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3

Genetically Based Measures of Uniqueness

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The understanding of organic diversity has been a major continuing goal of biology. The earliest component of such endeavors is systematics, which already in pre-Darwinian times had recognized the major discontinuities whereby organic diversity could be classified and quantified. Much of the pre-Darwinian legacy (for example, Ray distinguishing monocots from dicots, and Lamarck separating the vertebrates from the invertebrates) is still with us. Taxonomic divisions, then and now, were seen as reflective of a natural order, with the proviso that, in these post-Darwinian times, the epithet "natural" is reflective not of inherent design but of evolutionary divergence and history. However, the sense of early accomplishment that came with pigeonholing organic diversity into phyla, classes, orders, families, and species was not long-lived. Even Linnaeus became concerned with variation and with hybridization among his different species. Later, evolutionists were quick to point out that the difficulties of applying a rigorous species concept were not necessarily to be found in the deficiencies of taxonomy, but in the continuing dynamic nature of the evolutionary process. By the middle of this century, the exploration and clarification of intraspecific variation had become a major goal of experimental taxonomists and evolutionary biologists. It was evident that the variation in every species had a complex structure: subspecies, races, and ecotypes were the rule rather than the exception. And even if discontinuities were hard to recognize and name, clines and genetic variants were commonplace and thus became a major focus for understanding the genetics of the evolutionary process.

At the beginning of this century, however, experimental genetics developed relatively independently of evolutionary biology. Indeed, experimental geneticists regenerated, albeit subconsciously, a disturbingly archaic, typological view of the species. They spoke of a "wild type" and of "mutants," as if there was a species ideal from which deviations were aberrant forms of great experimental value, but of only passing natural interest.

The advent of electrophoresis, and the discovery of large amounts of genetic variation at the protein level, overthrew the idea of a wild type; and the problem of organic diversity at the intraspecific level fell squarely into the laps of population geneticists. We now know that about 30 to 40 percent of the genes in a population may exist in different allelic states. Given that an individual might contain 10,000 or so different genes, the potential number of gene combinations is enormous. If each of the 23 chomosome pairs in the human genome

carried a single polymorphic locus, containing two alleles, the number of possible genotypes would be 3^{23} or 9.4×10^{10}—a number well in excess of the current world population! The discovery of electrophoretic variation introduced much complexity, but also some simplification. Unified measures of difference and diversity became possible, with their units being the units of population genetics, namely allelic frequency. Such measures could be applied to every population, and comparisons could be made across species, genera, and higher taxa.

Most recently the problem of genetic diversity has also become a central concern of molecular biologists. Large-scale DNA sequencing is now a plausible reality. The genome was formerly visualized as a "string of beads," but now it is clear that the enormity of the information content present among the beads pales by comparison with the information content within each bead. Each "gene" may contain several thousand DNA base pairs, and this sequence may vary in complex ways. Base pairs may be substituted, added, and deleted. Whole regions may duplicate, transpose, and invert. Furthermore, those translated coding regions that we have imagined as the repositories of genetic information and which produce the structural genes analyzable by electrophoresis, turn out to be minor regions, interrupted by untranslated sequences, and flanked by large regions concerned with control and other more important or nonexistent functions (we don't yet know). The string has become as important as the beads.

Thus within each of the several million species on the earth, there are several thousand genes, each of which in turn may have several thousand base pairs in it and around it. It is the purpose of this paper to outline how such diversity can be measured and how uniqueness can be identified. How this is done at a higher taxonomic level is well understood, and is the core of modern systematics. I will not attempt to review this. Instead I will concentrate on variation at and below the species level. Already from a brief history of the subject, we have come to several important conclusions: (1) No species is genetically uniform. (2) The concept of a "wild type" is erroneous: allelic variants are abundant and commonplace. (3) The number of possible genetic combinations usually far exceeds the number of individuals in a population (or in a species): every individual is genetically unique, and its particular genotype may never reappear.

These conclusions may seem self-evident. But they are still resisted when taxonomists search for a "type" and when they deem it worthwhile to pursue endless discussions on "What is a species?" These conclusions are also regularly ignored by ecologists who use the species as their unit of description.

Given this variability, several important issues are posed:

1. How does one categorize and measure this enormous diversity and uniqueness? Are the measures we propose useful as a basis for conservation strategies?

2. What should our conservation strategies be at the intraspecific level? Why should we conserve genetic variants?

3. Finally, are genetic resources renewable? Mutations occur continuously,

ly reflects our perception that plants are much more plastic phenotypically than animals. However, even in plants, it is remarkable that in nearly every case where well-established populations living in contrasting habitats have been studied, their phenotypic differences have been shown to have at least a partial genetic basis (Heslop-Harrison, 1964; Langlet, 1971).

Increasing resolution of genetic effects can be achieved using the methods of quantitative genetics (Falconer, 1981; Mather and Jinks, 1982). Such methods, while giving substantial insight into the amount of genetic variation in a trait, cannot identify individual loci or their alleles. These techniques are also difficult to apply on a large scale, and therefore may not be feasible for a practicing conservation biologist. However, differences among populations can be studied using "transplant" or "common garden" experiments, and such experiments should be encouraged. Where this cannot be done, distinct phenotypic differences among populations can cautiously be considered to reflect, at least in part, genetic differentiation.

Phenetic diversity is usually measured by the variance of a particular trait. Where several traits are measured simultaneously, multivariate measures of variance (such as the determinant of the variance-covariance matrix) are used. Partitioning variance into between- and within-group effects is normally done by analysis of variance and variance component analysis.

Assessment of the structure of such phenetic variance is the province of numerical taxonomy (Sneath and Sokal, 1973). It involves the establishment of a "similarity matrix" that expresses the degree of similarity among groups. This similarity matrix usually takes the form of a correlation matrix, for closely related groups, indicating the correlations between each pair of populations with regard to a set of measured traits. This similarity matrix may then be subjected to a cluster analysis (which identifies groups at various levels of similarity) or an ordination analysis (which places the groups in a reduced hyperspace such that their distance from each other can be visualized readily). With closely related groups, principal component analysis on the correlation matrix is often used. Distances between groups can then be measured in terms of their differences in principal component scores. These distances (perhaps with the aid of a further cluster analysis) can then be used to identify sets of similar groups, and to describe how the overall variation is partitioned.

The use of these approaches is illustrated in the work of Adams (1977), who used chemical and morphological characteristics to assess variation among bean (*Phaseolus vulgaris*) varieties. Principal component analysis identified clusters of similar varieties, and the resulting groupings were consistent with genetic relationships based on pedigree analysis (Figures 5 and 6). Such multivariate methods are being used with increasing frequency in the analysis of crop resource data (e.g., Martinez et al., 1983; Witcombe and Rao, 1976; Murphy and

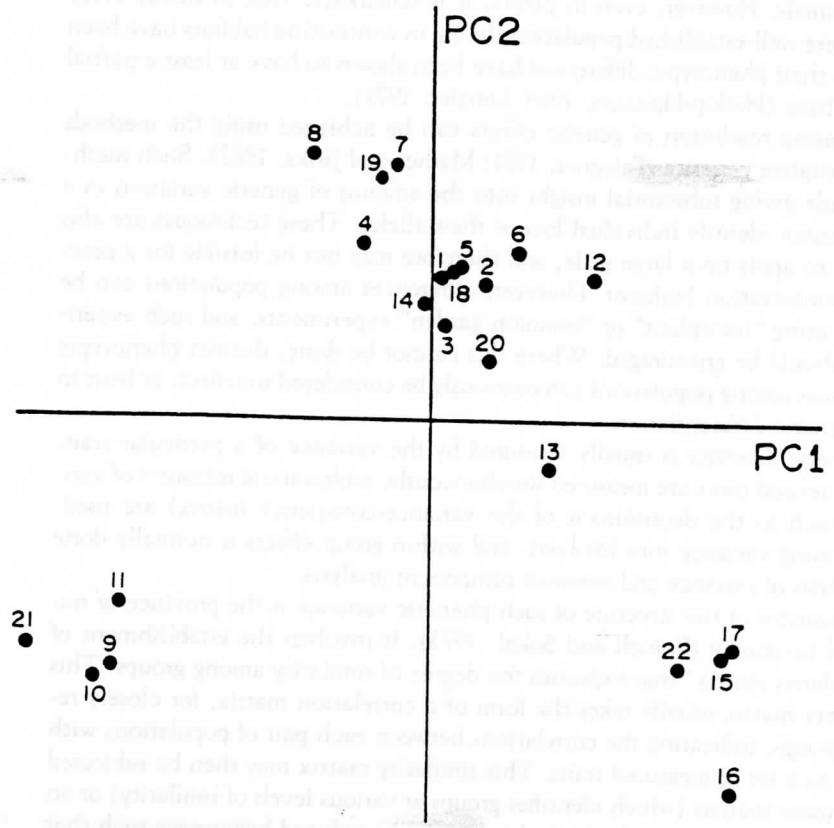

FIGURE 5. Relationship between phenetic distance derived by principal component analysis, varietal membership, and degree of genetic relationship among bean cultivars (after Adams, 1977). The display shows twenty-two cultivars on principal axes 1 and 2 derived from principal component analysis of eighteen chemical and agronomic characteristics.

Key to cultivars: (1) Red Mexican U.I. 34; (2) Red Mexican U.I. 36; (3) Gr. Northern U.I. 31; (4) Gr. Northern U.I. 59; (5) Gr. Northern U.S. 1140; (6) Gr. Northern Neb. 1; (7) Pinto U.I. 111; (8) Pinto U.I. 114; (9) Cal. Dk. Red Kid.; (10) Royal Red Kid.; (11) Idaho Lt. Red Kid.; (12) Big Bend Red Mex.; (13) Cal. Sm. Wh. 59; (14) Black Turtle Soup; (15) Sanilac Navy; (16) Gratiot Navy; (17) Seafarer Navy; (18) Gr. Northern U.I. 61; (19) Gr. Northern Tara; (20) Idaho Fl. Sm. Wh.; (21) Redkote Kidney; (22) Michelite 62 Navy.

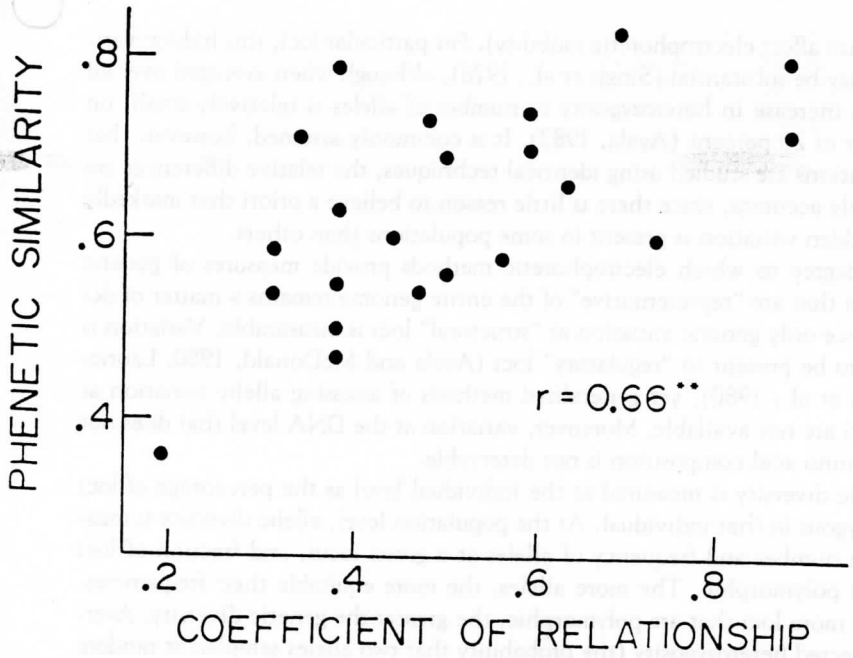

FIGURE 6. Comparison of phenetic similarity (= 1−distance) based on six principal component scores derived from principal component analysis of eighteen chemical constituent characteristics (see Figure 5) with relationship coefficients derived from ancestry patterns among seven cultivars.

Wilcombe, 1981) and in the analysis of morphological variation in natural populations (Hamrick, 1975; Clay and Antonovics, 1985; Johnston and Selander, 1971).

Phenetic traits have the advantage that they are easily measured, and their ecological or practical utility is either obvious or can be readily inferred. They have the disadvantage that their genetic basis is difficult to assess precisely, and standardized comparisons are difficult when populations or taxa are measured for qualitatively different traits.

Allelic Diversity

Measures of allelic diversity require knowledge of the allelic composition at individual loci. This information is generally obtained using electrophoretic analysis of enzyme variants. Allelic variants may also be recognizable as overt polymorphisms, but currently electrophoretic techniques are the most efficient for analyzing allelic variation at a large number of loci (usually 10 to 30). Diversity may be underestimated if there are "hidden alleles" (i.e., amino acid changes

that do not affect electrophoretic mobility). For particular loci, this hidden variability may be substantial (Singh et al., 1976), although when averaged over all loci, the increase in heterozygosity or number of alleles is relatively small, on the order of 20 percent (Ayala, 1982). It is commonly assumed, however, that if populations are studied using identical techniques, the relative differences are reasonably accurate, since there is little reason to believe a priori that markedly more hidden variation is present in some populations than others.

The degree to which electrophoretic methods provide measures of genetic variation that are "representative" of the entire genome remains a matter of debate, since only genetic variation at "structural" loci is measurable. Variation is known to be present in "regulatory" loci (Ayala and McDonald, 1980; Laurie-Ahlberg et al., 1980), yet generalized methods of assessing allelic variation at such loci are not available. Moreover, variation at the DNA level that does not affect amino acid composition is not detectable.

