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GENETIC DIVERSITY AND THE CONSERVATION OF ENDANGERED SPECIES

By
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INTRODUCTION

Genetic diversity is the basis of the twin evolutionary processes of speciation and adaptation (Darwin, 1859; Dobzhansky, 1970; Mayr, 1963; Lewontin, 1974; Wright, 1968,1969,1978). The evolutionary process, within and between species, i.e. of both macro- and micro-evolution, is critically dependent on the availability of heritable variation and its constraints. This conclusion applies notwithstanding the ongoing neutralist-selectionist debate on the nature of polymorphisms in natural populations, because the debate is primarily quantitative: how much variation at the molecular level is adaptive? Likewise, the conclusion is true regardless of our colossal ignorance of the complex translation of genetic into phenotypic diversity during embryogenesis and development (e.g. Edelman, 1988). Since change, both physical and biotic, is the hallmark of nature, biological evolution is critically dependent on genetic diversity to cope with, and adapt to, the constantly changing environments in nature. An in-depth analysis of genetic diversity at the protein and DNA levels is crucial to understanding the major evolutionary processes of adaptation and speciation and to prevent the disappearance of species, i.e. extinction.

I will first comment briefly on each of these three aspects, then summarize local, regional and global studies of genetic diversity and differentiation in natural populations of animals and plants, some of which are derived from long-term studies conducted at the Institute of Evolution, University of Haifa, and from the studies on cheetah. I will then draw conclusions and suggest ideas and prospects for future planning and management.

Adaptation: the central evolutionary process

Organisms have structures and functions that adapt them to survive and reproduce (Darwin, 1859). Darwin's theory predicts adaptations not as perfect entities built for promoting life. Notwithstanding the unit of selection, whether genes, individuals, populations or species, any such unit must vary genetically and reproduce, in order to evolve. While criticism on the adaptationist programme (e.g. Gould and Lewontin, 1979; see also several essays in Dupre, 1987, primarily by Sober, Maynard Smith and Lewontin) may continue, adaptation remains the central core of evolution. What indeed needs careful scrutiny is its critical evaluation, not total disposal; not even in order to avoid confusion in language and thinking, as suggested by Krimbas (1984). A critical evaluation of adaptation will search for efficient causes, patterns and processes which best explain the structures and functions under research out of multiple potential alternative stories. These explanatory models must be testable, falsifiable, and at least partly predictable.

Nonadaptive factors may certainly be important in evolutionary change, due to many obvious reasons. The latter include, inter alia, adaptive compromises and imperfections, historical and epistatic constraints, pleiotropy, genetic hitchicking, genetic drift, stochasticity, or lack of appropriate genetic variation. Nevertheless, despite the obvious obstacles faced by natural selection,

these factors, singly or in combination, do not seem to undermine the major role of natural selection assigned to it first by Darwin (1859) in orienting evolutionary change of whole organisms. This appears to be true from the molecular (Nevo *et al.*, 1984; Nevo, 1988a, b) to the phenotypic levels. The evolution of the subterranean mole rats of the *Spalax ehrenbergi* superspecies and their intimate relationship with the environment in space and time is explicable only along the adaptationist programme (Nevo, 1985,1986a, b 1989a, b).

The aforementioned inter- and multi-disciplinary reviews summarize the massive evidence displaying convergent adaptations in *S. ehrenbergi* to the subterranean ecotope in general (Nevo, 1979) and divergent adaptations associated with the speciation and adaptive radiation into four climatic regimes in particular (Nevo, 1985,1986a, b). While certainly not perfect, the pluralistic adaptive strategies described for *Spalax* are effective in increasing fitness. The significant differential mortality of the four chromosomal species found in a standartized laboratory environment reveals their differential fitness in accordance with their different climatic origins and adaptations. A critical evaluation of the adaptationist programme provides a clue to understanding organic nature and its evolutionary history. Stripped from adaptation, organic evolution will always remain as in the pre-Darwinian period: chaotic and inexplicable by material and lawful regularity. Adaptation from the gene through organisms, species, and communities, is the heart of the evolutionary process and diversity at all levels is the key to life.

Speciation: How many species are there on earth?

The answer to the basic problem of our understanding nature, that of speciation and species diversity, remains a major enigma at all levels, involving the modes, mechanisms and genetics of specation as well as the number of extant species. Focussing here on the latter, i.e., on "how many species are there on earth"?, our ignorance concerning present and past organic diversity is truly colossal (May, 1988). About 1.5 million species are currently classified and estimates of the total number range from under 5 million to more than 50 million. Theoretically, as emphasized by May (1988) we can not explain from first principles any estimate of the global total species numbers. May (1988) surveyed various kinds of empirical and theoretical studies pertaining to the enigma of the total species on Earth or in a given environment. These studies analyze food supplies and patterns of species abundance in relation to size and environment. While no answers are given, the questions are more sharply focused.

