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A Role for Molecular Genetics in the Recognition and Conservation of Endangered Species

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Taxonomies based on morphological traits alone sometimes provide inadequate or misleading guides to phylogenetic distinctions at the subspecies and species levels. Yet taxonomic assignments inevitably shape perceptions of biotic diversity, including recognition of endangered species. Case histories are discussed in which the data of molecular genetics revealed prior systematic errors of the two possible kinds: taxonomic recognition of groups showing little evolutionary differentiation, and lack of taxonomic recognition of phylogenetically distinct forms. In such cases, conservation efforts for 'endangered species' can be misdirected with respect to the goal of protecting biological diversity.

In conservation biology, most discussions of genetics have focused on how best to preserve variability within threatened species, the assumption being that higher genetic variation enhances the probability of a population's survival over ecological or evolutionary time. For example, genetically-motivated concerns about minimum viable population size (MVP) led to the much disputed '50/500 rule' (reviewed in Refs 1 and 2), which suggests that an effective population size of $N_e \simeq 50$ may be sufficient to avoid appreciable short-term inbreeding depression, and that $N_e \simeq 500$ is required to avoid long-term erosion of genetic variation in quantitative traits with high heritability.

Lande[3] has recently argued that demographic and behavioral considerations should be of greater immediate importance than genetic concerns in the formulation of conservation plans. Individuals in many species show decreased reproduction at low population densities for non-genetic reasons, such as lack of social interactions necessary for breeding, difficulty of finding mates, or other density-dependent ecological factors collectively known as the Allee effect[4]. Lande[3] discusses case histories for two endangered taxa [the northern spotted owl (*Strix caurina occidentalis*) and the red-cockaded woodpecker (*Picoides borealis*)] in which management plans based on population genetic principles 'threaten the existence of the populations they were designed to protect because basic demographic factors were ignored'. There are additional reasons for question-

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ing management strategies based solely on maximizing intrapopulation genetic variation: there appears to be wide variation among species in the fitness cost of inbreeding[5]; many species in nature have breeding systems (e.g. self fertilization or sib mating) or geographic population structures that reduce heterozygosity far below its expected value under outcrossing and high gene flow; and matings between dissimilar individuals, while increasing variation in progeny, may sometimes disrupt favorable gene combinations and result in 'outbreeding depression'[6].

Nonetheless, attention to intrapopulation genetic variation is likely to continue, because heterozygosity (as estimated by various molecular genetic techniques) is known to be dramatically reduced in some threatened species[7-10], and because such reductions are sometimes associated with lowered components of fitness[11,12]. However, the connections between heterozygosity and population viability are complex, and in this respect molecular genetic data cannot provide unambiguous guidelines for the management of rare species.

Molecular genetic information can still be of considerable value in another context, involving the appraisal of phylogenetic discontinuities within and among 'species'. Taxonomic assignments at the subspecies and species level, many of which were proposed in the last century from small numbers of morphological characters, continue to provide the systematic framework within which endangered forms are recognized. Yet these taxonomic assignments too often provide inadequate or even incorrect partitions of phylogenetic diversity. An updated taxonomy that includes input from molecular genetics should provide a firmer foundation for the proper recognition and hence management of biotic diversity.

As examples, I will briefly summarize two case histories involving North American endangered 'species' in which the existing taxonomies improperly summarized the evolutionary genetic relationships of the populations involved. Full details and background references can be found in Refs 13 and 14, respectively.

Taxonomy-based mismanagement of endangered species

Colonial pocket gopher

In 1898, *Geomys colonus* was described as a distinct species, with range confined to Camden County, Georgia. This form remained essentially unnoticed and unstudied until the 1960s, when gophers in Camden County were 'rediscovered'. The population referable to 'colonus' then consisted of less than 100 individuals, and was subsequently listed and managed as an endangered species by the State of Georgia.

Subsequently, a molecular genetic survey was conducted using multilocus protein electrophoresis, karyotypic examination, and restriction enzyme analysis of mitochondrial DNA (mtDNA). None of these genetic methods detected any consistent distinction between 'colonus' and nearby populations of a common congener *G. pinetis*. This result was not attributable to a lack of sensitivity of the techniques employed, because each method revealed dramatic genetic differences among a broader geographic array of *G. pinetis* populations. The conclusion in this case was clear: '*G. colonus*' did not warrant recognition as a distinct species. Either the species description in 1898 was inappropriate, or an original valid *G. colonus* species had gone extinct and was replaced by recent *G. pinetis* immigrants into Camden County.