Allelic diversity is measured at the individual level as the percentage of loci heterozygous in that individual. At the population level, allelic diversity is measured in number and frequency of alleles at a given locus, and fraction of loci that are polymorphic. The more alleles, the more equitable their frequencies, and the more loci that are polymorphic, the greater the genetic diversity. Average expected heterozygosity (the probability that two alleles sampled at random will be different) is a commonly used overall measure. This measure is equal to the average number of heterozygotes per locus assuming Hardy-Weinberg proportions.

The partitioning of allelic variation within and among populations is generally carried out using the Shannon-Weaver diversity index, and by means of Wright's *F*-statistics. The Shannon-Weaver index measures the "information content" provided by the allelic variation, at both within- and between-group levels (Lewontin, 1972). *F*-statistics use the difference between observed and expected heterozygosities as a measure of within-individual, within-population, and between-population estimates of genetic substructuring (see Weir and Cockerham [1984] for a recent treatment).

Assessment of the structure of genetic variance among populations is carried out using measures of "genetic distance." The most commonly used measure is that of Nei (1975, 1978). First, one calculates genetic identity, *I*, a measure of the probability that two alleles chosen at random from two different populations will be identical, relative to the probability that these same alleles chosen from within each population will be identical. Genetic identity is then converted to genetic distance, *D*, by averaging over all loci, and using the relationship $D = -\ln I$. Nei (1975, 1978) has shown that *D* reflects the average number of allelic substitutions that have occurred between two populations since they diverged, based on the assumption that divergence has been by random spread of neutral mutations. Assuming that mutation rates within the populations are

similar, and that the chosen loci are representative of the genome as a whole, D is proportional to time since the populations diverged.

Other measures of genetic distance use the kinship (or coancestry) coefficient, f. This is defined as the probability that alleles sampled from two individuals (or populations) are identical by descent (i.e., have been derived by replication from the same ancestral gene). Cavalli-Sforza and Bodmer (1971) show that if two populations are assumed to have diverged only by genetic drift, with no mutation, the time of divergence is proportional to $-\ln(1 - f)$. This measure is therefore more appropriate than that of Nei when dealing with small populations that have diverged over relatively short periods. Precise methods of estimating the coancestry coefficient from gene frequency data have recently been described by Reynolds et al. (1983). The measure of Nei will probably continue to be the most commonly used because of its intuitive appeal, its well-established status, and its rough and ready translation into average number of allelic substitutions since population divergence.

Detection of allelic variation by electrophoresis has the advantage that it can be precisely quantified to provide comparative measures of genetic variation. However, it has the disadvantage in that it may not be representative of variation in the genome as a whole. It has the further disadvantage that its functional significance or selective importance is generally not known. Particular alleles may have specific phenotypic effects and may be subject to selection (e.g., Koehn et al., 1980), but in most cases electrophoretic variants can be used successfully as neutral markers of past historical events, or neutral markers to assess breeding system events. One of the most elegant demonstrations of such use is provided by the studies of Ward and Neel (1970), who showed a strong correlation between genetic relationship and village history in South American Indian tribes (Figures 7 and 8).

Sequence Diversity

Two techniques are currently used for assessing diversity in DNA sequences. The first involves the use of restriction enzymes that recognize a particular small base sequence (usually four to six bases), and cleave DNA at this site. Any changes in base composition may either prevent cleavage by the restriction enzyme at this site or generate new restriction sites, thereby producing a different fragment length. Differences in length of DNA fragments produced by the action of a particular restriction enzyme therefore reflect changes in base sequence, and can be detected electrophoretically. The use of several such enzymes permits "sampling" of the DNA for changed bases. Since the restriction enzymes are usually of bacterial origin, there is no a priori reason to suppose any one recognition site will be more abundant or evolve in a different manner from any other. This technique is most applicable to small DNA molecules, because in any large DNA molecule the restriction sites are likely to be so numerous as to

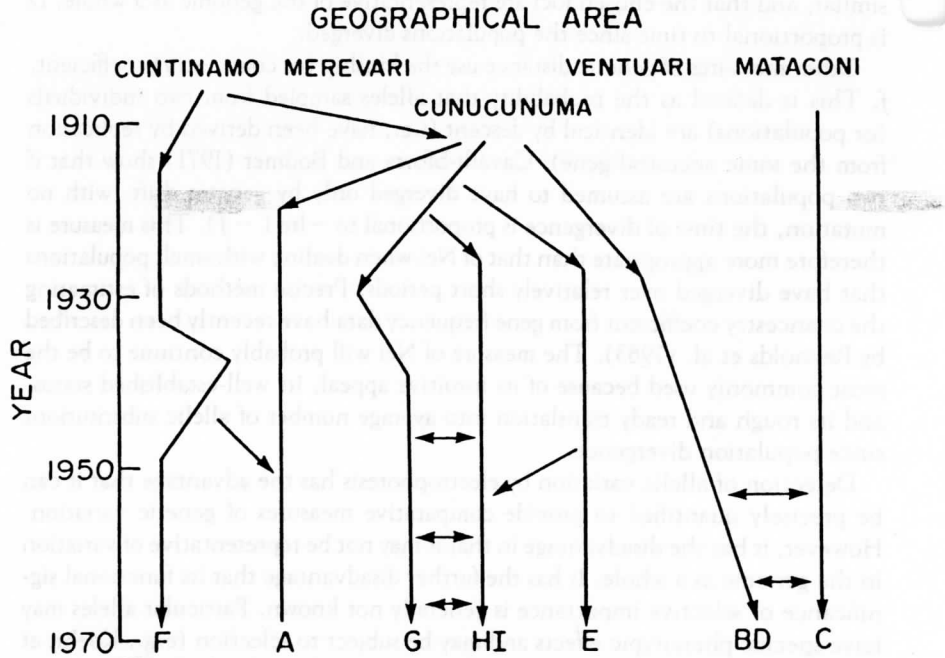

FIGURE 7. Relationship between village history and genetic distance among villagers of the Makiritare tribe (after Ward and Neel, 1970). The diagram shows the historical relationships and migration patterns during sixty years leading to the establishment of seven Makiritare villages. The time scale is shown on the left and the five main geographical areas at the top.

produce a confusing continuum of fragment lengths. Therefore, most analyses at the population-intraspecific level have involved mitochondrial genomes in animals and chloroplast genomes in plants (e.g., Clegg et al., 1984). Differences in DNA sequence are usually estimated in terms of the average number of pairwise differences in base pair composition, assuming that each altered restriction site represents a single base pair change (see Table 1 for an example in *Peromyscus*).

Numerous genes have been cloned and sequenced, but such techniques only now are being developed to a sufficient degree that they can be applied to studies of the same gene in a substantial number of individuals within a species. In one such study (Kreitman, 1983) of the Adh locus in the fruitfly *Drosophila melanogaster*, where previously only two electrophoretic variants were known, a large number of other polymorphisms (forty-two) were revealed at the DNA level which did not result in amino acid changes (Figure 9 and Table 2). Given this complexity and functional diversity at the DNA level, the analysis of DNA sequence data is rapidly developing into a sophisticated branch of genetic statis-

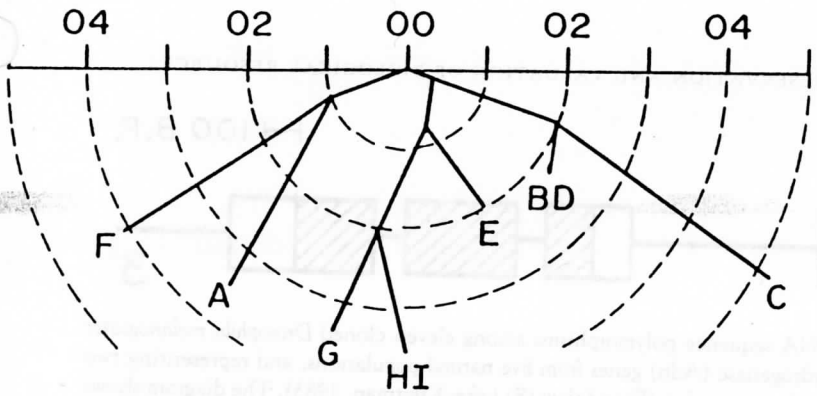

FIGURE 8. Genetic networks derived from the pairwise genetic distances (see Figure 7) based on eleven loci. The networks are plotted to scale on polar coordinates with units of genetic distance read along the radius of the diagram.

TABLE 1

Estimated genetic distance in base substitutions per nucleotide between *Peromyscus* populations at various stages of evolutionary divergence.

Comparison	Mean Distance Between Collections	Four Base Enzymes	Six Base Enzymes
Within geographic locality			
P. leucopus	500 feet	—	0.000
maniculatus	¼ mile	—	<0.010
polionotus	1 mile	0.004	0.002
Between geographic localities			
P. maniculatus	1,000 miles	0.042	0.031
P. polionotus	80–500 miles	0.006	0.015
Sibling species			
P. maniculatus vs. *P. polionotus*		0.166	0.132
Nonsibling species			
P. leucopus vs. *P. maniculatus* and *P. polionotus*		—	0.214

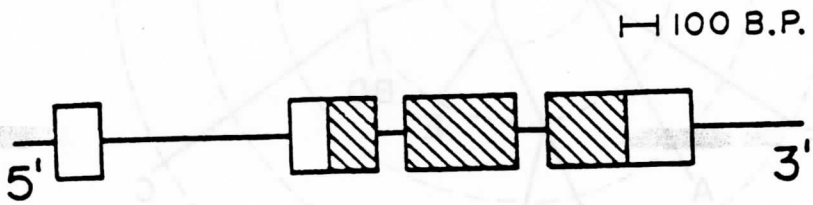

FIGURE 9. DNA sequence polymorphisms among eleven cloned *Drosophila melanogaster* alcohol dehydrogenase (Adh) genes from five natural populations, and representing two electrophoretic variants, fast (F) and slow (S) (after Kreitman, 1983). The diagram shows the structure of the Adh gene. Boxes are Exons 1–4, among which are Introns 1–3. The protein coding region is shaded. Scale = 100 base pairs.

tics (Weir, 1983). However it will probably be several years before standardized methods for dealing with DNA sequence data are developed.

Comparison of Phenetic, Allelic, and Sequence Data

At the intraspecific level, there is in general a broad concordance between phenetic and allelic measures of diversity. Populations are less different from each other than are races, and these in turn are less different than subspecies and species. This concordance appears not to hold particularly well with regard to higher taxonomic levels. Thus species differences within genera may reflect different degrees of electrophoretic divergence depending on the group being considered (Avise and Aquadro, 1982); and large morphological differences may reflect small genetic distances (Cherry et al., 1978). Even at the population level, discordant estimates of divergence have been obtained using various methods. Usually the most common discordance is the observation of substantial morphological or chromosomal differentiation, but relatively little isozyme differentiation (Jain et al., 1980; Turner, 1974; Avise et al., 1975; Heywood and Levin, 1984). Clearly, large morphological and chromosomal changes may occur without substantial evolution at the electrophoretic level. Often discordance is claimed, but the data are too limited either with regard to electrophoretic or morphological data to provide a rigorous comparison (e.g., Snyder and Linton, 1984; Giles, 1984). At other times, discordance is claimed where agreement between electrophoretic and taxonomic data is certainly not perfect, but is substantial (Heywood and Levin, 1984).

It is often difficult to reach firm conclusions about concordance, because the types of data collected in morphological and electrophoretic studies differ in units and scale. Comparison is therefore tenuous, and null hypotheses of what would constitute no difference are difficult to formulate. Too often authors seem eager to excite the reader by emphasizing the existence of discordance, rather than clearly arguing how such discordance might be manifest and how it might be quantified.

TABLE 2

DNA sequences (variable sites only) of fast and slow electrophoretic alleles of Adh from isochromosomal lines sampled for several localities. The reference nucleotide sequence on the top line is the most common Adh-S nucleotide at each of the polymorphic sites.

Strain Origin	Enzyme Mobility	5′ Flanking	Exon 1	Intron 1	Exon 2		Intron 2	Exon 3	Intron 3	Exon 4		3′ Flanking
		CCG		CAATATGGG▽C▽G	C	T	AC	CCCC	GGAAT	CTCCA*CTAG	A▽C	AGC▽C▽T△
Seattle	S	. . .		. . . . . AT	.	.	. .	TT . A	CA . TA	AC	. . .	. . . . . O
Florida	S	. . C		. . . . .	.	.	. .	TT . A	CA . TA	AC	. . .	. . . . . O
Africa	S	. . .		. . . . .	.	.	. .	. . . .	. . . . .	. . . . . A	. . .	. . TO . 1A .
France	S	. . .		. . . . .	.	.	GT	. . . .	. . . . .	. . . . . A	−1 .	TA . . . . .
Florida	S	. . .		AG . . . A . TC	A	G	GT	. . . .	. . . . .	. . . . .	C3 .	. . . . .
Japan	S	. . C		. . . . .	.	G	. .	. . . .	. . . . .	. . . T . T . CA	C4 .	. . . . T . . .
Florida	F	. . C		. . . . .	.	G	. .	. . . .	. . . . .	. . GTCTCC .	C4 .	. . . . .
France	F	TGC		AG . . . A . TCOGO .	.	G	. .	. . . .	. . . . .	. . GTCTCC .	C4G	. . . . .
Seattle	F	TGC		AG . . . A . TCOGO .	.	G	. .	. . . .	. . . . .	. . GTCTCC .	C4G	. . . . .
Africa	F	TGC		AG . . . A . TCOGO .	.	G	. .	. . . .	. . . . .	. . GTCTCC .	C5G	. . . . .
Japan	F	TGC		AGGGGA . . . O . . T	.	G	. .	. . A .	. . C . .	. . GTCTCC .	C4 .	. . . . −1 . .
No. of polymorphic sites		3	0	11	1	1	2	4	5	7	2	5
Average no. of nucleotides		63	87	620	70	99	65	405	70	204	178	767

▽/△ = insertion/deletion polymorphisms, where numbers are the differences in homopolynucleotide run lengths compared with the consensus sequence.

