributed, but such populations cannot be subdivided into ESUs and MUs.

## ESUs

We begin by considering the criterion for ESU recognition. Imagine the extreme case in which a daughter population is founded from a parent population under the condition that each population contains only a single female in the generation immediately following this event. Regardless of the past size of the parent population or the subsequent size of either population, these two populations will immediately be reciprocally monophyletic and will qualify for ESU status. Now imagine a more realistic situation in which the daughter population is founded by a group small enough to attain mtDNA monophyly quite rapidly, but the parent population is larger. The parent population is then expected to be paraphyletic relative to the daughter population for some time—in other words, some lineages in the parent population will share a more recent common ancestor with lineages in the daughter population than they do with other lineages in the parent population. The question is, how much time? Neigel and Avise (1986) simulated a range of scenarios, including one similar to that just described (DAT 7 in their Fig. 9). In this case they found that the parent population was paraphyletic relative to the daughter population in more than 50% of simulations after  $N$  generations ( $N$  = female effective population size of the parent population) and that approximately  $4N$  generations were required before reciprocal monophyly was achieved with high frequency (approximately 90% of cases).

What are the implications of this? Consider a large mammal with a generation time of 10 years. Imagine that a peripheral population becomes isolated and starts

down an evolutionary path independent from that of the parent population. If the parent population is very small ( $N = 400$ ), the probability approaches 0.5 that ESU status will be achieved in 4000 years ( $N$  generations). If  $N$  is very large (say 100,000), there is an approximately 10% chance that ESU status will not be achieved after  $4N$  generations, or 4 million years. In this example the probability of the daughter population achieving ESU status is dependent on two factors: the size of a population from which it is now completely independent and, due to the large variance in expected time to reciprocal monophyly, a considerable amount of chance.

One of the most important contributions made by population genetics to our understanding of the tempo and mode of evolution was the realization that genetic changes in small, isolated populations could, under certain circumstances, proceed much more quickly than usual (Templeton 1980). Therefore, the type of scenario outlined above may be of broad relevance to evolution.

As a practical example, consider the case of the polar bear (*Ursus maritimus*), a species thought to have appeared in the mid-Pleistocene, perhaps when a small population of a widely distributed and relatively abundant parent species (the brown bear, *U. arctos*) became isolated during a glacial episode (Kurtén 1964). If this history is correct, then the finding that brown bears have maintained several well-diverged clades of mtDNA lineages, whereas polar bears have become fixed for lineages within one of these clades (Talbot and Shields 1996)—that is, that brown bears are paraphyletic relative to polar bears—is in keeping with expectation.

Although no biologist would suggest that polar bears are not a distinct species because of the mtDNA data, this case illustrates that groups far surpassing a reasonable biological threshold for ESU recognition can fail to get that recognition on genetic grounds if the population to which they are being compared has had large  $N$  since the two groups diverged. Of course, there is also a possibility of over-splitting groups that have had small  $N$ , but the real concern is that morphologically cryptic groups with a history of isolation and divergence similar to that of the polar bear might fail to receive protection because of a lack of mtDNA reciprocal monophyly. In short, reciprocal monophyly for mtDNA is not a necessary criterion for identifying ESUs, although it may be a sufficient criterion as long as there is no evidence to suggest that both populations involved have had a history of being very small.

I cannot suggest a simple alternative algorithm that could be used for defining ESUs under all conditions. Rather, I make the unoriginal (Ryder 1986) suggestion that ESU definitions should be based on as many sources of information, genetic or otherwise, as are available. For example, Talbot and Shields (1996) used sequence divergence to estimate that polar bear mtDNA lineages diverged from the closest brown bear lineages some

200,000–250,000 years ago. If nothing else were known about the biology of these groups, this estimate would at least suggest isolation in keeping with ESU recognition.

## MUs

We now consider the criterion for MU recognition. This criterion is less specific than the one for ESUs because neither the type nor number of loci used in searches for allele frequency differences were specified (Moritz 1994). There are many examples illustrating that the power of a genetic system to detect population structure depends on the variability and number of markers used and the sample size of individuals (e.g., Moritz et al. 1995). In lieu of a practical theoretical basis for relating genetic data to MU status, one possibility is to calibrate genetic data in populations for which movement patterns are known. The limitation of such empirical “ground-truthing” is that the analytical methods would have to provide a resolution between different scenarios that could lead to similar genetic results.

Perhaps the most important analytical issue currently limiting extrapolation from genetic data to movement patterns is that it must be possible to distinguish genetically between continuous and subdivided populations and to identify the subdivisions that exist; only when this has been done should the issue of assessing the relationships between those subdivisions arise. This issue is often ignored by geneticists who treat the study areas forming the basis of their sampling as cohesive natural groups and move straight to the task of quantifying the relationships between those sampled areas. Such an approach is adequate for learning about the general partitioning of genetic diversity across a species distribution, but not for identifying MUs.

Another analytical problem arises when the groups under consideration are not at equilibrium. This can be illustrated with two hypothetical scenarios; one where an isolated population is established with animals translocated from another population and the second where a genetically homogeneous population becomes split into two isolated groups by anthropogenic habitat alteration. In these cases the allele distributions in the respective population pairs will initially be identical (excluding sampling error), but the isolated populations will, by biological definition, be MUs. Although genetic differences will accumulate through time until the isolated populations meet the genetic criterion for MU recognition, there are many instances, particularly in conservation biology, where we would prefer not to wait for what could be tens of generations before we are able to recognize the effects of changes in population structure. In both of these cases, movement data could form a sensible basis for MU recognition from the mo-

ment after the changes in population structure took effect.

It is possible to imagine situations where the current limitations of genetic methods are not excessive—for example, insular populations with no recent record of departures from equilibrium—and existing problems may eventually be overcome by developments in the analytical methods used in genetic studies. But it does not seem practical to make routine use of genetic methods to identify MUs at this time. If promising new genetic methods become available, an important part of their development will be testing them empirically on populations for which movement patterns are known.

## Conclusions

Genetic studies can make important contributions to defining groups for conservation, but the criteria proposed by Moritz (1994) have severe limitations, and these criteria should be applied with caution. Nonetheless, discussion about the problems with the status quo, which I have tried to stimulate here, is the first step forward, and I am optimistic that continued refinement of ideas and improvement in analytical methods will overcome some of the current limitations associated with the application

of genetics to identifying natural groups and quantifying their independence.

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## Literature Cited

- Kurtén, B. 1964. The evolution of the polar bear, *Ursus maritimus* Phipps. *Acta Zoologica Fennica* **108**:1–30.
- Moritz, C. 1994. Defining 'evolutionary significant units' for conservation. *Trends in Ecology and Evolution* **9**:373–375.
- Moritz, C., S. Lavery, and R. Slade. 1995. Using allele frequency and phylogeny to define units for conservation and management. *American Fisheries Society Symposium* **17**:249–262.
- Neigel, J. E., and J. C. Avise. 1986. Phylogenetic relationships of mitochondrial DNA under various demographic models of speciation. Pages 515–534 in E. Nevo and S. Karlin, editors. *Evolutionary processes and theory*. Academic Press, New York.
- Ryder, O. A. 1986. Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology and Evolution* **1**:9–10.
- Talbot, S. L., and G. F. Shields. 1996. Phylogeography of brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. *Molecular Phylogenetics and Evolution* **5**:477–494.
- Templeton, A. R. 1980. The theory of speciation via the founder principle. *Genetics* **94**:1011–1038.