For most of the history of life on Earth that is preserved in the fossil record, rates of extinction and rates of speciation have been roughly commensurate. If we assume that roughly half of the extant species evolved in the last 50 to 100 million years, and that maybe half of all extant species will become extinct at the next 50 to 100 years if current rates of tropical deforestation continues, then contemporary rates of speciation are of order 1 million times slower than rates of extinction (A.P Dobson in May, 1988). These alarming circumstances elevate conservation biology (Frankel and Soule, 1981; Schonewald-Cox *et al.*, 1983; Soule and Wilcox, 1980; Soule 1986,1987) to one of the most urgent fields of theoretical and practical studies of evolution and conservation, i.e., management of the biosphere to prevent a global ecological catastrophe. Rational short- and long-term strategies of preserving the environment become crucial to life on earth, including human life.

Extinction: Patterns. causes and consequences of species disappearance

Most past species have disappeared from the evolutionary scene, and their hypothetical numbers are in the billions (e.g. Simpson, 1952). Massive extinctions played a major evolutionary role in the history of life (Raup, 1986). Eight major episodes of biological extinction of marine families over the past 250 million years stand significantly above local background (Raup and Sepkoski, 1986). Likewise, several major mass extinctions have been described for non-marine tetrapods (Benton, 1985), and these may be correlated with non-marine extinctions (Rampino, 1988). Furthermore, it has been recently suggested that extinctions, for example, the end Cretaceous mass extinction, were not a geologically instantaneous event and were selective in character (Hallam, 1987).

Population genetics parameters of mutation rates and secondarily population size, were suggested as partial explanatory factors in the Cretaceous extinction (Tsakas and David, 1987). Selectivity was also suggested in the last mammalian extinction of the later Pleistocene (Tsakas, 1988). Mass extinctions are selective events since heterogeneous ecologies, demographies and genetics lead to differential extinction probability. Most theories of extinction deal with statistical properties of large assemblages of species, ignoring details of the species ecology, demography and life history; hence these theories cannot predict the extinction of particular species (Lande, 1988). I suggest that genetic diversity, ecological heterogeneity, population structure and behaviour play major roles, not only in speciation and adaptation, but also in differential extinction. Heterozygosity may provide directly or indirectly a buffering shield preventing a total extinction.

Extinction due to vanishing tropical rain forests with their high species diversity is now reaching alarming rates, by far higher than the background rates of extinction (Myers, in Soule, 1986) . This collosal extinction is comparable to Late Cretaceous extinction 65 MYA in which the majority of species, then living on earth, perished. The current catastrophic rate of extinction has multiple destructive implications on the biosphere as a whole and, on the technologies of man, i.e. agriculture, medicine and industry and recreation, in particular. Ultimately, the destruction of natural ecosystems may destabilize regional and global climate with potentially disastrous effects (Ehrlich and Ehrlich, 1981; Southwick, 1983). The current global pollution and environmental deterioration by man affects disastrously also temperate and polar regions. This is very noticeable in Mediterranean biota and particularly in the ecosystems of cold or hot deserts across the globe, where species diversity is initially low (for hot deserts see 2 volumes of Evenari *et al.*, 1985,1986).

Clearly, as human populations grow and explode, habitats for wild plants and animals shrink and extinction often results. It has been estimated that 15-20% of all species on earth may become extinct by the year 2000 (Global report, 1980) . Hence the urgency for the short-term, but primarily long-term planning of the following

i) scientific assessment of species numbers and their ecological correlates;
ii) scientific conservation planning and management of numerous endangered species and ecosystems;
iii) in-depth understanding of genetic diversity, at the protein and DNA levels and its relevance to the evolutionary processes of:
  a) Adaptation;
  b) Speciation;
  c) Extinction.

It is therefore imperative to survey the population genetics of biological conservation in natural populations based on extensive surveys of heterozygosity. What is the regularity of heterozygosity in nature?

Genetic Diversity in Nature: Patterns and theory

The evolutionary significance of genetic diversity in natural populations of plants and animals was reviewed by Nevo (1988b and references therin) using the environmental-genetic correlation methodology at three geographical levels:

1. local: several species of wild cereals, land snails, and barnacles in Israel;
2. regional: 38 species in Israel; of these, 21 share the same ecological gradient ranging from the Mediterranean region to the Negev desert; also included were two species of wild cereals in the Near East Fertile Crescent; and
3. global: 1111 species of animals and plants ranging across the planet.

The species involved in these local, regional and global analyses are largely taxonomically unrelated. They vary in their ecologies, ranges, demographies, life histories, and other biological variables. They were mostly tested for allozymic diversity by routine horizontal starch gel electrophoresis at 25 gene loci on average (range 14-50 loci). In addition, two studies were reviewed on DNA polymorphisms (restriction fragment length polymorphisms, RFLPs) in animals and plants in Israel and the correlation was explored between RFLPs in animals and plants in Israel and the correlation was explored between RFLP and allozymes. The following results were found at all three geographical levels:

1. The levels of genetic diversity vary nonrandomly among populations, species, and higher taxa; and
2. Genetic diversity is partly correlated with, and predictable primarily by, ecological factors. These results corroborate the adaptive, environmental theory of genetic diversity, and they were confirmed for several allozyme loci in controlled laboratory experiments on pollution biology (Nevo, 1986c). The genetic patterns obtained are inconsistent with the neutral theory of molecular evolution. By contrast, natural selection in its various forms appears to be a major differentiating and orienting force of evolutionary change in protein and probably DNA polymorphisms as well.