* Thr-Lys amino acid replacement polymorphism. All other polymorphisms are either silent or noncoding.

With both phenetic and allelic measures, the overall picture is one of continuity of difference from population to species. Highly divergent populations that have been given the rank of races, ecotypes, or subspecies are more different from each other than are populations within these groups, and their differences approach those found among species. In particular instances, certain closely related species may be less differentiated than races within another species.

GENETIC UNIQUENESS

The Uniqueness of Individual Alleles and Traits

Studies of allelic variation among populations within a geographical region show that common alleles are generally "universal" (i.e., found in all populations). Usually only rare alleles are confined to one or few populations. Such "private" alleles may be restricted in distribution or they may be ubiquitous but rarely sampled in the average population survey because of their low frequency. The value and importance of such rare alleles are difficult to assess. Where they are relatively universal, they are powerful indicators of gene flow (Slatkin, 1985); otherwise they may be rare because they are disadvantageous, because they are novel mutations, or because they occur as a result of chance effects. Where unique alleles are found, only rarely can a strong case be made for their preservation. Usually their effect on the phenotype is not known, nor does their rarity provide any clue to their origin. Their collection may be of value in increasing the range of allelic variants as genetic markers, or for functional studies of enzyme expression.

A similar picture emerges from studies of individual phenetic traits: frequency distributions of these traits usually overlap extensively. Unique phenotypes commonly represent developmental or genetic abnormalities (Spencer, 1947). The preservation of such "odd" variants is hard to justify.

Within species, very few alleles or phenotypic traits are unique. Uniqueness characteristically arises only when there are distinct habitat differences, where populations are isolated, when there is inbreeding, or where populations have divergent histories (Table 3). While the richness of allelic variation may lead us to think that all evolutionary avenues are open to species, this is not true, because limits to selection are imposed by the availability of appropriate variation. In studies of the adaptation of plant species to mine tailings, for example, certain species fail to adapt, and their failure can be directly attributed to a lack of genetic variance for tolerance (Bradshaw, 1983). Different populations within species may likewise have an uneven distribution of genetic variance.

The Uniqueness of Allelic and Trait Combinations

It is harder to assess the importance of unique *combinations* of alleles and traits. At a phenetic level, combinations of character states appear to be very

TABLE 3
Examples of the different sources of ecological adaptation in plant breeding programs (after Bradshaw, 1983).

Sources	Adaptations
From original gene pools	
Potato	Blight resistance within *Solanum tuberosum*
Alfalfa	Spotted aphid resistance
Sugar beet	Sugar content
Rye	Reduced height
From other gene pools—other cultivars	
Barley	Yellow dwarfness from Abyssinian cultivars
Wheat	Dwarfing genes from Japanese cultivars
Grapes	Root aphid resistance from American material
Cotton	Blackarm resistance from African cultivars
From other gene pools—other species	
Oats	Mildew resistance from *Avena ludoviciana*
Bread wheat	Stem rust resistance from *Triticum dicoccum*
Bread wheat	Eye spot resistance from *Aegilops ventricosa*
Rice	Grassy-stunt resistance from *Oryza nivara*
Delphinium	Red flower color from *Delphinium cardinale*
Potato	Blight resistance from *Solanum demissum*

important. Thus closely related species are usually distinguished on the basis of character combinations rather than on single "key characters"; and such combinations are often frustratingly ambiguous, as anyone who has ever tried to use a key knows. Within species, populations are distinguished by character complexes (Clausen and Hiesey, 1958), which may occur at a very low level, in outbreeders (Antonovics and Bradshaw, 1970) as well as in inbreeders (Hamrick, 1975). Even within one population, such complexes may have considerable integrity (Clay and Antonovics, 1985; Morishima et al., 1984). Moreover, many characters of value in plant breeding do not appear as single genes, in isolation from other traits, but as character complexes. For example, Qualset (1975) found that resistance to yellow dwarf mosaic virus in barley was found only in Ethiopia, and there it was associated with many other distinct morphological traits.

It is pertinent to ask whether such complexes are "unique," in the sense of being difficult to reassemble from component traits, or component alleles. If these complexes are the result of coordinate changes at many loci, and if these many loci are themselves interspersed and closely linked, then reassembling the

complex may be very difficult or nearly impossible. The difficulty of disentangling such complexes is illustrated in the work of Davies (1971), who showed that correlated responses to selection for abdominal and thoracic bristle number in *Drosophila* were due to linkage of many interspersed loci, determining bristle number in either of the two body regions. Pleiotropic loci (affecting both characters simultaneously) were relatively rare.

Unique and important combinations may occur in all populations. In outbreeding species, however, such combinations are likely to be ephemeral and readily broken down. Combinations are therefore likely to have clear identity only where populations also show differentiation. This view is supported by the difficulty of finding linkage disequilibrium (nonrandom allelic associations) among all but extremely closely linked loci ("supergenes") in outbreeders. In inbreeders the situation is quite different, since heterozygotes and hence opportunities for recombinational events are far fewer. It is here that most character complexes have been identified (Hamrick, 1975). Unfortunately there have been very few studies on whether the component characters or alleles of such complexes do indeed enhance fitness (singly or in combination), or whether the complex is the result of chance associations resulting from "hitchhiking" of neutral characters on a few particular traits that are under selection.

The evolutionary literature is replete with references to "coadapted gene complexes," and such complexes have been postulated to play a major role in the evolutionary process. However, such complexes have only rarely been studied in depth. They have been inferred either from observed allele and character associations or from experimental studies showing loss of fitness following interpopulation crosses (Dobzhansky, 1950; Price and Waser, 1979). The development of conceptual frameworks and methods for the study of allelic associations, and for the study of evolution in correlated traits, is currently a very active area of evolutionary biology. But our current knowledge is inadequate to assess fully the importance and uniqueness of complex traits at the intraspecific level. Uniqueness in trait and allele combinations remains the least understood of the categories we consider.

GENETIC CONSERVATION AND UNIQUENESS

Four major goals in genetic conservation, listed in increasing order of complexity and conceptual difficulty, can be recognized. The first is preservation of relatives of useful species, as potential sources of useful variation for breeding programs. The second is preservation of genetic variation to maintain viability in rare species, particularly in captive populations. The third is maintenance of genetic variation for continued evolution of wild species. The fourth goal is preservation of genetic variants within wild species for aesthetic reasons and for as yet unforeseen potential utility.

TABLE 4
Strategies for sampling extant genetic variation from natural populations (after Marshall and Brown, 1975).

Model	Allelic Profile 1	2	3	4	5
Allele					
A_1	0.25	0.76	0.63	0.49	0.80
A_2	0.25	0.20	0.23	0.22	0.005
A_3	0.25	—	0.09	0.12	0.05
A_4	0.25	—	—	0.07	0.05
Remainder	—	0.04	0.05	0.10	0.05
Sample size (n)	19	15	37	43	80
Probability (P)	1.00	1.00	1.00	0.99	0.98

Sample sizes (n) required to be 95 percent certain of obtaining at least one copy of each common allele (frequency > 0.05) and probability of achieving this objective if n = 100 for five contrasting allelic profiles.

Preservation of Relatives of Useful Species

It is widely recognized that there has been serious loss of genetic variability in relatives of our cultivated plants and animals. The process of domestication—with its associated founder effects, severe inbreeding, strong selection, and rapid varietal turnover—has resulted in a rapid erosion of genetic variability. The preservation of wild relatives and crop plants has been a matter of international concern over the past twenty-five years. A number of symposia have addressed this issue, and the principles of genetic conservation are now well established (Frankel and Bennett, 1970; Frankel and Hawkes, 1975; Holden and Williams, 1984).

Much of the genetic uniqueness and variability of crop species is concentrated in "centers of diversity," and much effort continues to be spent on collecting from these areas and characterizing them genetically so as to further aid sampling strategies (e.g., Witcombe and Rao, 1976).

Marshall and Brown (1975) have calculated the numbers of individuals that need to be collected within a population to have a reasonable chance of sampling all the common alleles. They find that sample sizes of fifty should suffice in most cases (Table 4) and that vast collections per population are not necessary. Samples of larger size may be useful, however, in providing baseline information from which future sampling strategies may be further improved. Larger samples give a clearer view of gene frequencies and also permit analysis of character complexes and associations (Qualset, 1975).

TABLE 5

Theoretical values of optimal number of plants to sample per site and optimal number of sites to sample per day for a range of genetic models.

Population	Modern Cultivars (1)	Primitive Cultivars (2)	Wild Relatives (3)	Outbreeding Species (4)	Outbreeding Species (5)
P	0.01	0.05	0.10	0.50	0.75
p	0.95	0.20	0.05	0.05	0.05
a/b ratio		Number of plants per site (n)			
25	1	10	15	30	36
100	2	15	39	50	55
a b		Number of sites per day (N)			
25 1	18	14	12	9	8
50 0.5	10	8	7	6	6

P = proportion of total variation represented by population.
p = proportion of genetic variation per population represented by an individual.
a = amount of effort expended for each site visited.
b = amount of effort expended to sample each plant.

Marshall and Brown (1975) use data on the distribution of genetic variation within and among populations to calculate how sampling resources should be divided between, among, and within population samples. It is quite feasible to collect most of the extant variation in a region in a relatively short period (Tables 5 and 6), since, among outbreeders at least, most of a region's variation can be found within populations. Sampling extant genetic variation is therefore not a daunting task.

In the relatives of a domesticated species, it is clear that uniquely different genes and gene combinations are more likely to be found among relatives that are distant either historically, geographically, or taxonomically. However, genes from more widely divergent populations are correspondingly more difficult to transfer back to the domesticated variety. For any particular domesticated species we can conceptualize an optimum allelic or phenetic distance, which is determined by the trade-off between increased probability of finding uniqueness and decreased probability of gene transfer. This optimum distance will not be constant, but will increase as developing technology permits more efficient gene transfer from distant relatives. Indeed, transspecific gene transfer is now one of the major goals of biotechnology.

TABLE 6
Number of days required to collect 95 percent of variation using a maximally efficient sampling procedure under a range of genetic models.

Population		Modern Cultivars (1)	Primitive Cultivars (2)	Wild Relatives (3)	Outbreeding Species (4)	Outbreeding Species (5)
P		0.01	0.05	0.10	0.50	0.75
p		0.95	0.20	0.05	0.05	0.05
a	b	Days to collect 95% of variation				
25	1	16	5	5	1	1
50	0.5	30	8	5	1	1

Preservation in Rare and Captive Populations

Rare or captive species generally live in small populations. As such they are subject to (1) loss of alleles by chance effects (Franklin, 1980), (2) inbreeding due to mating among close relatives, and (3) selection for performance in the captive environment (i.e., "domestication"). Loss of alleles will lead to decreased genetic variance, increased disease susceptibility (Antonovics and Ellstrand, 1984), and decreased probability of future evolutionary response should conditions change. Inbreeding may lead to reduced vigor and the appearance of abnormal types (Ralls and Ballou, 1983; Senner, 1980), while selection under domestication will lead to preservation of unnatural traits and decreased probability of survival in the wild. In such situations the goals should be twofold: maintenance of variation and elimination of the deleterious effects of inbreeding or domestication (Templeton and Read, 1983).

Preservation of Evolutionary Potential

The dangers of arrested evolution are inherent in small or permanently subdivided populations, because such populations may be genetically depauperate. Large, interconnected natural populations usually contain abundant genetic variation that permits long-term continued evolutionary change. It has been argued that long-term evolutionary considerations must also be an aspect of any genetic conservation strategy (Frankel and Soulé, 1981). However, it is unclear how such long-term considerations can be implemented practically. Structuring preserved populations so that genetic variation is maintained may be best for the maintenance of long-term evolutionary potential. Seldom are preserves designed in such a way as to make this possible.

Preservation of Genetic Variants in Wild Species

From a genetic perspective it is hard to escape the conclusion that the use of the species as a unit of conservation is coarse, artificial, and arbitrary. It is nonetheless difficult to come up with alternative, ready-made solutions. The enormity of genetic diversity precludes a glib simplistic approach to its conservation. The Noah's ark approach of species conservation cannot be used at the genotype or allelic level. Limits, and the choices that these limits entail, require that criteria be developed whereby the value of a particular variant can be judged. The criteria for preserving genetic variants "for their own sake" will be complex. Genetic data are likely to be only a small component of the decision process. It is also for this reason that electrophoretic data are likely to be much less useful than phenetic data. Thus it would be totally arbitrary to designate a particular genetic distance as a criterion beyond which different populations should be preserved. Such a criterion does not take into account discordances of genetic and morphological distances and does not consider that we usually do not know what electrophoretic variants represent biologically; it is also simplistic, since other criteria of aesthetics, potential utility, and so forth, are ignored. For example, different mimicry morphs in butterflies are determined by different alleles at only one locus (albeit perhaps a complex switch gene), yet on aesthetic grounds it would be extremely hard to advocate forgoing their preservation.

An example which illustrates several of these issues is provided by two "species" of sandwort, *Arenaria alabamensis* and *A. uniflora*, found in the Carolinas. The former is extremely rare and restricted to a few granite outcrops. Recent studies by Wyatt (1984) have revealed that *A. alabamensis* represents a polyphyletic group of independently derived inbred populations, resembling each other in floral morphology (related to their inbreeding syndrome) but each resembling the local *A. uniflora* populations in other morphological and electrophoretic traits. Therefore, Wyatt (1984) has advocated that on taxonomic grounds, *A. alabamensis* should not be considered a distinct monophyletic species. Should this preclude efforts for its conservation? The arguments for its preservation are strong: it is morphologically distinct; its populations have enormous scientific interest because of the large breeding system differences among them and because they are a paradigm for one type of speciation process. Moreover, preserving these populations would essentially involve preserving its unique habitat and other associated rare species. While arguments for preservation of *A. uniflora* var. *alabamensis* are compelling, a species-centric view would doom it to extinction.