Dusky seaside sparrow

In 1872, a melanistic form of seaside sparrow was discovered and subsequently described as a distinct species, *Ammodramus nigrescens*. Its range was confined to Brevard County, Florida, whereas other seaside sparrow populations (*A. maritimus*) occur in coastal marshes from Massachusetts to South Texas. In the 1960s, the population of duskies (by then, technically reduced to subspecies status, *A. maritimus nigrescens*) was listed as endangered by the United States Fish and Wildlife Service. By 1980, the few remaining birds were brought into captivity and mated to individuals from a Gulf Coast subspecies in a last-ditch effort to preserve in hybrids some 'dusky' genes for eventual reintroduction to Brevard County.

A recent molecular genetic survey

of mtDNA showed that populations of *A. maritimus* consist of two fundamental phylogenetic stocks, one confined to all Gulf coast locales and the other to Atlantic coast locations. The dusky seaside sparrow proved indistinguishable from other Atlantic populations, but genetically quite distinct from the Gulf population to which it had been hybridized in the captive breeding program. Because traditional taxonomies for the seaside sparrow complex (which have ranged from recognition of one to three species and from four to nine subspecies) include no apparent cognizance of an Atlantic/Gulf separation, they had not captured what is perhaps the single most salient phylogenetic feature in the evolutionary history of the assemblage.

Thus, in the cases of both the pocket gophers and seaside sparrows, conservation efforts had focused on populations showing little evolutionary separation from other conspecifics, and had neglected other populations showing considerable evolutionary genetic distinctiveness.

Acting on endangered species

The Endangered Species Act of 1973 was recently revitalized by the United States Congress, with annual appropriations of roughly $60 million authorized through 1992[15]. The program's charge is to prepare a list of plants and animals threatened or endangered, and then develop monitoring and recovery plans for those species. Listings are usually based on the ecological and demographic status (i.e. sizes and ranges) of populations with previously designated subspecies or species epithets. Little attention is paid to the adequacy of the taxonomic assignments, despite the fact that many descriptions trace to meager morphological evidence derived (as in the colonial pocket gopher and dusky seaside sparrow) from cursory surveys in the last century.

Once a Latin binomial or trinomial is in the literature, the group to which it refers usually assumes an aura of reality that may not always be commensurate with its true evolutionary distinctiveness. Given the high monetary and ecological stakes involved in endangered species management, it would seem prudent to base taxonomic decisions on a broad and reliable information base, which should now include (but not be limited to) the data of molecular genetics. In applying molecular genetic information to descriptions of biotic diversity, several non-

conventional issues in conservation biology will arise:

(1) *Evaluations of taxonomic status*

Management personnel will have to keep an open mind regarding the prospect of taxonomic revision, particularly in groups that have been problematic or poorly studied. Most systematists are well aware of the provisional nature of existing taxonomic assignments, particularly at the subspecies and species levels. But such reservations are difficult to convey to government managers, who have been granted a legislative mandate to preserve taxonomic entities that are often perceived as sacrosanct. In the future, management personnel should be prepared to evaluate the taxonomic status of endangered species where appropriate, and to identify groups that may benefit from molecular genetic analysis.

(2) *Conflicts among data bases*

Inevitably, conflicts will occasionally arise when multiple data bases are used to assess taxonomic and evolutionary relationships. In the past, morphology was the major source of information for phylogenetic investigation. Molecular assays are valuable because they provide access to a specified and usually significant sample of genetic material, whereas conventional taxonomic characters typically have unknown or limited genetic basis. Indeed, some morphological characteristics upon which taxonomies have been erected may exhibit ontogenetic or phenotypic plasticity[16–18], while others are obviously under intense selection, such that they can sometimes be misleading markers of evolutionary relationship.

On the other hand, there is also a danger of 'molecular chauvinism'. For example, even if the dusky seaside sparrow was indisputably no more distinct than many other local Atlantic populations in overall genetic composition, there might have remained valid sentiment for exceptional efforts to preserve that particular population because of its unusual phenotypic appearance. The darker plumage in the dusky sparrow could have a simple and recently evolved genetic basis, yet be deemed of sufficient 'aesthetic' consequence as to be afforded disproportionate weight in a population preservation program. Such value judgements imply that the connections between molecular genetic findings and management strategies will not always be straightforward, even when the phylogenetic results are clear. Man-

agers must continue to weigh a host of biological, social, political, economic and aesthetic factors.

(3) *Levels of resolution*

McKitrick and Zink[19] advocate an extreme version of the 'phylogenetic species concept'[20] in which taxa to be recognized are the smallest distinguishable clusters of individuals sharing a monophyletic character. In my view, this suggestion cannot be applied to conservation policy. Most species exhibit genetic differences across their ranges, in part attributable to varying degrees of phylogeographic population structure[21]. As increasingly sophisticated methods of descriptive molecular genetics are applied to natural populations (or as more DNA sequence data become available), opportunities for finer distinctions will result, and in the extreme, virtually every local population, family unit, and even individual may prove distinguishable from all others by some recently derived genetic trait.