Genetic diversity in nature and the probability of extinction

A comprehensive reanalysis of genetic diversity in natural populations (Nevo *et al.*, 1984) generated the following results (Fig 1):

1. The levels of genetic diversity vary nonrandomly among populations, species, and higher taxa; ecological parameters (life zone, geographic range, habitat type and range, climatic region); demographic parameters (species size and population structure, gene flow, and sociality); and a series of life history characteristics (longevity, generation length, fecundity, origin, and parameters related to the mating system and mode of reproduction).
2. Genetic diversity is higher:

    i) in species living in broader environmental spectra;

    ii) in large species with patchy population structure and limited migration, as well as in solitary rather then in social species; and

    iii) in species with small body size, annuals or long-lived perennials, older in time, with smaller diploid chromosome numbers, primarily outcrossed; and plant species reproducing sexually and pollinated by wind. Species with the above characteristics harbour generally more genetic diversity than their opposite counterparts, which are therefore more susceptible to extinction.

3. Genetic diversity is partly correlated and predictable by 34 variable combination of ecological, demographic, and life history variables, largely in this order. Ecological factors account for the highest proportion of the 20% explained genetic variance of all species as compared with demographic and life history factors (90%, 39% and 3.5% respectively). Within individual higher taxa the explained portion of genetic diversity increases considerably (mean 44%, and maximum of 74% in molluscs). However, significant small intercorrelations (r = mostly 0.1-0.3) occur both within and between the subdivided biotic variables. Therefore, additional critical tests at the population microgeographical levels,complemented by biological, biochemical and physiological experimentation (e.g. Zera *et al.*, 1985), may verify the inferences of causal relationships between biotic factors and genetic diversity.

Following are some general patterns which are directly relevant for endangered species Species living under the following conditions are characterized by low genetic diversity: arctic life zone, endemics, underground specialists (only in vertebrates), arid climates, territorial isolates (in vertebrates and mammals), small species size, large body size (in vertebrates and mammals) perennials, large generation length, and recent in origin. Generally, species characterized by one or more of the above parameters have lower levels of heterozygosity, hence are more vulnerable to extinction. These species should be the prime candidates for biological conservation and management.

Domestication of plants and animals: A global human experiment in erosion of genetic diversity and its biological consequences.

The biggest diversity experiment conducted by man with drastic consequences is that of domestication. While crop yields have been generally increasing recently, the genetic base of most of the important food crops has been rapidly narrowing (Plucknett *et al.*, 1983). The genetic diversity of cultivated plants is derived from the wild progenitors, modified in response to cultivation. A major problem preventing effective crop improvement, and a cause of growing concern, is the drastic genetic erosion of the advanced cultivars as compared with those of their ancestors, either the wild progenitors or the land races. This genetic erosion is caused by the global extension of modern pure-line breeding practices primarily during our century, which increase genetic homogeneity (Frankel and Soule, 1981; Plucknett *et al.*, 1983; Nevo, 1988b). The loss of genetic diversity of some of the world's crops has accelerated in recent decades with many crops becoming increasingly susceptible to diseases, pests, and environmental stresses, resulting in large losses of yield. A global network of gene banks has been established to provide plant breeders with crops that will maintain stable and high yields (Plucknett *et al.*, 1983). This global domestication experiment which resulted in diminishing diversity, should provide us with a severe warning. Homozygotization leads lo increased vulnerability and potential extinction. The domesticates survive not because of their ecological superiority as compared with their progenitors, but because of their economic importance for man and his protection.

Genetic basis for species vulnerability in a wild mammal: The Cheetah

A dramatic example of the genetic basis for species vulnerability in nature is that of the cheetah by O'Brien and colleagues (O'Brien *et al.*, 1985). A population genetic survey of over 200 structural loci previously revealed that the South African cheetah (*Acinonyx jubatus jubatus*) has an extreme paucity of genetic variability, probably as a consequence of a severe population bottleneck in its recent past. The genetic monomorphism of the species has been extended to the major histocompatibility complex. The apparent consequences of such genetic uniformity to the species include:

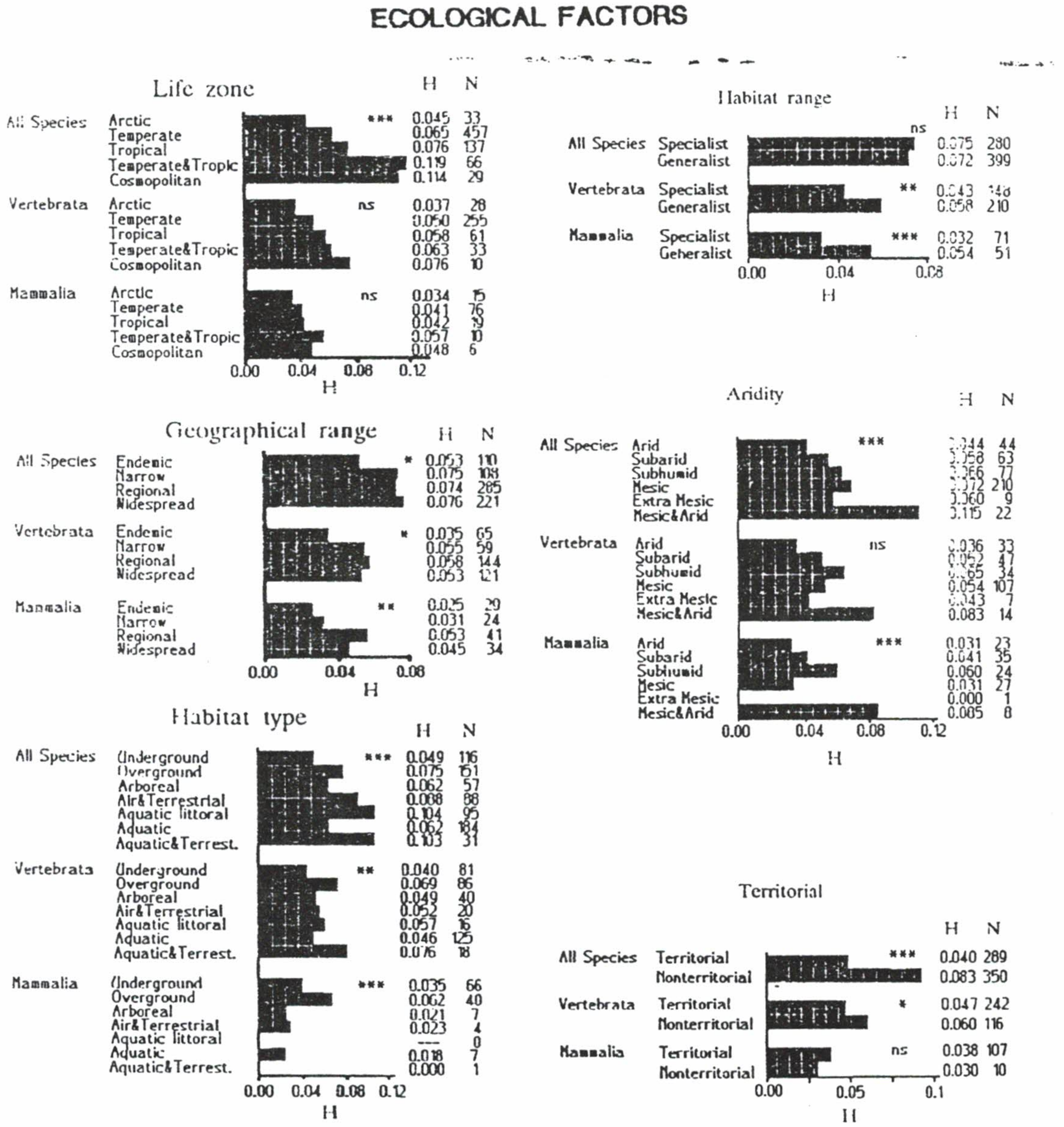
- great difficulty in captive breeding
- a high degree of juvenile mortality in captivity and in the wild, and
- a high frequency of spermatozoal abnormalities in ejaculates.

The species vulnerability of the cheetah was demonstrated by an epizootic of coronavirusassociated feline infectious peritonitis in an Oregan breeding colony in 1983. Exposure and spread of the coronavirus, which has a very low morbidity in domestic cats (approximately 1%), has decimated a heretofore productive and healthy captive population. The extreme genetic monomorphism, especially at the major histocompatibility complex, and the apparent hypersensitivity of the cheetah to a viral pathogen maybe related, and provide a biological basis for understanding the adaptive significance of abundant genetic variation in outbred mammalian species (O'Brien *et al.*, 1985).

A combined population genetic and reproductive analysis was undertaken to compare freeranging cheetahs from east Africa (*Acinonyx jubatus raineyi*) with the genetically impoverished and reproductively impaired South African subspecies (O'Brien *et al.*, 1987). Like that of their South African counterparts, the quality of semen specimens from east African cheetahs was poor, with a low concentration of spermatozoa (253 x 106 pr ejaculate) and a high incidence of morphological abnormalities (79%). From an electrophoretic survey of the products of 49 genetic loci in *A. jubatus raineyi*, two allozyme polymorphisms were detected; one of these, for a nonspecific esterase, shows an allele that is rare (less than 1% incidence) in South African specimens. Estimates of polymorphism (2-4%) and average heterozygosity (0.0004 - 0.014) affirm the cheetah as the least genetically variable felid species. The genetic distance between southern and eastern African cheetahs was low (0.004), suggesting that the development of genetic uniformity preceded the recent geographic isolation of the subspecies. O'Brien *et al.*, (1987) propose that at least two population bottlenecks followed by inbreeding produced the modern cheetah species. The first and most extreme was ancient, possibly late Pleistocene (circa 10,000 years ago); the second was more recent (within the last century) and led to the South African populations. The cheetah represents a tragic example of the loss of genetic diversity in a wild mammalian species and its grave consequences.