Very often a subspecies or genetic variant may be as interesting and valuable as a species. Some genetic variants are remarkable in themselves (such as albino tigers in the zoo). Others may be of potential commercial value (such as chemical races of lichens, variants of thyme with unique flavors, or metal tolerance races for recolonizing waste spoils from mining operations). The potential uses

of wild species are legion (Myers, 1983). Yet such utility is often not fully realized unless specific traits are amplified by breeding programs that use the extant genetic variance or that of close relatives.

How can such a diversity of goals and issues be accommodated? First, what might be the generalized "political" procedures that we could use for genetic preservation? Second, what criteria would be used or how would these criteria be applied?

Genetic Impact Statements

By analogy with the process whereby some species can be declared "endangered," we can also envisage species to be "genetically endangered." Assessment of such a status would require a "genetic impact statement." Indeed, it is now an accepted practice to provide such a statement for any species that is endangered, captive, or existing in small isolated populations (Schonewald-Cox et al., 1983), although such statements as yet have no legislative imperative. Such a "genetic impact statement" could identify justifiable reasons for the preservation of genetic variants within a species, whether these variants be subspecies, races, particular populations, or particular genotypes. Justification for such special attention might be: (1) genetic uniqueness (Is the population morphologically and genetically distinct?); (2) current and potential commercial utility (Is the population a member of a species of commercial importance, or is it a relative of a commercially important species?); (3) research importance (Is the population of research interest for evolutionary biologists, ecologists, agronomists?); (4) aesthetic importance (Is the population of interest to collectors, of interest to naturalists, a source of wonder and curiosity to the public?).

Strong cases for genetic conservation could be made on one or any combination of these factors. Clearly uniqueness per se is insufficient; every individual is genetically unique and genetically ephemeral. Every population, separated from others spatially or distinct ecologically, will be different. Criteria other than purely genetic measures have to be invoked. I would anticipate that in the process of establishing priorities for saving the world's genetic resources, certain species might be sacrificed for genetically unique populations.

RENEWABILITY OF UNIQUENESS

Genetic variation can be regenerated by mutation; however, mutation rates are extremely low. Therefore, large populations, long time periods, and specific methods of selecting rare phenotypes are necessary for recovery of mutant types. Even with the use of mutagenic agents, large numbers of individuals and great expenditure of effort are necessary because such mutagens cause high mortality. Many recessive mutations are only detectable as segregants in subsequent

generations, and even then particular desired mutations may be rare. Where general phenetic traits are concerned, spontaneous mutation appears to be a useful steady source of variation. This is presumably because many such traits are affected by numerous loci, thus giving substantial rates of mutation per generation per character (Sprague et al., 1960; Mukai, 1964). There is the further problem that the frequency of induced mutations may not reflect the frequency of spontaneous mutations; evidence for this comes from the classic fine-structure mapping of the R II locus in phage by Benzer (1955), and from simple considerations of molecular mechanisms of mutation, as well as from studies of mutation breeding in crop plants. Therefore, although a large number of crop varieties produced by mutation breeding have been released (for review, see Gottschalk and Wolff, 1983), such "mutation breeding" has rarely been proposed as a complete substitute for genetic preservation. This is not surprising, because much extant variation in natural populations is probably maintained and influenced by selection processes that have acted on the spontaneous spectrum of mutations over a considerable period. Moreover, selection has also built up gene and character combinations that would be almost impossible to reconstruct de novo, given even a relatively low level of complexity.

CONCLUSIONS

1. Populations contain large amounts of genetic variation at a genotypic level; every individual in an outbreeding population is genetically unique.

2. Differences among individuals, populations, and species can be measured in terms of phenetic, allelic, or sequence diversity. Such measures are concordant in reflecting a continuum of increased divergence from the population to species level, but may be quite discordant in particular cases, and are not easily generalizable across highly divergent taxa.

3. Unique alleles and traits tend to be found in populations that are divergent geographically, ecologically, and historically.

4. Unique character combinations ("character complexes") are perhaps common at the intraspecific level. In populations of outbreeders, unique combinations are quickly broken up, but they may persist in inbreeding species. The latter species are especially likely to show substantial geographic variation in which sets of characters are fixed. The genetic basis of such complex traits is not well understood: it is therefore difficult to assess whether such complexes can be easily regenerated.

5. Unique alleles and gene combinations have the greatest importance in relation to useful "domesticated" species. It is here that "genetic erosion" has been severe because of bottleneck effects, inbreeding, and selection. Wild relatives and primitive races are therefore a useful source of variability in breeding programs.

6. If species are endangered or captive, special efforts may have to be made to preserve allelic variation and to avoid inbreeding.

7. A strong case can be made for preserving variants at the intraspecific level. The justification can be made in terms of aesthetics, actual and potential utility, and research interest.

8. Genetic resources are partly renewable by mutation, spontaneous or induced. Mutation spectra for spontaneous and induced mutations (using different mutagens) are not identical. The use and identification of induced mutations require large populations and extensive resources: the process is therefore unlikely to be useful as a mode of genetic recovery in small populations.

9. It is clear that the use of the species as a unit of genetic conservation is inadequate. Genetic uniqueness can occur within species, useful variants are often restricted to particular populations or regions, and genetic variants per se may have a potential utility.

10. A "genetic impact statement" should become an integral part of protection plans for endangered species, and could serve as a mechanism whereby a species or population could be declared "genetically endangered."

11. Mechanisms should be developed that permit preservation of potentially valuable variants and populations at the intraspecific level.

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REFERENCES

Adams, M. W. 1977. An estimation of homogeneity in crop plants with special reference to genetic vulnerability in the dry bean, *Phaseolus vulgaris* L. *Euphytica* 26:655–679.

Antonovics, J., and A. D. Bradshaw. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. *Heredity* 25:349–362.

Antonovics, J., and N. C. Ellstrand. 1984. Experimental studies on the evolutionary significance of sexual reproduction. I. A test of the frequency dependent selection hypothesis. *Evolution* 38:103–115.

Avise, J. C., and C. F. Aquadro. 1982. A comparative summary of genetic distances in the vertebrates: Patterns and correlations. *Evolution. Biol.* 15:157–185.

Avise, J. C., R. A. Lansman, and R. O. Shade. 1979. The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. I. Population structure and evolution in the genus *Peromyscus*. *Genetics* 92:279–295.

Avise, J. C., J. J. Smith, and F. J. Ayala. 1975. Adaptive differentiation with little genetic change between two native California minnows. *Evolution* 29:411–426.

Ayala, F. J. 1982. The genetic structure of species. In *Perspectives on Evolution*, ed. R. Milkman, 60–82. Sunderland, Mass.: Sinauer.

Ayala, F. J., and J. F. McDonald. 1980. Continuous variation: Possible role of regulator genes. *Genetica* 52/53:1–15.

Ayala, F. J., M. L. Tracey, D. Hedgecock, and R. Richard. 1974. Genetic differentiation during the speciation process in *Drosophila*. *Evolution* 28:576–592.

Benzer, S. 1955. Fine structure of a genetic region in bacteriophage. *Proc. Nat. Acad. Sci. (USA)* 41:344–354.

Bradshaw, A. D. 1983. The importance of evolutionary ideas in ecology and vice versa. In *Evolutionary Ecology*, ed. B. Shorrock, 1–25. Oxford: Blackwell.

———. 1984. Ecological significance of genetic variation between populations. In *Perspectives on Plant Population Ecology*, ed. R. Dirzo and J. Sarukhan, 213–228. Sunderland, Mass.: Sinauer.

Briggs, D., and S. M. Walters. 1984. *Plant Variation and Evolution*. 2d ed. Cambridge: Cambridge University Press.

Bryant, E. H., H. van Dijk, and W. van Delden. 1981. Genetic variability of the face fly, *Musca autumnalis* De Geer, in relation to a population bottleneck. *Evolution* 35: 872–881.

Cavalli-Sforza, L. L., and W. F. Bodmer. 1971. *The Genetics of Human Populations*. San Francisco: Freeman.

Cherry, L. M., S. M. Case, and A. C. Wilson. 1978. Frog perspective on the morphological difference between humans and chimpanzees. *Science* 200:209–211.

Clausen, J., and W. M. Hiesey. 1958. *Experimental Studies on the Nature of Species. IV. Genetic structure of ecological races*. Carnegie Institution of Washington Publication 615. Washington, D.C.

Clay, K., and J. Antonovics. 1985. Quantitative variation of progeny from chasmogamous and cleistogamous flowers in the grass *Danthonia spicata*. *Evolution* 39:335–348.

Clegg, M. Y., A. M. D. Brown, and P. R. Whitfield. 1984. Chloroplast DNA diversity in wild and cultivated barley: Implications of genetic conservation. *Genet. Res.* 43: 339–343.

Coyne, J. A. 1976. Lack of genetic similiarity between two sibling species of *Drosop.* as revealed by varied techniques. *Genetics* 84:593–607.

Davies, R. W. 1971. The genetic relationship of two quantitative characters in *Drosophila melanogaster*. II. Location of the effects. *Genetics* 69:363–375.

Dobzhansky, T. 1950. Genetics of natural populations. XIX. Origin of heterosis through natural selection in populations of *Drosophila pseudoobscura*. *Genetics* 35:288–302.

Falconer, D. S. 1981. *Introduction to Quantitative Genetics*. 2d ed. London: Longman.

Frankel, O. H., and E. Bennett, eds. 1970. *Genetic Resources in Plants: Their Exploration and Conservation*. Oxford: Blackwell Scientific Publications.

Frankel, O. H., and J. G. Hawkes, eds. 1975. *Crop Genetic Resources for Today and Tomorrow*. IBP 2. Cambridge: Cambridge University Press.

Frankel, O. H., and M. E. Soulé, eds. 1981. *Conservation and Evolution*. Cambridge: Cambridge University Press.

Franklin, I. R. 1980. Evolutionary change in small populations. In *Conservation Biology: An Evolutionary-Ecological Perspective*, ed. M. E. Soulé and B. A. Wilcox, 135–149. Sunderland, Mass.: Sinauer.

Giles, B. E. 1984. A comparison between quantitative and biochemical variation in the wild barley *Hordeum murinum*. *Evolution* 38:34–41.

Gottschalk, W., and G. Wolff. 1983. *Induced Mutations in Plant Breeding*. New York: Springer-Verlag.

Hamrick, J. L. 1975. Correlations between quantitative characters and enzyme genotypes in *Avena barbata*. *Evolution* 29:438–442.

Heslop-Harrison, J. 1964. Forty years of genecology. *Adv. Ecol. Res.* 2:159–247.

Heywood, J. S., and D. A. Levin. 1984. Allozyme variation in *Gaillardia pulchella* and *G. amblyodon* (Compositae): Relation to morphological and chromosomal variation and to geographical isolation. *System. Bot.* 9:448–457.

Highton, R., and T. P. Webster. 1976. Geographic protein variation and divergence in populations of the salamander, *Plethodon cinereus*. *Evolution* 30:33–45.

Holden, J. H. W., and J. T. Williams. 1984. *Crop Genetic Resources: Conservation and Evaluation*. London: Allen and Unwin.

Jain, S. K., L. Wu, and K. R. Vaidya. 1980. Levels of morphological and allozyme variation in Indian amaranths: A striking contrast. *J. Hered.* 71:283–285.

Johnston, R. F., and R. K. Selander. 1971. Evolution in the house sparrow. II. Adaptive differentiation in North American populations. *Evolution* 25:1–28.

Koehn, R. K., R. I. E. Newell, and F. Immerman. 1980. Maintenance of an aminopeptidase allele frequency cline by natural selection. *Proc. Nat. Acad. Sci. (USA)* 77: 5385–5389.

Kreitman, M. 1983. Nucleotide polymorphism at the alcohol dehydrogenase locus of *Drosophila melanogaster*. *Nature* 304:412–417.

Langlet, O. 1971. Two hundred years of genecology. *Taxon* 20:653–722.

Laurie-Ahlberg C. C., G. Maroni, G. C. Bewley, J. C. Lucchesi, and B. S. Weir. 1980. Quantitative genetic variation of enzyme activities in natural populations of *Drosophila melanogaster*. *Proc. Nat. Acad. Sci. (USA)* 77:1073–1077.

Lewontin, R. C. 1972. The apportionment of human diversity. *Evolution. Biol.* 6:381–397.

Marshall, D. R., and A. H. D. Brown. 1975. Optimum sampling strategies in genetic conservation. In *Crop Genetic Resources for Today and Tomorrow*, ed. O. H. Frankel and J. G. Hawkes, 53–80. IBP 2. Cambridge: Cambridge University Press.

Martinez, O. J., M. M. Goodman, and D. H. Timothy. 1983. Measuring racial differentiation in maize using multivariate measures standardized by variation in F2 populations. *Crop Sci.* 23:775–781.

Mather, K., and J. L. Jinks. 1982. *Biometrical Genetics*. 3d ed. London: Chapman and Hall.

Morishima, H., Y. Sano, and H. J. Oka. 1984. Differentiation of perennial and annual types due to habitat conditions in the wild rice *Oryza perennis*. *Plant System. Evol.* 144: 119–135.

Mukai, T. 1964. Genetic structure of natural populations of *Drosophila melanogaster*. I. Spontaneous mutation rate of polygenes controlling viability. *Genetics* 50:1–19.

Murphy, P. J., and J. R. Witcombe. 1981. The analysis of plant genetic resources data by multivariate techniques. FAO/UNEP IBPGR Technical Conference on Crop Genetic Resources, Rome.

Myers, N. 1983. *A Wealth of Wild Species*. Boulder, Colo.: Westview Press.