In my opinion, one very important key to taxonomic assignments should involve evidence for clear phylogenetic discontinuities resulting from long-term population separation. These discontinuities should be evidenced by concordance in the phylogenies constructed from unlinked genes or unrelated suites of characters. A tree constructed from a given gene or character can be different from a population phylogeny, particularly when the divergence time between taxa is short[22,23]. But as divergence times between taxa increase (relative to effective population size), so too do the expected numbers of independent character states that concordantly identify the clades as monophyletic. In addition, historical biogeographic information will contribute importantly to the recognition of phylogenetic separations, particularly when geographic and genetic subdivisions are concordant.

Conclusion

There are currently over 500 species listed in the United States as endangered or threatened[24], with perhaps 1000 more awaiting formal assessment[15]. Clearly, because of the time and expense involved, not all such taxa can be evaluated extensively by molecular genetic methods, nor need they be. Many endangered species are indisputably unique, with no close living relatives; conversely, identification of morphologically cryptic species by molecular methods may not be a high priority in conservation biology

when protection efforts for known species are already inadequate. Given the problems of environmental deterioration and species extinction on a global scale, it might be unwise to divert a large fraction of the limited resources earmarked for conservation to molecular genetic evaluations.

Nonetheless, in certain situations molecular genetic assessments are clearly a necessary and important guide to the description of biotic diversity. Furthermore, general management implications may often stem from studies funded as 'pure' research in molecular evolution. For example, Bermingham and Avise[25] found that populations within each of several species of freshwater fishes in the southeastern United States exhibit marked and geographically concordant genetic differences, probably due to historical patterns of drainage isolation and coalescence. These phylogenetic subdivisions should aid in the development of a regional management program applicable to many fish species in the southeast of the country.

Molecular genetic techniques should be increasingly employed as an aid to phylogeny reconstruction, and hence biotic diversity assessment. The need for increased attention to molecular descriptions of phylogenetic differences, particu-

larly at the level of populations and species, is a special aspect of the broader call to revive the field of systematics in conservation biology[26]. Considerable conservation resources are devoted to the management of rare taxa; commensurate attention should be devoted to the adequacy of the biotic descriptions.

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Chaos and Ecology

Chaotic Evolution and Strange Attractors

by David Ruelle, *Cambridge University Press, 1989. £25.00/$39.50 hbk, £8.95/$12.95 pbk (112 pages) ISBN 0 521 36830 8*

Chaos

edited by Arun V. Holden, *Manchester University Press and Princeton University Press, 1986. £45/$50 hbk, £17.95/$19.95 pbk (324 pages) ISBN 0 691 08423 8*

Chaos in Biological Systems

edited by H. Degn, A.V. Holden and L.F. Olsen, *Plenum Press, 1987. $75 hbk (323 pages) ISBN 0 306 42685 4*

Until recently, most ecologists assumed that if a population was influenced only by simple density-dependent factors, with no environmental or other randomness, then it would tend to remain roughly con-

stant. It is now increasingly realized, however, that simple and deterministic relations can produce stable points, or stably cyclic oscillations, or apparently random, 'chaotic', fluctuations in population density, depending on the severity of the nonlinear or density-dependent effects. Originating largely from work in population biology, and from Lorentz's studies in meteorology, 'chaos' is now a burgeoning subject, finding an increasing range of applications in the physical and biological sciences (see, for instance, Ref. 1).

Unfortunately, it is not yet clear exactly what the implications of chaotic dynamics and strange attractors may be for ecologists. Hassell[2] has reviewed, with examples, ways in which the presence of deterministically chaotic population fluctuations might undercut conventional methods for analysing data. Schaffer and Kot[3] have discussed the possibility that many recorded observations of population densities over

time ('time series'), which show quasi-periodic or irregular fluctuations, may be interpreted as strange attractors; a group including Schaffer, Kot, Pimm, Ellner, Gilpin, Sugihara and others (what might be called a strangely attractive collective!) is currently pursuing these ideas with as many long-term time series as they can find.

The books briefly reviewed here serve, in different ways, to guide the interested novice into the unfamiliar world of deterministic chaos.

In Ruelle's title, 'evolution' has nothing to do with Darwin, but rather refers to the development of dynamical patterns in chaotic systems; the book has the subtitle *The Statistical Analysis of Time Series for Deterministic Nonlinear Systems*. The book in fact derives from notes prepared by Stefano Isola from lectures given by Ruelle, and it gives an exceptionally clear and concise account of basic mathematical ideas, with an emphasis on intuitive arguments and on what the mathematics