The Evolutionary model of active speciation and adaptive radiation of the Spalax ehrenhergi superspecies in Israel

Generally, small size population effects and repeated bottlenecks are considered biologically hazardous (e.g., Lande, 1988; O'Brien *et al.*, 1987). In small populations, inbreeding can gretly reduce the average individual fitness, and loss of genetic variability from random genetic drift can



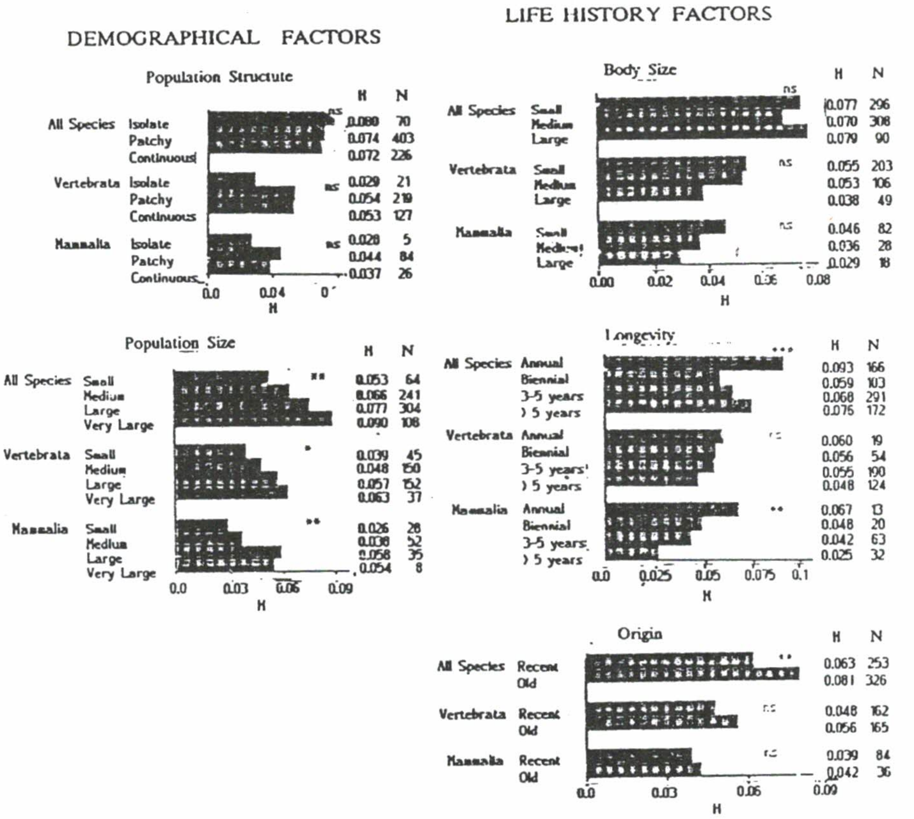


Fig. 1.Levels of heterozygosity of biotic factors (ecological, demographic and life history variables) for (i) all species tested; (ii) vertebrates; and (iii) mammals (Nevo et al, 1984). The estimates of heterozygosity (H) and number of species in each category (N) appear next to each bar. Levels of significance: * = p smaller than 0.05; ** = p smaller than 0.01; *** = p smaller than 0.001; ns = p greater than 0.05.

diminish future adaptability to a changing environment. Theory and empirical examples summarized by Lande (1988) suggested to him that demography is usually of more immediate importance than population genetics in determining the minimum viable sizes of wild populations. Since the discussion on small-size population effects is intimately linked with speciation and extinction it may be relevant to review here the *S. ehrenbergi* case which leads me to the conclusion that ecological genetic factors may sometimes override demographic factors in the evolutionary biology of species. The same conclusion was earlier drawn and reviewed here in the analysis of genetic diversity and differentiation in nature. Ecological factors appear to be of prime importance in genetic differentiation in nature (Nevo, 1988a, b; Nevo *et al.*, 1984).

Subterranean mole rats of the *S. ehrenbergi* superspecies in Israel represent a dynamic case of ecological speciation in action (Nevo, 1985,1986a, b, 1988c, 1989a-c) . The complex consists of four chromosomal species (2n = 52, 54, 58 and 60), which display progressive stages of late chromosomal speciation. Their adaptive radiation in Israel from the Lower Pleistocene to Recent times is closely associated with fossoriality and increasing aridity. Each of the four chromosomal species is adapted genetically and phenotypically at all organizational levels (morphology, physiology and behaviour), to its own climatic regime characterized by a unique combination of humidity and temperature. Populations are largely continuously distributed in their main ranges, but become semi-isolated, particularly in the peripheral steppes and deserts surrounding the chromosomal species 2n = 60. These peripheral isolates may be the cradles of future peripatric speciation (Mayr, 1982).

Speciation in the *S. ehrenbergi* superspecies proceeded probably peripatrically with little genomic differentiation (Nevo and Cleve, 1978; Catzeflis *et al.*, 1989).