Nei, M. 1975. *Molecular Population Genetics and Evolution*. New York: Elsevier.

———. 1978. The theory of genetic distance and the evolution of human races. *Japanese J. Human Genetics* 23:341–369.

Price, M. V., and N. M. Waser. 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. *Nature* 277:294–297.

Qualset, C. O. 1975. Sampling germplasm in a center of diversity: An example of disease resistance in Ethiopian barley. In *Crop Genetic Resources for Today and Tomorrow*, ed. O. H. Frankel and J. G. Hawkes, 81–96. IBP 2. Cambridge: Cambridge University Press.

Ralls, K., and J. Ballou. 1983. Extinction: Lessons from zoos. In *Genetics and Conservation: A Reference for Managing Wild Animals and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 164–184. Menlo Park, Calif.: Benjamin/Cummings.

Reynolds, J., B. S. Weir, and C. C. Cockerham. 1983. Estimation of the coancestry coefficient: Basis for a short-term genetic distance. *Genetics* 105:767–779.

Schonewald-Cox, C. M., S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. 1983. *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Menlo Park, Calif.: Benjamin/Cummings.

Senner, J. W. 1980. Inbreeding depression and the survival of zoo populations. In *Conservation Biology: An Evolutionary-Ecological Perspective*, ed. M. E. Soulé and B. A. Wilcox, 209–224. Sunderland, Mass.: Sinauer.

Singh, R. S., R. C. Lewontin, and A. A. Felton. 1976. Genetic heterogeneity within electrophoretic "alleles" of xanthine dehydrogenase in *Drosophila pseudoobscura*. *Genetics* 84:609–629.

Slatkin, M. 1985. Rare alleles as indicators of gene flow. *Evolution* 39:53–65.

Sneath, P. H. A., and R. R. Sokal. 1973. *Numerical Taxonomy: The Principles and Practice of Numerical Classification*. San Francisco: Freeman.

Snyder, T. P., and M. C. Linton. 1984. Population structure in black flies: Allozymic and morphological estimates for *Prosimulium mixtum* and *P. fuscum* (Diptera: Similiidae). *Evolution* 38:942–956.

Soulé, M. E., and B. A. Wilcox, eds. 1980. *Conservation Biology: An Evolutionary-Ecological Perspective*. Sunderland, Mass.: Sinauer.

Spencer, W. P. 1947. Mutations in wild populations of *Drosophila*. *Advances in Genetics* 1:359–402.

Sprague, G. F., W. A. Russell, and L. H. Penny. 1960. Mutations affecting quantitative traits in the selfed progeny of doubled monoploid maize stocks. *Genetics* 45:855–866.

Templeton, A. R., and B. Read. 1983. The elimination of inbreeding depression in a captive herd of Speke's gazelle. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 241–261. Menlo Park, Calif.: Benjamin/Cummings.

Turner, B. J. 1974. Genetic divergence of Death Valley pupfish species: Biochemical vs. morphological evidence. *Evolution* 28:281–294.

Ward, R. H., and J. V. Neel. 1970. Gene frequencies and micro-differentiation among the Makiritare Indians. IV. A comparison of a genetic network with ethno-history and migration matrices; a new index of genetic isolation. *Amer. J. Human Genetics* 22: 538–561.

B. S. 1983. *Statistical Analysis of DNA Sequence Data.* New York and Basel: Marcel Dekker.

Weir, B. S., and C. C. Cockerham. 1984. Estimating *F*-statistics for the analysis of population structure. *Evolution* 38:1358–1370.

Witcombe, J. R., and A. R. Rao. 1976. The genecology of wheat in a Nepalese centre of diversity. *J. Applied Ecol.* 13:915–924.

Wyatt, R. 1984. The evolution of self-pollination in granite outcrop species of *Arenaria* (Caryophyllaceae). I. Morphological correlates. *Evolution* 38:804–816.

Commentary

David S. Woodruff

In his paper Janis Antonovics provides a comprehensive survey of methods used to identify and conserve genetic variants. He views the goals of genetic conservation as the preservation of genetic variants of economically, scientifically, or aesthetically useful species by conserving their populations and those of closely related species. He argues that genetic considerations are likely to play only a minor role in decisions affecting which desirable variants or unique populations are to be saved. Antonovics concludes that the classic Noah's ark approach to species conservation is inappropriate for the preservation of intraspecific variants and that viewing the species as the unit for conservation is inadequate.

Antonovics's emphasis on intraspecific variant conservation reflects his expertise as a botanist interested in population-level adaptations. My own interest in species-level phenomena in animals leads me to slightly different views. As a zoologist I am more comfortable with the biological evolutionary species concept than are many botanists (e.g., Levin, 1979). Species are more easily recognized in many groups of animals than they are in plants, where phenotypic plasticity, polyploidy, and asexual reproduction often obscure phylogenetic relationships. Even in the genus *Cerion*, regarded by various authorities as the most difficult land snails to classify, species can be recognized using a combination of genetic, morphological, and biogeographic criteria (Woodruff and Gould, 1981). Also, my work on the characterization of species in taxonomically difficult groups of animals has led me to downplay the significance of intraspecific variation (Wilson and Brown, 1953). I believe that geneticists will play a significant role in the conservation of biological diversity, and that they can contribute to the management of variants, populations, and species. Species, far from being inadequate

conservation units, are, in my opinion, key natural units upon which many conservation decisions will focus. Moreover, most of the present legal framework for the conservation of diversity focuses on species-level taxa; for example, the Endangered Species Act of 1973 (1982), CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), Strategy Conference on Biological Diversity (U.S. Department of State, 1982), and World Conservation Strategy (IUCN, 1980; Thibodeau and Field, 1984).

Nonetheless, I agree with Antonovics that conservation genetics is currently a population-level science and that management will have to focus at the population level. Regrettably our understanding of species-level genetics is in its infancy. We need to know much more about the significance of coadapted gene complexes (Templeton, 1981; Lande, 1983; Templeton et al., 1986), genetic structuring of populations (Brussard, 1984), and the processes of genetic differentiation in small populations (Carson and Templeton, 1984) before we can hope to develop a species-level approach to genetic conservation.

THE MEASUREMENT OF DIVERSITY AND UNIQUENESS

The maintenance of genetic diversity is probably the most fundamental issue in population genetics (Clarke, 1979; Cook, 1984; Hamilton, 1984), and it has a direct bearing on conservation biology, since variability determines a population's ability to respond to environmental change and coevolutionary challenges. Several points, however, deserve additional mention. First, Antonovics had inadvertently omitted karyotype analyses from his list of techniques relevant to the measurement of genetic uniqueness. Studies of chromosomal polymorphism within and between species have been very important in evolutionary biology (White, 1978) and are proving useful to conservationists (see Briscoe et al., 1982, for cases involving rock wallabies; Benirschke, 1983, for primates and deer; and Ryder, 1984, for zebras).

The stress placed on multivariate approaches to phenetic variation in Antonovics's paper is also appropriate. Single variable analyses have led to incorrect decisions regarding conservation priorities. The strength of multivariate covariation analyses is well illustrated by studies of the variable land snail *Cerion*, where this approach has enabled us to synonymize hundreds of taxonomically confused morphospecies (Woodruff and Gould, 1981; Gould and Woodruff, 1978, 1986).

Single gel electrophoresis on starch or acrylamide slabs is one of the most useful genetic techniques available to the conservation biologist (see Milkman, 1982; Nei and Koehn, 1983; Oxford and Rollinson, 1983, for recent reviews). For data on levels of genetic variability in over 1,000 species of organisms see Nevo et al. (1984) and Hamrick (1983). The problem of hidden (undetectable) variation, once thought to conceal the presence of two of three alleles, is not extensive enough to grossly alter estimates of variation based on approximately

twenty loci and thirty to fifty individual organisms from a population (Ayala, 1975, Selander and Whittam, 1983). Allozymic variation is now characterized routinely in established laboratories, but it is important to remember that the genes surveyed constitute a very small fraction of the whole genome. Regulatory genes may well be more important than structural genes in determining a population's evolutionary uniqueness, but they remain difficult to study. Conservation biologists should note progress in determining regulatory gene divergence based on the study of developmental schedules of gene expression in F_1 hybrids (Philipp et al., 1983b; Parker et al., 1985). Such considerations are relevant to the manager's problem of outbreeding depression and the handling of organisms from natural hybrid zones (Woodruff, 1979, 1981; Barton and Hewitt, 1983; Philipp et al., 1983a).

The relationship of enzyme variation, genetic distance, and taxonomic separation is very complex (Avise, 1983; Thorpe, 1983). It is clear that Nei's distance (D) or identity values can rarely be interpreted simply—as absolute proof of conspecificity or of significant divergence. Nevertheless, within a higher taxonomic category (genus or family) they provide the conservationist with the best available measure of genetic differentiation. Nonetheless, they do not always work. Examples of difficulties include (1) $D = 0$ in green and white lacewing species that differ by perhaps only three loci (Tauber and Tauber, 1977), and (2) $D = 1.5$ for two sibling species of salamanders (Highton and Larson, 1979). Similarly, the relationship between D and time of divergence (t) is more complex than originally conceived by those who believed in the regularity of molecular clocks. Avise and Aquadro (1982) found a twentyfold difference in divergence rates based on D in five classes of vertebrates. Fortunately, this problem should be of little concern to conservation biologists who are typically involved with closely related populations.

Antonovics notes that sequence diversity—as measured by restriction enzyme mapping of mtDNA, chloroplast DNA, and rDNA—is in its infancy. Results obtained to date generally parallel those obtained with cheaper allozyme techniques (e.g., Sytsma and Schaal, 1985; Ashley and Wills, 1987). Yet, because mtDNA is inherited maternally, it affords the manager a powerful tool for detecting interpopulation hybridization—a natural phenomenon that may occur at much higher frequency in "managed" populations inadvertently made up of several geographic races or sibling species (Harlan, 1983; Carr and Dodd, 1983; Cade, 1983).

Another approach to the measurement of genetic uniqueness mentioned by Antonovics involves pedigree analysis and estimation of kinship. Such techniques are useful only for those few populations for which pedigree data are available. Nevertheless, improved algorithms for microcomputer users are being developed and this approach should become more popular (Ballou, 1983).

I agree with Antonovics's conclusion that unique and important combinations

of loci occur in every individual and in all populations of a species. Furthermoi in outbreeding species, individual uniqueness is ephemeral, since the genome passes through meiotic recombination each generation. There is, then, no simple way of defining or of preserving genetic uniqueness, and Antonovics concludes that other factors will be more important in setting conservation goals. Although the latter may have been true in the past, I see no reason why genetics cannot make more significant contributions to conservation in the future. Present tendencies of conservationists to insist on preserving every local "variety," and zoo curators to get credit for the number of "types" they exhibit, indicate the extent to which genetics has been ignored. In the remainder of this commentary I will try to indicate areas where geneticists can make major contributions.

HOW CAN GENETICISTS CONTRIBUTE TO BIOLOGICAL CONSERVATION?

Proper Identification of Biologically Meaningful Conservation Units

Antonovics defines the goals of genetic conservation in terms of the preservation of variants and populations of useful species and their relatives. I take a broader view: the primary goal should be the maintenance of evolutionarily significant units as communities of species. Accordingly, I would add to Antonovics's list of species deserving attention the "keystone" species (*sensu* Orians and Kunin) and the coevolved pollinators and mutualists of useful species. Oldfield (1981, 1984) discusses the importance of this broader ecological view. Unfortunately, neither approach helps us decide which species or variants are useful. This is a serious problem and we run the risk of overloading the ark with naturally rare species, endemics, and specialists before we have developed appropriate selection criteria (Western, 1985; Norton, 1986). The charismatic megavebrates will undoubtedly receive more than their fair share of our resources some time to come.

Once a taxon has been identified in general terms as needing conservation, geneticists can define biologically meaningful units for *in situ* and *ex situ* management. The literature contains numerous examples of cases where past conservation efforts failed to recognize such biologically meaningful units as the following ones.

1. Until very recently, Bornean and Sumatran orangutans (*Pongo pygmaeus*) were managed as a single species. It is now clear, however, that the two island populations are chromosomally distinct (Seuanez et al., 1979) and reputable zoos are excluding hybrids from their breeding programs.

2. Northern and southern isolates of the African white rhinoceros (*Ceratotherium simum*) are widely regarded as being only regional varieties of a formerly widespread species. Recently, however, George et al. (1983) discovered that the ctDNA of representatives of the northern and southern races show more differences than one would expect for conspecific populations. Unfortunately, this

finding may have come too late, since less than fifteen northern white rhinos survive in Garamba, Zaire.

3. The Sonoran topminnow (*Poeciliopsis occidentalis*) is an endangered species in Arizona. Studies of allozyme variation throughout the range of this species revealed that the wrong stocks are being employed in restocking efforts (Vrijenhoek et al., 1985). Largemouth bass have been mismanaged on a larger scale (Philipp et al., 1983a). Future management will hopefully pay more attention to the genetic variability of hatchery fish and the natural variation of the species they represent.

Other cases where genetic considerations are playing a role in the management of captive populations are discussed by Benirschke (1983). Surprisingly, very few of the species managed by zoos are well defined genetically. This is evident from the number of ongoing debates concerning endangered mammals where genetic data are badly needed for management decisions. Most of these debates involve the question whether individuals from geographically different populations should be mixed or maintained separately. Obviously, the greater the geographic distance between source populations, the more likely hybridization will result in outbreeding depression and a decline in fitness. Unfortunately, relevant genetic data are simply unavailable to the managers of sea otters in California and Alaska, of Asian elephants from Sri Lanka and India, and of Sumatran rhinos from Sabah and peninsular Malaysia. Although past practice would have involved mixing such geographic races indiscriminately, it is now recognized that the integrity of evolutionarily significant units should be maintained whenever possible. This leads us back to the central problem of deciding which populations to conserve. It is clear, for example, that zoos cannot afford to maintain self-sustaining populations of all eight subspecies of tiger. Similarly, ow does one decide which populations of black rhino to concentrate on? The ,000 surviving animals representing seven subspecies are scattered across seventeen African countries in over fifty isolated populations (Western and Vigne, 1985). Efforts to conserve every odd variant of a species are unjustifiable economically and may be unnecessary biologically. Hopefully, genetic data will be obtained before too many more decisions to preserve either "generic" or "pure" populations are made.

