Genic Variability and Strategies of Adaptation in Animals
(allozymes/heterozygosity/polymorphism/environmental grain)

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ABSTRACT  Levels of genic heterozygosity, as measured by surveys of allozymic variation, are much lower in populations of large, mobile animals (most vertebrates) than in those of small, relatively immobile animals (most invertebrates). This difference is not consistent with theories relating variability to population size (species number) or dispersal ability (gene flow), but it is predicted by Levins’ theory of adaptive strategies in relation to environmental uncertainty (“grain”). Mobility and degree of homeostatic control apparently are important factors influencing levels of genic heterozygosity in natural populations. The results argue indirectly that at least a major proportion of allozymic variation is maintained by natural selection.

Although classical research on viability and morphologic characters had suggested the existence of much cryptic genic variation in plants and animals (1), the concept of a high level of polymorphism as the usual condition in populations was not firmly established until 1966, when surveys of allozymic variation yielded direct estimates of genic heterozygosity (mean proportion of loci in heterozygous state per individual) for Drosophila pseudoobscura (2) and the British human population (3). Extrapolations from these and other surveys of electrophoretically demonstrable variation in proteins lead to the conclusion that most diploid organisms are polymorphic at thousands of structural gene loci and that every individual has a unique protein complement (4, 5).

The rationale behind the approach of estimating total genic heterozygosity in genomes by electrophoretic analysis of randomly selected samples of loci encoding enzymes and other proteins is discussed by Hubby and Lewontin (6). Because of our profound ignorance of the composition of genomes and, particularly, the number and proportion of structural genes (7), the degree of confidence to be attached to extrapolations from small samples of loci is uncertain. Additionally, the contribution of individual loci to estimates of overall heterozygosity is so variable (5, 8–10) that sampling error among loci undoubtedly is an important source of variation. Yet the general consistency of estimates for very different types of organisms suggests that they index some basic parameter of genetic variability. This idea is supported by recent demonstrations of positive correlations between degrees of morphologic and allozymic variability in some plants and animals (11).

Table 1. Estimates of genic heterozygosity per population

<table>
<thead>
<tr>
<th>Organism</th>
<th>No. of species</th>
<th>No. of loci</th>
<th>Heterozygosity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Invertebrates</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drosophila</td>
<td>19</td>
<td>11–33</td>
<td>0.145</td>
</tr>
<tr>
<td>Field cricket</td>
<td>1</td>
<td>20</td>
<td>0.145</td>
</tr>
<tr>
<td>Land snails</td>
<td>3</td>
<td>17</td>
<td>0.207</td>
</tr>
<tr>
<td>Horseshoe crab</td>
<td>1</td>
<td>25</td>
<td>0.097</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td></td>
<td>0.1507</td>
</tr>
<tr>
<td>Vertebrates</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish (Tetra)</td>
<td>1</td>
<td>17</td>
<td>0.112</td>
</tr>
<tr>
<td>Lizards</td>
<td>4</td>
<td>15–29</td>
<td>0.058</td>
</tr>
<tr>
<td>Sparrow</td>
<td>1</td>
<td>15</td>
<td>0.059</td>
</tr>
<tr>
<td>Rodents</td>
<td>14</td>
<td>18–41</td>
<td>0.056</td>
</tr>
<tr>
<td>Seal</td>
<td>1</td>
<td>19</td>
<td>0.030</td>
</tr>
<tr>
<td>Man (European)</td>
<td>1</td>
<td>70</td>
<td>0.067</td>
</tr>
<tr>
<td>Total</td>
<td>22</td>
<td></td>
<td>0.0584</td>
</tr>
</tbody>
</table>

Species and references: Drosophila pseudoobscura, D. persimilis, D. obscura, D. subobscura, D. willistoni, D. equinoxialis, D. paulistorum (23), D. tropicalis (10), D. melanogaster, D. simulans (8), and nine species of the D. virilis group (L. H. Throckmorton and J. L. Hubby, in preparation); Gryllus integer (Seland er, in preparation); Helix aspersa, Mesodon roemeri, and Rab dotus mooreanus (Kauffman and Seland er, in preparation); Limulus polyphemus (24); Astyanax mexicanus (25); Uta stans buriana, Sceloporus graciosus, S. grammicus, and Anolis carolinensis (26); Zonotrichia capensis (27); Dipodomys ordii and D. merriami (16), Eutamias panaminitinus Mus musculus, Sigmodon hispidus, S. arizonicus, Thomomys bottae, T. umbrinus, Peromyscus polionotus, and P. floridanus (28), P. leucopus and P. gossypinus (Smith, Seland er & Johnson, in preparation), Geomya persona andus, and G. arenarius (Kauffman et al., in preparation); Mirounga leonina (29); Homo sapiens (30).
average, and it is not unusual to find 10 or more alleles segregating at esterase loci (12). Proportions of polymorphic loci range generally from 10 to 20% in vertebrates and from 25 to 50% in invertebrates. Thus, several indices demonstrate a major difference in level of genic variability between vertebrates and invertebrates.