In a recent study Nevo (1989a) compared and contrasted 14 genetic and phenotypic variables of the continuous populations of the chromosomal species 2n=52, 54, and 58, but particularly 2n=60 with its peripheral post-Würm relictual semi-isolates and isolates. Separated from the main range by several kilometers to tens of kilometers of inhospitable steppe and desert environment, they consist of low effective population sizes (N= 10 to several hundred individuals about 100 in the main Sede Boqer isolate studied). The results indicate that:

1. Notwithstanding their small effective population sizes, Ne, semi-isolates and isolates harbour genetic polymorphisms and phenotypic variances that are similar in nature to those of the continuous populations, but lower in their levels of polymorphism and number of segregating alleles.
2. Chromosomal, allozymic, mtDNA and nuclear DNA polymorphisms are correlated with climatic factors of water availability and temperature.
3. Based on currently available molecular and organismal evidence, no signs of genetic revolution or major genome reorganizations are discernible in the isolates. In a few systems though, such as in Myosin heavy chain (Ben-Shlomo and Nevo, 1989), unique alleles have been found in the Sede Boqer isolate not found elsewhere (Fig 2). Likewise, these small isolates, if not frequently extirpated, may also involve Robertsonian chromosomal mutations which may initiate speciation (Nevo, 1989a).

These results suggest that peripatric speciation in the isolates may occur primarily because of their multiple genetic and phenotypic adaptations to their new ecological open frontier, and to the

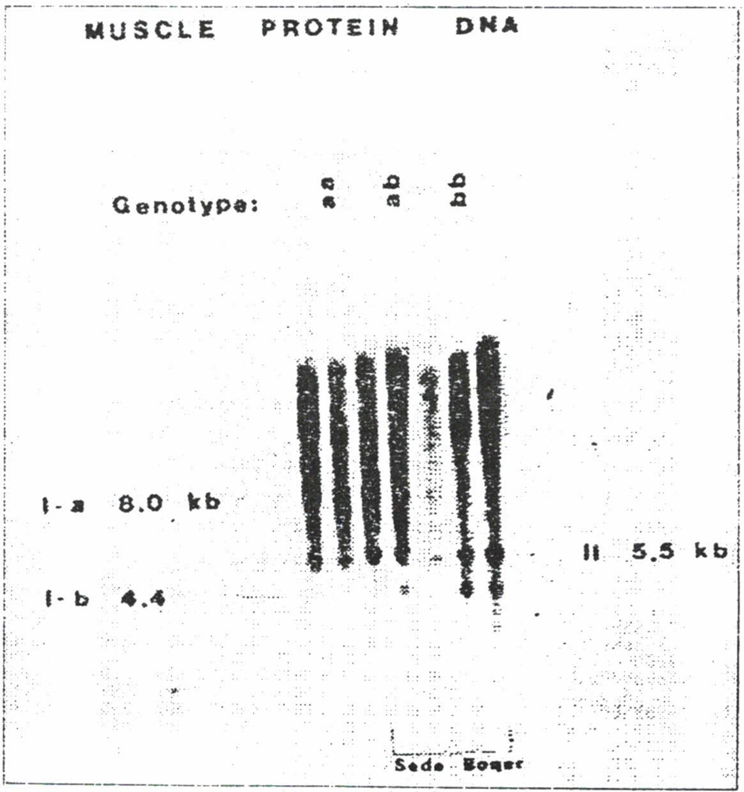


Fig. 2. Muscle protein DNA variation in mole rats of the *Spalax ehrenbergi* superspecies in Israel. Note the unique alleles in three individuals from the desert isolate of Sede Boqer. This allele was not found elsewhere in the entire range of the four chromosomal species of *S.ehrebergi*.

unique combination of evolutionary forces operating in small isolated populations. These forces, involving natural selection, genetic drift, segregation distortion, and inbreeding, may facilitate, singly or in combination, the initiation of reproductive isolation primarily by Robertsonian mutations. Speciation evolves slowly and gradually until complete reproductive isolation is established, thereby intimately combining adaptation and speciation and merging micro- into macro-evolution without any sign of drastic punctuationism (Nevo, 1985, 1986a, b, 1988c, 1989a). The relative role of peripatric speciation among actual and potential modes of speciation is still unknown; its determination will depend on future multidisciplinary evaluation of many and diverse taxonomic, ecological, demographic and life history cases, particularly of actively speciating taxa.

The S. ehrenbergi case illustrates that small isolates (N= 10-100) are not necessarily highly homozygous due to inbreeding. Natural selection maintains presumably genotypic polymorphisms and phenotypic variation at the molecular and organismal levels, respectively. Although the level of these polymorphisms and the number of segregating alleles may indeed be lower, they do not totally disappear from these small populations. By contrast, these unique populations, if not extirpated, may provide the cradles of new species by peripatric speciation (Mayr, 1982). Thus, safeguarding such potentially important populations, which may give rise to new species, is of paramount importance in future conservation biology.