To reiterate, population genetic characterization is a prerequisite for effective conservation, be it at the level of the population, geographic race, or species. Morphology, the criterion used traditionally to define management units, is often unreliable. However, as Antonovics points out, morphology, coupled with genetic characterization, provides the conservationist with a means of defining evolutionarily significant units. The strength of the combined use of phenetic and genetic techniques is well illustrated in the following three cases.

1. The cephalopod *Nautilus pompilius* is widely distributed in the Indo-Pacific region and is quite variable in size and coloration. The larger-shelled animals

from Palau in Micronesia were recently recognized as a morphologically distinct species, *N. belauensis* (Saunders, 1987). The possibility remained, however, that they were just a locally large race of *N. pompilius*. This possibility was ruled out when studies of allozyme variation revealed a much greater difference between *N. pompilius* and *N. belauensis* ($D > 0.30$) than between several populations of the former (Woodruff et al., 1983; Woodruff and Carpenter, 1986).

2. In salamanders of the genus *Plethodon*, morphological divergence is unrelated to the amount of electrophoretically detectable genetic differentiation occurring among populations. Recent studies have shown that *P. dorsalis* is actually two allopatrically distributed species that are virtually identical in appearance but differ dramatically ($D = 1.5$) in 80 percent of their structural genes (Highton and Larson, 1979). The same authors report that three geographically isolated morphologically defined "subspecies" of *P. nettingi* have actually diverged as much as several well-characterized sympatric species.

3. Traditional taxonomy, based entirely on shell characteristics, would badly mislead a conservationist working with the West Indian land snails of the genus *Cerion*. On small New Providence Island in the Bahamas conchologists had described seventy-one living "species," many of which have since gone extinct as a result of the recent growth of the city of Nassau. Gould and Woodruff (1986), in contrast, found that there were really only two, imperfectly isolated species on the island. These species are characterized on the basis of the pattern of multivariate morphometric character *covariation*, allozyme variation, and biogeography. These taxa are not threatened, since they are common elsewhere in the Bahamas.

These examples show how easy it is to focus on biologically inappro[illegible]e units. In the future, geneticists should be able to make significant contributions to conservation biology by defining and characterizing evolutionarily meaningful units for management purposes.

Genetically Sound Breeding Plans for Closely Managed Populations

I will mention this important area only briefly, since numerous books are available on the application of genetics to breeding domesticated species in addition to the chapters and papers in the recent conservation biology literature (Soulé and Wilcox, 1980; Frankel and Soulé, 1981; Schonewald-Cox, et al., 1983; and especially Ralls and Ballou, 1986). Among the general principles appropriate for most closely managed populations are the following ones.

1. Increase population size as fast as possible to avoid loss of genetic variance and allelic diversity through genetic drift. The founder event itself may or may not have a profound effect on the genetics of the survivors. One species of mammal that exists only in captivity—the Arabian oryx (*Oryx leucoryx*)—has apparently lost most of its original genetic variability (Woodruff and Ryder,

1986). The challenge for managers is to retain as much of the remaining variation as possible.

2. Avoid inbreeding, because its associated costs may be significant (Ralls and Ballou, 1983). When this is impractical, as with Speke's gazelle, where the founding population numbered only four animals, it is possible to reduce the deleterious effects of inbreeding depression by careful selection of mating pairs (Templeton and Read, 1983). This has apparently happened naturally in species with a long history of inbreeding, such as Père David's deer (*Elaphurus davidianus*).

3. Maximize the effective population size (N_e) by subdividing the population and equalizing the contribution of all the founders. This latter principle, probably the most powerful weapon in the hands of captive breeders (Frankel and Soulé, 1981:40), is seldom employed.

4. Exchange enough genes each generation to maintain qualitative or quantitative genetic similarity between various subpopulations. Application of this principle would involve far more planning and cooperation among conservation organizations than now occurs.

5. Increase the variability of previously mismanaged populations by introducing more alleles from the wild. The endangered Indian lion is represented in U.S. zoos by the descendents of only three full sib pairs. The problem is even more serious in the case of major crop plants; for example, the North American soybean industry was launched in 1930 with six plants from one site in China (IUCN, 1980; King, 1984).

6. Avoid outbreeding depression. Crossing two differently coadapted populations may result in an increase in gametic incompatibility, zygotic and embryonic inviability, and hybrid mortality in the F_1, F_2, or backcross generations (Shields, 1982; Templeton et al., 1986). Such outbreeding depression in heterogeneous populations can severely hamper breeding programs (Benirschke, 1983). In at least one case, where Turkish and Nubian ibex were mixed with the Tatra Mountain ibex in Czechoslovakia, the hybrids were so poorly adapted that the entire population went extinct (Greig, 1979; Templeton et al., 1986). Methods should be discussed for the detection of outbreeding depression, for distinguishing inbreeding from outbreeding depression, and for the management of outbreeding depression. Ideally, the genetic characterization of evolutionarily meaningful conservation units through the study of natural populations will result in less disruption of coadapted gene complexes in closely managed situations in the future.

7. Avoid artificial selection for phenotypic conformity, since this will undoubtedly affect other traits and ultimately reduce the population's fitness. Highly selected, "domesticated" populations are notoriously maladapted for life under natural conditions. Norway brown trout, for example, do very well in hatcheries

but are useless as stock for reintroduction into the wild. Cutthroat trout raised in one hatchery for fourteen years had a 57 percent reduction in the proportion of polymorphic loci (Allendorf and Phelps, 1980). We need to develop techniques of genetic reinvigoration of remnant populations with genetic disease and highly selected inbred populations.

These genetic principles enable a conservationist to preserve the genetic diversity present in a closely managed population. Their application should increase the chances of the managed population's sustained long-term propagation and suitability for reintroduction into the wild.

Several of these principles are aimed at reducing the rate at which genetic diversity is lost in small populations. In this connection it should be stressed that there is no single "right" amount of genetic variation for a population or a species. Optimal levels of genetic polymorphism and heterozygosity vary with mating systems and demographic history (Soulé, 1980; Beardmore, 1983; Selander, 1983). Some species have paradoxically low levels of variation, such as the cheetah (O'Brien et al., 1985), the northern elephant seal (Bonnel and Selander, 1974), various gastropods (Selander and Ochman, 1983), and Torrey pines (Ledig and Conkle, 1983). Others show considerable geographic variation in levels of genetic variation. Isolated peripheral populations are often less variable than continuously distributed central populations (Briscoe et al., 1982; Brussard, 1984). The challenge for the geneticist is to characterize the variability of the population or species to be conserved and assist the manager in maintaining the variability.

Unfortunately, the application of these genetic management principles is by no means routine. Although ecological principles have long guided conservation practice, it is only recently that genetic principles were considered re nt (Frankel, 1982). This arose because of a shift from short-term to long-term conservation issues. The Species Survival Plan program of the American Association of Zoological Parks and Aquariums represents a pioneering attempt to incorporate genetic principles into the management of selected species in the collections of participating institutions. Although there are SSPs for only about forty species of endangered animals, the lessons learned with these will undoubtedly be transferred to other less closely managed species.

Integration of Genetic Principles in the Design and Management of Nature Reserves

As the costs of maintaining self-sustaining populations of free-ranging organisms are often two to four orders of magnitude less than the costs of captive propagation (Western, 1985), the need to further improve field management techniques should be obvious. Geneticists can contribute to ongoing discussions concerning the determination of minimal viable population size (MVP) of selected species. To quote Shaffer (1981:132), "A minimum viable population for any given species in any given habitat is the smallest isolated population having

a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes." The genetic determinants of MVP sizes are still unclear: "their resolution hinges primarily on a better knowledge of the breeding structure and genetic variability . . . and, most importantly, the role of genetic variability in population growth and regulation" (p. 134). Factors relevant to designing or modifying nature reserves stem from considerations of this type. Reserve acquisition can be based on genetic criteria (Hopper et al., 1982), and genetic arguments for the need for multiple reserves have yet to be put into practice. Another problem requiring attention concerns the empirical determination of optimal levels of gene flow and interpopulation hybridization (e.g., James, 1982; Harlan, 1983). Incorrect decisions can be costly (Hall-Martin, 1984). Finally, the conservation of taxa threatened by hybridization with neighboring taxa presents still other challenges for geneticists (Briscoe et al., 1982; Novak, 1982).

The increased application of genetics to the management of wild plant and animal populations presupposes greater cooperation between laboratory-bound geneticists and traditionally field-oriented conservation biologists. The various specialist groups of the International Union for the Conservation of Nature/Species Survival Commission (IUCN/SSC) facilitate such interdisciplinary planning. Oldfield (1984) discusses several other national and international organizations (including the National Council on Gene Resources, and the National Academy of Sciences 1978 report on germ plasm conservation) and suggests ways of strengthening conservation legislation relevant to our genetic heritage. Antonovics's call for genetic impact statements marks another positive step in the increased involvement of geneticists in conservation.

EPILOGUE

At the beginning of this commentary I suggested that Antonovics and I differ in our view of the goals of conservation genetics: he emphasizes the preservation of representative samples of genetic diversity and the preservation of existing variants of domesticated and useful wild species; I am more concerned with the future survival of wild species and the need to conserve genetically coadapted populations representative of such taxa. This dichotomy of opinion is representative of the variety of opinion about conservation genetics in the extensive literature on that subject. I use the term "conservation genetics" for the emerging applied science that seeks to define the genetic conditions for the continued evolution of wild biota. Antonovics's view is clearly closer to that of Bennett (1965), who introduced the near synonym "genetic conservation" for the preservation of genetic material used by plant breeders. This dichotomy, however, is only one of relative emphasis (Frankel, 1970, 1982, 1983; Frankel and Soulé, 1981). Both conservation genetics and genetic conservation are based on a com-

mon set of scientific principles and have important roles to play in conservation biology.

REFERENCES

Allendorf, F. W., and S. R. Phelps. 1980. Loss of genetic variation in a hatchery stock of cutthroat trout. *Trans. Amer. Fish. Soc.* 109:537–543.

Ashley, M., and C. Wills. 1987. Analysis of mitochondrial DNA polymorphisms among Channel Island deer mice. *Evolution* 41:854–863.

Avise, J. C. 1983. Protein variation and phylogenetic reconstruction. In *Protein Polymorphism: Adaptive and Taxonomic Significance*, ed. G. S. Oxford and D. Rollinson, 103–130. London: Academic Press.

Avise, J. C., and C. F. Aquadro. 1982. A comparative summary of genetic distances in the vertebrates: Patterns and correlations. *Evolution. Biol.* 15:151–185.

Ayala, F. J. 1982. The genetic structure of species. In *Perspectives on Evolution*, ed. R. Milkman, 60–82. Sunderland, Mass.: Sinauer.

Ballou, J. 1983. Calculating inbreeding coefficients from pedigrees. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 509–520. Menlo Park, Calif.: Benjamin/Cummings.

Barton, N. H., and G. M. Hewitt. 1983. Hybrid zones as barriers to gene flow. In *Protein Polymorphism: Adaptive and Taxonomic Significance*, ed. G. S. Oxford and D. Rollinson, 341–360. London: Academic Press.

Beardmore, J. A. 1983. Extinction, survival, and genetic variation. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 125–151. Menlo Park, Calif.: Benjamin/Cummings.

Benirschke, K. 1983. The impact of research on the propagation of endangered speci in zoos. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 402–413. Menlo Park, Calif.: Benjamin/Cummings.

Bennett, E. 1965. Genecological aspects of plant introduction and genetic conservation. *Scottish Plant Breeding Station Record* 1965:27–113.

Bonnel, M. L., and R. K. Selander. 1974. Elephant seals: Genetic variation and near extinction. *Science* 184:908–909.

Briscoe, D. A., J. H. Calaby, R. L. Close, G. M. Maynes, C. E. Murtagh, and G. B. Sharman. 1982. Isolation, introgression and genetic variation in rock-wallabies. In *Species at Risk: Research in Australia*, ed. R. H. Groves and W. D. L. Ride, 73–87. Berlin: Springer-Verlag.

Brussard, P. F. 1984. Geographic patterns and environmental gradients: The central-marginal model in *Drosophila* revisited. *Ann. Rev. Ecol. Syst.* 15:25–64.

Cade, T. J. 1983. Hybridization and gene exchange among birds in relation to conservation. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 288–309. Menlo Park, Calif.: Benjamin/Cummings.

Carr, A. F., and C. K. Dodd. 1983. Sea turtles and the problem of hybridization. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 277–287. Menlo Park, Calif.: Benjamin/Cummings.

Carson, H. L., and A. R. Templeton. 1984. Genetic revolutions in relation to speciation phenomena: The founding of new populations. *Ann. Rev. Ecol. Syst.* 15:97–131.

Clarke, B. 1979. The evolution of genetic diversity. *Proc. Roy. Soc. London B* 205:453–474.

Cook, L. M. 1984. The problem. In *Evolutionary Dynamics of Genetic Diversity*, ed. G. S. Mani, 1–12. Berlin: Springer-Verlag.

Frankel, O. H. 1970. Variation, the essence of life. Sir William Macleay Memorial Lecture. *Proc. Linn. Soc. N.S.W.* 95:158–169.

———. 1982. The role of conservation genetics in the conservation of rare species. In *Species at Risk: Research in Australia*, ed. R. H. Groves and W. D. L. Ride, 159–162. Berlin: Springer-Verlag.