THEORETICAL AND EMPIRICAL ASPECTS OF CONSERVATION BIOLOGY

Heterozygosity and fitness in natural populations

The central problem of conservation genetics is the relationship between change in genetic diversity and fitness (Frankel and Soule, 1981). As indicated above, genetic diversity varies spatiotemporally within and between populations. Recent theoretical and empirical studies (e.g. Lerner, 1954; Turelli and Ginzburg, 1983; Karlin and Feldman, 1981; Mitton and Grant, 1984; Zouros, 1987) suggest that the level of heterozygosity of individuals is a major organizing principle of both plants and animals. Many enzymes in natural populations are polymorphic, and these served as the basis of heterozygosity estimates reported by Nevo *et al.*, (1984). For those enzymes whose kinetics have been investigated there are typical differences in biochemical and physiological performance among genotypes (Zera *et al.*, 1985). These genotypic differences are also detectable at the level of the whole organism and math with its performance in nature. Empirical studies summarized by Mitton and Grant (1984) report associations among individual heterozygosity (i.e., the number of heterozygous loci) and measures of performance such as growth rate, development stability and oxygen consumption in plants, animals and humans. This is true even if associative overdominance overwhelms the direct dominance effects of the scored loci, and is mainly responsible for the observed correlations. Hence heterozygosity must be investigated on its own merit, as concluded by Zouros (1987). The catastrophic results reported for the cheetah by O'Brien *et al.* (1985 and 1987), where vulnerability presumably results from the extreme genetic monomorphism, should serve as an extreme caution for future management of animals in nature. Clearly, drastic bottlenecks can lead as in the cheetah's case to extreme homozygosity and vulnerability.

These conclusions are of paramount importance for theory and practice alike. They must be the solid foundations of breeding and conservation programmes. Lande (1988) suggested that predicting the extinction of single populations or species requires ecological and evolutionary information. He emphasized the role played by primary demographic factors affecting population dynamics, including social structure, life history variation caused by environmental fluctuation, dispersal in spatially heterogeneous environments, and local extinction and colonization. He stressed the fact that in small populations inbreeding can greatly reduce the average individual fitness and loss of genetic variability from random genetic drift can diminish future adaptability. He concludes that demography is usually of more immediate importance than population genetics in determining the minimum viable size of wild populations. This conclusion needs much more research and quantification in the wild for establishing generality. It contrasts with the pattern of genetic variation in nature described earlier (Nevo *et al.*, 1984) and is not supported by the *Spalax* evidence, though it is clearly supported by the cheetah and other cases (O'Brien *et al.*, 1985,1987). In such future studies, quantification should dearly distinguish between relictual populations and new endemics or bottlenecked populations such as the cheetah. Genetic monitoring of zoo populations could provide specific recommendations for the evaluation of captive populations and for the monitoring of breeding programmes by using biochemical and morphological characters (Wayne *et al.*, 1986, see also Schonewald-Cox *et al.*, 1983).

Inbreeding and heterozygosity

Inbreeding leading to homozygosity always reduces fitness in animals. Large out crossing populations that suddenly decline to a few individuals usually experience reduced viability and fecundity (inbreeding depression) (Lande, 1988 and references therein). The decline of reproductive traits, or inbreeding depression, resulting from a 10% increase in the inbreeding coefficient, is usually between 5% and 10%. For total reproductive performance, the decline may be 2 to 5 times as high. Behaviour traits and competitive ability are also depressed by inbreeding. Intense inbreeding in animals results in the loss of 90% or more lines unless the stock has a long history of domestication or slow inbreeding is 1%. This translates into an effective population size of fifty, or more if the loss of heterozygosity (or increase in homozygosity) is not to surpass 1% (Frankel and Soule, 1981). Notably, however, gradual inbreeding or reduction of population size creates relatively little permanent inbreeding depression since selection purges the population of deleterious recessive alleles when they become homozygous (Wright, 1977).

The situation is drastically different in inbreeding plants which have overcome inbreeding depression through gradual elimination of the population of deleterious alleles resulting in a "clonal" population structure. Inbreeding plants have very low between many homozygous clones within a population which are associated with microniche ecological differentiation (Nevo *et al.*, 1984; Nevo and Beiles, 1989a and unpublished studies). Here clonal diversity replaces individual heterozygosity in adaptation to microsite environmental variation. In our wild cereal studies at the Institute of Evolution, we have established through a series of microgeographical studies that diverse genotypes or homozygous clones are associated with different microclimatic niches, soil types, topographies, and years. Thus, the solution of inbreeding plants to ecological heterogeneity is to spread the variation between individual genotypes or clones adapted to microniche heterogeneity, whereas in outbreeders it is situated within each individual.

CONCLUSION AND PROSPECTS

Genetic diversity in nature is subdivided within and between species and is the key to life and its evolution on our planet. However, generally our little knowledge of the organism-environment interrelations and of spatiotemporal changes, impede reliable prediction of extinction patterns and rates. In small populations inbreeding and random processes can reduce heterozygosity in the absence of factors acting to maintain genetic diversity, such as mutation, immigration, or selection favouring heterozygotes or heterozygosity. The expected rate of loss of heterozygosity is $^{1}/_{(2N_e)}$ per generation (Lande, 1988). Reduction in heterozygosity will usually reduce individual fitness, thereby diminishing future adaptability to a changing environment.