———. 1983. Foreword. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas. Menlo Park, Calif.: Benjamin/Cummings.

Frankel, O. H., and M. E. Soulé, eds. 1981. *Conservation and Evolution*. Cambridge: Cambridge University Press.

George, M., L. A. Puentes, and O. Ryder. 1983. Genetische Unterscheide zwischen den Unterarten des Breitmaulnashorns. In *Internat. Studbook African Rhinoceros*, ed. H. G. Klos and R. Frese, 60–67. Berlin: Zoologischen Garten.

Gould, S. J., and D. S. Woodruff. 1978. Natural history of *Cerion* VIII: Little Bahama Bank—A revision based on genetics, morphometrics and geographical distribution. *Bull. Mus. Comp. Zool.* 148:371–415.

———. 1986. Systematics of *Cerion* on New Providence Island: A radical revision. *Bull. Amer. Mus. Nat. Hist.* 182:391–490.

Greig, J. C. 1979. Principles of genetic conservation in relation to wildlife management in southern Africa. *S. Af. J. Wildlife Res.* 9:57–78.

Hall-Martin, A. 1984. Kenya's black rhinos in Addo, S. Africa. *Af. Elephant and Rhino Group Newsletter* 3:11.

Hamilton, W. D. 1984. Pathogens as causes of genetic diversity in their host populations. In *Population Biology of Infectious Diseases*, ed. R. M. Anderson and R. M. May, 269–296. New York: Springer-Verlag.

Hamrick, J. L. 1983. The distribution of genetic variation within and among plant populations. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 500–508. Menlo Park, Calif.: Benjamin/Cummings.

Harlan, J. R. 1983. Some merging of plant populations. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 267–276. Menlo Park, Calif.: Benjamin/Cummings.

Highton, R., and A. Larson. 1979. The genetic relationships of the salamanders of the genus *Plethodon*. *System. Zool.* 28:579–599.

Hopper, S. D., N. A. Campbell, and G. F. Moran. 1982. *Eucalyptus caesia*, a rare mallee of granite rocks from south-western Australia. In *Species at Risk: Research in Australia*, ed. R. H. Groves and W. D. L. Ride, 46–61. Berlin: Springer-Verlag.

International Union for the Conservation of Nature and Natural Resources (IUCN). 1980. *World Conservation Strategy*. International Union for the Conservation of Nature and Natural Resources/United Nations Environment Programme/World Wildlife Fund. Gland, Switzerland.

James, S. H. 1982. The relevance of genetic systems in *Isotoma petraea* to conservation practice. In *Species at Risk: Research in Australia*, ed. R. H. Groves and W. D. L. Ride, 63–71. Berlin: Springer-Verlag.

King, F. W. 1984. Preservation of genetic diversity. In *Sustaining Tomorrow: A Strategy for World Conservation and Development*, ed. F. R. Thibodeau and H. H. Field, 41–55. Hanover, N.H.: Tufts-University Press of New England.

Lande, R. 1983. The response to selection on major and minor mutations affecting a metrical trait. *Heredity* 50:47–65.

Ledig, F. T., and M. T. Conkle. 1983. Gene diversity and genetic structure in a narrow endemic, Torrey pine (*Pinus torreyana* Parry ex Carr.). *Evolution* 37:79–85.

Levin, D. A. 1979. The nature of plant species. *Science* 204:381–384.

Loveless, M. D., and J. L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. *Ann. Rev. Ecol. Syst.* 15:65–95.

Milkman, R., ed. 1982. *Perspectives on Evolution*. Sunderland, Mass.: Sinauer.

Nei, M., and R. K. Koehn, eds. 1983. *Evolution of Genes and Proteins*. Sunderland, Mass.: Sinauer.

Nevo, E., A. Beiles, and R. Ben-Schlomo. 1984. The evolutionary significance of genetic diversity: Ecological, demographic and life history correlates. In *Evolutionary Dynamics of Genetic Diversity*, ed. G. S. Mani, 13–213. Berlin: Springer-Verlag.

Norton, B. G., ed. 1986. *The Preservation of Species: The Value of Biological Diversity*. Princeton, N.J.: Princeton University Press.

Novak, R. 1982. The red wolf recovery program. In MAB Symposium: Application of genetics to the management of wild plant and animal populations. Speakers' abstracts. August 9–13, 1982, Washington, D.C.

O'Brien, S. J., et al. 1985. Genetic basis for species vulnerability in the cheetah. *Science* 227:1428–1434.

Oldfield, M. L. 1981. Tropical deforestation and genetic resources conservation. *Stud. Third World Soc.* 14:277–345.

———. 1984. *The Value of Conserving Genetic Resources*. Washington, D.C.: U.S. Department of the Interior, National Park Service.

Oxford, G. S., and D. Rollinson, eds. 1983. *Protein Polymorphism: Adaptive and Taxonomic Significance*. London: Academic Press.

Parker, H. R., D. P. Philipp, and G. S. Whitt. 1985. Relative developmental success in interspecific *Lepomis* hybrids as an estimate of gene regulatory divergence between species. *J. Exp. Zool.* 233:451–466.

Philipp, D. P., W. F. Childers, and G. S. Whitt. 1983a. A biochemical genetic evaluation of the northern and Florida subspecies of largemouth bass. *Trans. Amer. Fish. Soc.* 112:1–20.

Philipp, D. P., H. R. Parker, and G. S. Whitt. 1983b. Evolution of gene regulation: Iso-

ruff. 1986. Local adaptation, coadaptation, and population-boundaries. *Zoo. Biol.* 5(2): 115–126.

Templeton, A. R., and B. Read. 1983. The elimination of inbreeding depression in a captive herd of Speke's gazelle. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, 241–261. Menlo Park, Calif.: Benjamin/Cummings.

Thibodeau, F. R., and H. H. Field. 1984. *Sustaining Tomorrow: A Strategy for World Conservation and Development.* Hanover, N.H.: Tufts-University Press of New England.

Thorpe, J. P. 1983. Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation. In *Protein Polymorphism: Adaptive and Taxonomic Significance*, ed. G. S. Oxford and D. Rollinson, 131–152. London: Academic Press.

U.S. Department of State. 1982. *Proceedings of the U.S. Strategy Conference on Biological Diversity.* November 16–18, 1981. Department of State Publication 9262. Washington, D.C.

Vrijenhoek, R. C., M. E. Douglas, and G. K. Meffe. 1985. Conservation genetics of endangered fish populations in Arizona. *Science* 229:400–402.

Western, D. 1985. The role of captive populations in global conservation. In Primates: The Road to Self-sustaining Populations. Zoological Society of San Diego Conference, June 1985. Manuscript.

Western, D., and L. Vigne. 1985. The deteriorating status of African rhinos. *IUCN/SSC African Elephant and Rhino Specialist Group Newsletter.*

White, M. J. D. 1978. *Modes of Speciation.* San Francisco: W. H. Freeman.

Wilson, E. O., and W. L. Brown. 1953. The subspecies concept and its taxonomic application. *System. Zool.* 2:97–111.

Woodruff, D. S. 1979. Postmating reproductive isolation in *Pseudophryne* and the evolutionary significance of hybrid zones. *Science* 203:561–563.

———. 1981. Towards a genodynamics of hybrid zones: Studies of Australian frogs and West Indian land snails. In *Essays on Evolution and Speciation in Honor of M. J. D. White*, ed. W. R. Atchley and D. S. Woodruff, 171–197. Cambridge: Cambridge University Press.

———. 1987. Fifty years of interspecific hybridization: Genetics and morphometrics of a controlled experiment on the land snail *Cerion* in the Florida Keys. *Evolution* 41: 1022–1045.

Woodruff, D. S., and M. P. Carpenter. 1986. Genetic variation and phylogeny in *Nautilus*. In *Nautilus: The Biology and Paleobiology of a Living Fossil*, ed. W. B. Saunders and N. H. Landman, 65–83. New York: Plenum Press.

Woodruff, D. S., and S. J. Gould. 1981. Geographic differentiation and speciation in *Cerion*: A preliminary discussion of patterns and processes. *Biol. J. Linn. Soc. London* 14:389–416.

Woodruff, D. S., M. Mulvey, W. B. Saunders, and M. P. Carpenter. 1983. Genetic variation in the cephalopod *Nautilus belauensis*. *Proc. Nat. Acad. Sci.* (USA) 136: 147–153.

Woodruff, D. S., and O. A. Ryder. 1986. Genetic characterization and conservation of endangered species: Arabian oryx and père David's deer. *Isozyme Bull.* 19:35.

Summary of the Discussion

Lawrence Riggs

Gordon Orians opened the session by focusing attention on how genetic knowledge and research techniques might be applied in determining what genetic materials are valuable, in identifying criteria for selecting materials for preservation, and in selecting technologies appropriate for preservation of valuable materials. The group discussion continued for over two hours, ranging across many topics and referring to examples drawn from the experience of many of the participants.

SELECTION CRITERIA

Deborah Rabinowitz raised two provocative issues for discussion based on Janis Antonovics's observations that the genetic criteria for uniqueness are frequently not adequate justification for preservation, and that information about phenetic traits (morphological, physiological, or behavioral) may be more useful than genotypic data or composite indices.

Antonovics pointed out that the measures providing the most accurate specification of genetic information (e.g., DNA sequence data) are the most difficult to relate to their phenotypic effects, while methods affording a less accurate description of genetic substrates (e.g., phenetics) are better understood biologically. Isozyme data may fall somewhere in between.

The most difficult task for the geneticist, according to Antonovics, is to decide the level at which uniqueness should be measured. There are many unknowns in the mapping of genetic differences onto phenotypic differences. Single allelic variants are unique, and many phenotypic variants are distinctly different. Nearly all individuals in an outbreeding species are unique, but this level of resolution is not very useful in setting priorities for conservation. Systematists are still struggling to develop general methods that will distinguish species and subspecies in unequivocal ways on the basis of multiple trait differences. Techniques for recognizing important discontinuities in organic diversity below the species level are still being developed. Distributional information and historical data must be integrated with genetic and phenetic data on a case-by-case basis.

In concert with Antonovics, David Woodruff observed that genetics is not a sufficiently mature science to meet the challenges posed by management situations. Nevertheless he challenged assertions in Antonovics's paper that (1) genetic data are likely to be only a small component of the decision process and that (2) species may be inadequate units for conservation.

Other topics potentially relevant to the selection problem were broached but not pursued in detail; for example, the possibility of using electrophoretic

markers to aid the selection of genetic materials for preservation was mentioned. Such applications would require research on the association, if any, between the genetic markers and phenetic data. Arthur Weissinger outlined a series of questions that must be addressed: How much electrophoretic variation exists in isozymes? Is it important? Is it useful? If electrophoretic variation is not associated with phenotypic differences within any environment in which the organism is found, it may not represent anything important for conservation. Difficulties in using aggregate indices such as Nei's *D* in setting conservation priorities were also discussed briefly. Gardner Brown pointed out that the Nei index assumes that all allelic variants of a gene are equally important. An economic analysis carried out using those indicies would thus have to make the untenable assumption that physical changes in phenotype are equivalent for all allelic substitutions. While Nei's index may be the most useful one for evolutionary biologists seeking to calibrate divergence times at the lower end of the time scale, it may not be appropriate for setting criteria for genetic resource preservation. Either weighting criteria must be developed to permit disaggregation of allelic frequency data, rendering them useful to the selection problem, or different indices will have to be developed.

COADAPTED GENE COMPLEXES

The lack of strong evidence supporting the existence of coadapted gene complexes was noted by Antonovics, and this stimulated considerable discussion. Many of the participants saw adaptive gene combinations or coadapted complexes as a potentially important feature of genetic uniqueness, and one that might carry resource value whether or not detailed genetic information was available. Antonovics suggested that the probability of successfully assembling even ten to twenty-five genes in efforts to reconstruct gene complexes is very low, given current understanding and technology.

Arthur Weissinger outlined a study being implemented by Pioneer Hi-Bred International which will test the possibility of coadaptation between nuclear and cytoplasmic DNA in corn. The use of cytoplasmic sterility factors introduced to lower costs of hybrid seed production in corn in the late 1960s led to homogeneity of a portion of the genome apparently associated with disease resistance. In response to the severe corn blight epidemic of 1970, corn breeders ceased using single-cell derived cytoplasms and began research to determine how much cytoplasmic DNA variation might exist and how it might be deployed in commercial plantings to reduce vulnerability to disease outbreaks. Weissinger outlined studies documenting fairly limited genetic variability in breeding stock cytoplasms and experiments for which sixteen combinations of recognizable nuclear and cytoplasmic types were created by a complex series of backcrosses. He described the scope of testing efforts necessary to distinguish coadaptation

from environmental effects on yield parameters, and asked whether participants considered this kind of experiment possible with other organisms and effective in testing for the existence of coadapted gene combinations.

The population geneticists who were present recognized the technical feasibility of the approach described and its potential for addressing some questions of interest in evolutionary biology (e.g., for the study of male sterility mechanisms in natural plant populations, plant-pathogen interactions, etc.). However, the complexities of sorting out the possible combinations in populations considerably more variable and less well studied than breeding stocks of corn limit its application. It was concluded that, without specific knowledge of the genes involved in the expression of observable traits and of their location on chromosomes, and without appropriate measures of fitness, testing of coadaptation hypotheses would not be productive. *Drosophila* geneticists may be close to being able to conduct such experiments, given present knowledge of the *Drosophila* genome. In the meantime, the controlled recombination of cytoplasmic and nuclear variants may be the only experimental means to approach the issue of coadapted gene complexes. Basic population geneticists may find it difficult to conduct comparable studies, given the scope of the problem, and the fact that they rarely have access to the resources large firms such as Pioneer Hi-Bred have.

As a response to several questions, there was a review of the evidence supporting the validity of the coadapted gene complex concept. It was pointed out that the notion was developed at a time when DNA structure was represented by the "string of beads" analogy and gene expression was thought to be the simple result of translation and transcription. Since the picture has become more complicated with the recognition of extranuclear genes, the possibility of interspecific gene transfer through retroviral infection, and the observation of posttranscriptional changes in gene products, it has seemed less intuitively reasonable that genomic organization is necessarily adaptive, or that its structure is stable. Much of the evidence suggesting coadapted organization is weak. For example, from studies of parthenogenetic races of *Drosophila mercatorum*, Alan Templeton inferred the existence of alternative adaptive combinations of genes from the fact that members of each parthenogenetic line mate successfully with others of their own line but not with members of the parental population or other lines. While similar findings between species were advanced by Dobzhansky many years ago to explain hybrid dysgenesis and to support the plausibility of the coadapted gene complexes, such a criterion is not sufficient to test the hypothesis. As we know from a variety of studies, many other mechanisms can account for the failure of hybrid or between-line crosses, and not all represent adaptive responses.

Woodruff summarized the principal approach used by population geneticists to infer the existence of nonrandom associations of genes, the measurement of linkage disequilibrium; this makes no reference to adaptive explanations. A statistical test compares the observed associations of alleles at different marker

loci with that expected under the random segregation of alleles in an infinitely large population at demographic equilibrium. Strong associations of genes are indicated by significant departures from the null hypothesis, or "disequilibrium." Strong disequilibrium can be interpreted as evidence that the alleles under examination confer a higher (or lower if the alleles are negatively correlated) average fitness when they are associated in the genome. The argument for existence of coadapted gene complexes stems, in part, from the finding that allelic variants are often nonrandomly segregating. Other inferential data and examples were discussed. It was recalled that inbreeding has been credited with maintaining coadapted gene complexes in many genetically homogeneous species, and that outbreeding depression is often explained as the breaking up of gene complexes.

Without direct evidence for the existence and function of a coadapted gene complex, this concept can be applied to conservation efforts only indirectly. Woodruff offered an example based on studies of isozymic variability in populations of the slipper limpet, a bottom-dwelling mollusc found in San Diego harbor and on the coast of China. Much lower levels of variability in the Chinese population suggest its evolutionary derivation from North American populations. If asked to preserve the species for posterity, Woodruff would give priority to the North American population on the grounds that all of the variability (the isozymic variability at least) would be represented. However, if asked to address preservation of both forms, he would consider that sufficient evolutionary time had elapsed between divergence of the two populations that genetic coadaption could have developed in each, and they should be preserved separately rather than pooled in a single heterogeneous and interbreeding group.

Concern was voiced that the action of transposable elements ("jumping genes") might render the concept of coadapted gene complexes completely useless in conservation planning. Douglas Gill provided a cursory overview, mentioning the existence of substantial evidence for the movement of large segments of genetic material and for limitations on the locations of extraction and insertion sites within the genome. Movement of genetic material within an individual genome has been documented, and it is already known that the expression of genetic material may change depending on its location in the genome (the positional effect on eye color in *Drosophila*, for example). The determination of what genetic material is worth saving could be made impossibly complex: because genotypes are ephemeral, determination of the genotype might depend on what part of the individual organism one is examining. While no one in the group could provide a specialist's insight, it was felt that both the species concept and the notions of genotypic stability and germ line continuity are likely to be maintained as research progresses in this area. In addition to recommending that geneticists stay abreast of developments from studies of "selfish DNA," viral elements, and so forth, Antonovics suggested that retroviruses and other trans-

posable elements should, as a class, be deserving of a high priority for genetic conservation.

The take-home messages regarding the role of coadapted gene complexes in genetic conservation were the following: (1) the concept is relevant, though not necessarily critical to the definition of fundamental population units in nature (stocks, strains, varieties, etc.), and (2) to manage or sustain coadapted gene complexes in the absence of detailed information, as many individuals as possible should be sampled from natural populations.

SAMPLING VERSUS RECONSTRUCTION OF GENE COMBINATIONS

With seeming consensus that gene combinations, adaptive or otherwise, constitute one of the most "useful" aspects of genetic material, the question of how such combinations might best be preserved or otherwise obtained received considerable attention. Several comments by Margery Oldfield and Christine Schonewald-Cox suggested that collection from natural populations might be the best and perhaps the only practical way to obtain samples of adaptive genetic combinations. Maximum access to such material might be maintained through *in situ* management of populations.

There was no support for the notion that techniques of mutation breeding could be effective in reconstructing important gene combinations. However, Oliver Ryder argued that developing biotechnologies eventually will enable us to "cut and paste" genotypes to order, provided that a template is available. He suggested that samples of DNA could be preserved at very low temperatures until capabilities to isolate, identify, and study unique sequences eventually allow reintroduction of gene combinations into viable strains. Subsequently, Michael Rosenzweig suggested that tissue culture techniques might already be able to speed the process of recombining genes.

Antonovics highlighted several observations pertinent to the conservation of unique genetic combinations. Despite the incredibly large number of unique combinations generated by reproduction in outbreeding organisms, not all possible gene combinations occur in nature. Discontinuities ease the job of the taxonomist, but complicate life for the plant breeder, who often must search for traits to incorporate into commercial varieties from relatives of crop species. In most cases one can only guess at the existence of adaptive or "right" gene combinations from measures indicating nonrandom association of genes. Only in the most intensively studied species can we identify the genetic basis of particular traits and systematically assemble the desired gene combinations, using available technologies.

IMPACTS OF INBREEDING AND OUTBREEDING

The discussion of inbreeding and outbreeding effects revealed a considerable maturation of views on the application of genetics in this area. Whereas only a few years ago scientists and managers unequivocally condemned practices that might result in inbreeding, both groups have become more sophisticated. Descriptions of the mating systems in natural populations have shown certain levels of inbreeding to be acceptable, perhaps even desirable, and management of captive populations has provided examples in which promotion of outbreeding has been detrimental.

Citing Selander's work on Old World and New World species of slugs, Schonewald-Cox indicated the growing evidence that inbred and apomictic species of organisms have been highly successful colonists of natural habitats. She suggested that the often narrow and well-defined ecological requirements of such species could make them especially useful to managers attempting to install or intentionally modify biological communities in nonpristine habitats. She observed that the diversity of ways in which natural populations are genetically structured might suggest a broader range of possible management prescriptions than has been considered heretofore.

Ryder cited Alan Templeton's work on captive populations of zoo animals as evidence that inbreeding and outbreeding depression are temporal phenomena that can be alleviated by innovative management of subpopulations and some demographic good luck. Selective breeding of closely related individuals may be able to maintain numbers while homozygous recessive alleles are purged from the population. Recognition of genetically incompatible cytotypes of some cryptic species (e.g., spider monkeys) can help the manager avoid ineffectual crossbreeding.

Bruce Wilcox summarized Templeton's ongoing study of the collared lizard, *Crotaphytus collaris*, in the Ozarks as an example of how management might use knowledge of inbreeding and outbreeding effects. Habitat glades in the Ozarks are being managed as unique ecological areas, and efforts are being made to restore habitats and species. The problem in regenerating collared lizard populations was one of availability of source stocks. Lizard populations were extinct in many areas and very small in others. Templeton used allozyme markers and mitochondrial DNA analysis to examine population differentiation, and discovered fixed monomorphic differences between populations. This suggested that the risk of outbreeding depression might be high and that local adaptation might be more important than heterozygosity in establishing new populations. The data permitted "appropriate" breeding stocks to be selected for reestablishment of populations on particular glades. The assumptions behind the genetic models and the overall management strategy are being tested by implementation of his recommendations.

Challenged by Noll's remarks, Antonovics and others recounted examples of theoretical relationships and general observations in which geneticists do have confidence, and of contextual data that might influence professional judgments in particular management situations. For example, if a species is normally outbred in nature, imposition of inbreeding is likely to produce symptoms of inbreeding depression, including lower fecundity and lower survival. Although the exact consequences cannot be predicted for particular species, there is ample evidence to predict trends. Suggested examples of other "safe" generalizations included: (1) genetically uniform populations of organisms are susceptible to disease epidemics; (2) biological control is more effective if the organism being controlled is not highly variable genetically; and (3) population size is a critical parameter of survival for endangered species.

Several more detailed illustrations of how genetic and biological information might be used to recommend management action were given in the course of the discussion. Woodruff summarized work on topminnows found in springs in south central Arizona, where the species is endangered by habitat disturbance and an introduced predator, and in northern Sonora, where it is common. Restocking of unoccupied springs from a hatchery population is being attempted by the Arizona Department of Fish and Game, but the plan might be improved using recent genetic data. A survey of electrophoretic variation in populations from both areas, by Robert Vrijenhoek (1985), indicates that a large portion of overall genetic variability in the species is due to differences between geographic clusters of populations (53 percent) and between the populations themselves (26 percent). On the basis of these data, ecological information, and gen considerations on adaptation and inbreeding, Vrijenhoek recommended specific modifications of the restocking plan.

Riggs summarized an effort to integrate data from a variety of studies to recommend priorities for sampling Douglas-fir, an economically important forest tree species (NCGR, 1982). Evidence that local adaptation could be important to timber yield and viability of forest ecosystems provided the justification for establishing a high priority for sampling and conserving the genetic diversity of this common and widespread species. In the absence of a comprehensive study of genetic variation in Douglas-fir, data from a number of independent studies were used to develop a decision-making framework. Information on variation in isozymes, monoterpenes, and a large set of phenotypic parameters was available. Sampling priorities could have been established on any one of these traits alone, but the results would not have been in agreement. Variation patterns shown by the three different groups of genetic parameters were compared in an effort to develop a rationale for sampling some portions of the spectrum of genetic variability more closely than others.

There were various responses to the obvious need to establish priorities for research and conservation activities subject to budgetary constraint. It was sug-

Charnov suggested advantages for "intellectual opportunists," adducing, as an example, past discrepancies between the funding levels for coyote control and the study of factors important to coyote population dynamics.

Observations on the effects of EIS (environmental impact statement) and EIR (environmental impact report) requirements over the past fifteen years supported arguments both pro and con. William Kunin pointed out that voluminous EIS and EIR studies had been used for little else than fulfilling NEPA requirements. Without provisions for monitoring or follow-up studies, their conclusions could not be tested, and modification of development projects or management activities could not be justified. Riggs observed that constraints of time, budget, and personnel might often prevent the basic research biologist from pursuing those questions of greatest personal interest, and that past behavior of agencies made significant funding of associated basic research unlikely.

Comments on the complex and voluminous nature of EIS/EIR studies drew remarks from economists Brown and Noll. They noted that these features were endogenous—that is, explainable by the internal responses of organizations to procedural changes in public policy. Noll pointed out that this is itself an area of scientific inquiry, and recommended a recent publication by Serge Taylor (1984), describing how EIS requirements changed decision-making procedures within the Bureau of Land Management. He outlined the sequence of predicted responses: the procedural complexity that results from the legislated requirements increases the probability that disputes will involve litigation, and this in turn increases the need to anticipate information and documentation requirements, as well as the likelihood that appropriate expertise will be brought in earlier in the decision-making process. With this background, some of the costs and benefits of instituting genetic impact statements could be anticipated. A benefit would be that genetic principles and data would be considered at an earlier stage in the decision-making process. One negative effect might be a deflection of resources from other activities (on-the-ground management for example) and an increase in the overall expense of carrying out particular projects. Whether, on balance, the effect on preserving genetic resources would be good or bad is not easily predicted. Noll stated that such procedural changes are not to be recommended lightly; they call for the same kind of expertise and attention to detail that the impact statement itself would require in order to be worthwhile.

INSTITUTIONAL ROLES

Discussions of genetic impact statements, allocation of professional and monetary resources, and coordination of conservation efforts each focused attention on institutional roles in genetic conservation. Woodruff asserted that institutional impediments hamper progress on conservation, and he provided several examples. He observed that the species survival planning efforts of the Ameri-

of sophistication. Several examples of work that might benefit from more concerted professional attention were cited: (1) survey studies evaluating species and biological phenomena in ways that would permit interim management action on the basis of tentative "fuzzy" classification or generalizations; (2) integration of findings from diverse disciplines for the purpose of impact evaluation or other management and policy objectives; and (3) translation of research findings into a form easily applied by managers or planners. At least one commenter (Schonewald-Cox) called for institutional support of such activities.

An example of a relatively new institutional arrangement for bringing scientific and technical expertise to bear on planning efforts was outlined by Willa Nehlsen. She indicated how wildlife and fisheries management activities administered by the Bonneville Power Administration (BPA) in the Columbia River basin could be improved through adaptive management concepts introduced to the Northwest Power Planning Council by Kai Lee. The council operates under legislative mandate to integrate economic, social, scientific, and other considerations into resource plans recommended for implementation by BPA. One goal is to continuously test assumptions and interpretations of data used to justify management actions by careful design and execution of monitoring programs. It is hoped that recommendations to BPA's Fish and Wildlife Program will influence the way that BPA conducts its research programs and allocates money to research projects.

RESERVE DESIGN

Various comments throughout the discussion touched on the application of genetics to reserve design and management. Wilcox noted that data on species distributions and genetic variability could be used in identifying important locations for reserves and parks. Others did not hold out much promise for such efforts, pointing out that little is known about geographic patterns of overall genetic diversity and that, in any case, biologists have little to say in the selection of reserve locations.

Observing that the system of parks and reserves in the United States was established with little or no reference to distributions of species or species variants, Woodruff suggested that biologists must focus their efforts on recommendations to modify park boundaries and acquire the little remaining available land that might be most important to preservation of high priority species or populations. Ensuring that sufficient habitat is preserved and properly managed to maintain viable populations will also be a high priority, and, as was noted by both Woodruff and Schonewald-Cox, may be particularly critical for those species that are normally wide-ranging and outbreeding in nature.