Multiple reasons dictate the urgent need to conserve biodiversity. Ultimately ecosystem destruction by man may destabilize local, regional and global climate and biogeochemical cycles with potentially disastrous effects on the biosphere and the future of life (Ehrlich and Ehrlich, 1981; Southwick, 1983). Proximately, there are important practical reasons for conserving wild gene pools and habitats containing the actual and potential progenitors of medicaL agricultural, industrial and recreational values (Oldfield, 1984; Brown, 1988). Conceptually, extirpating life forms and biodiversity that evolved over millions of years, stood the test of time, and some of which provide adaptive shields for survival, is extremely unethical. It amounts to burning whole genetic libraries, that have been accumulating continuously through the history of life irreversibly and irreparably, thereby counteracting the evolution of life on our planet.

Awareness of the importance and benefits of conserving biodiversity is growing rapidly, but practices of saving these rich natural resources may lag in view of the current alarming rates of destruction. Our knowledge of genetic diversity and differentiation within and between populations across the entire geographic ranges of species is extremely meagre. This information is known for a few progenitors of important cultivars (e.g. for wild emmer wheat see Nevo and Beiles, 1989a), but is unknown for more than 99.9% of all extant species. Yet this is the only educated guid to evaluate local and regional adaptability. Wild emmer wheat, for example, displays an ecological and population genetics "archipelago" structure where common (greater than 10%) local and sporadic alleles constitute 70% of the genetic diversity of the species and only 30% are widespread. Moreover, the local and sporadic alleles display adaptation to climatic and soil variations. Hence, extinction of genetically unique populations deplete the genetic foundations of the species geographic variation and current distribution.

Nor do we know, in most cases, the physical and biotic factors causing genetic differentiation and the ecological and evolutionary dynamics of small populations to effectively manage and preserve them. But this information is crucial to a reliable prediction of populations' and species' extinction. Propagation of endangered species in zoos and in gene banks is important, but can not replace natural preserves (Soule, 1987). Protection and restoration of natural habitats is the best, and by far the most effective and cheapest method of preserving biodiversity and stability of the global ecosystem (Ehrlich and Ehrlich, 1981; Southwick, 1983; Brown *et al.*, 1988), and ecological, demographic and life history parameters of species are crucial for prediction and wise management (Lande, 1988).

However, our total ignorance emerges in view of the following open questions: What and how should we preserve? Should nature reserves be based on keystone species, or rather on general species diversity? Should we preserve primarily particularly endangered species or rather their natural habitats, as well as generally diversified habitats? Should we target on unique populations within a species, or rather on a spectrum of populations encompassing the entire ecological spectrum of the species range? Can zoos and gene banks replace natural populations?

Uniqueness is the hallmark of nature from the gene through the organism, population, species, higher taxa and biological communities. Despite centuries of biological studies our knowledge of nature at the interfaces of genetics-ecology-demography-life - history- systematics and evolution are astoundingly little for most species in nature. No wonder that current theories of the twin evolutionary processes of adaptation and speciation are criticized so severely from multiple angles in the present decade. Nevertheless, the current dynamism of biological conservation as a vital interdisciplinary new field of research and practice, is of utmost and critical importance for wise management in an attempt to safeguard the future of life and man on this planet.

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ABSTRACT

Genetic diversity is central to the twin evolutionary processes of speciation and adaptation, in providing adaptability to changing environments, and in shielding individuals, populations and species against extinction. The levels of genetic diversity vary nonrandomly among populations, species, higher taxa and ecological, demographic and life history parameters, at the local, regional, and global scales (Nevo 1988b). Predicting the extinction of single populations and species requires ecological and evolutionary information. Evolutionary factors affecting the levels of genetic diversity include ecological (life zone, geographic range, habitat type and raging, aridity index, territoriality); demographic (population structure, species size, adult mobility and young dispersal, social structure); and life history (body size, longevity, generation length, origin, mating type, mode of reproduction, chromosome number etc.). Average allozymic heterozygosity, H, of 968 species across phylogeny is H = 0.073 (standard deviation 0.076). H is usually lower than the average in species characterized by the following conditions: living in narrower environmental spectra (e.g. arctic life zone, endemics, underground, arid climates, territorial), small species size, isolates, migratory, social, monogamous, large body size, long lived perennials, recent in origin, with high chromosome numbers, and selfers (Nevo *et al.*, 1984). These species are more vulnerable to extinction than their counterparts and include many of the current endangered species on Earth.

The new interdisciplinary field of conservation biology addresses the dynamics and survival of populations, species, communities and ecosystems in view of the catastrophic environmental changes caused by man. Empirical and theoretical considerations suggest that preserving and managing biodiversity in nature must be based on the interfaces of ecology, genetics, demography, and life history. The importance of preserving biodiversity and ecosystems in nature could not be overemphasized. It amounts to safefuarding the evolution of life and man on our planet.

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