Clearly this difference cannot be related to dispersal ability, since both snails and flying insects are highly polymorphic. Nor is it likely that the difference can be related to total species number, following the argument of Kimura and Ohta (13), because the endemic Hawaiian species of *Drosophila*, which have numbers several orders of magnitude smaller than those of continental species, are on the average no less polymorphic (studies of 23 species by W. E. Johnson, personal communication). Even for the continental species of *Drosophila*, serious difficulties are encountered in attempting to explain observed levels of heterozygosity and the general geographic uniformity of allele frequencies in terms of genetic drift of neutral or nearly neutral alleles (14). For snails, with severely limited migration, the effective population size cannot be equivalent to the total species number or any significant part of it. In urban populations of *Helix aspersa*, for example, there is essentially no migration between colonies on adjacent city blocks (Selander and Kaufman, in preparation). If we exclude small insular populations and those having recently experienced severe reductions in numbers, there is no apparent relationship between level of genic variability and population size or extent of range (5, 15, 16).

The idea that types and levels of genetic variation in populations can be related to temporal and spatial patterns of environmental variation has been a persistent theme in evolutionary biology (17), although only recently have rigorous, quantitative statements and analyses of the problem been attempted. The theory of strategies of adaptation developed by Levins (18) in analyzing the effects of environmental uncertainty provides a general explanation for the observed variation in genic heterozygosity levels in animals and predicts in some detail the findings summarized in Table 1. The key point in his argument is that, primarily because of differences in mobility, small and large organisms tend to "experience" their environments differently. For small, relatively immobile organisms, environmental factors are experienced as sets of alternatives, and the environment is said to be "coarse-grained." Even if the proportions of the different environments are constant throughout the species range, the environment is uncertain for the individual. The notion of "grain" refers not only to sizes of patches of habitat relative to the size (and mobility) of the organism, but is generalized to include temporal and spatial variation in temperature, food, parasites, and other environmental factors. Levins argues that even when adults are mobile, as in *Drosophila* and other winged insects, the larval and pupal stages experience the environment as coarse-grained.

With increased mobility, environmental differences tend to become fine-grained, being experienced as a succession of many different conditions, the average of which is similar for all members of a population. The effective environment is therefore relatively less uncertain.

Physiological and behavioral homeostatic control of temperature, blood composition, and other internal conditions also increases the probability that the environment is experienced as fine-grained by buffering the individual against spatial and temporal changes. And for temperature and some other factors, larger size, itself, may increase homeostasis. Moreover, because the fitness set (an expression of individual developmental and functional tolerance relative to a range of environmental conditions) becomes more convex as homeostasis increases, there is a decreasing probability that adaptation will involve the maintenance of differentially adapted morphs. [Using a diffusion-model approach to explore relationships between genetic variability and environmental patchiness, J. Gillespie (in preparation) also has predicted that the likelihood of polymorphism in organisms decreases with increasing homeostatic control.]

Vertebrates, with generally larger body size, greater mobility, and greater homeostatic control, are expected to pursue a different adaptive strategy than invertebrates when the tolerance of the individual genotype is exceeded by the range of environmental conditions likely to be experienced ("concave fitness set" in Levins' terminology). For a population of organisms experiencing the environment as fine-grained, the optimum strategy is more often a single phenotype specialized to the most frequently encountered set of conditions. But a coarse-grained environment more often dictates a strategy in which specialized morphs occur in proportions dependent upon the frequencies of the different environmental patches. Thus, Levins' model predicts that the probability of the optimum adaptive strategy involving alternate or multiple phenotypic and genotypic equilibria decreases with increasing size and mobility, and that genetic polymorphism occurs less frequently in large, mobile organisms than in small, immobile ones. The estimates of genic heterozygosity in Table 1 are consistent with this prediction not only between vertebrates and invertebrates, but also within each group. The horseshoe crab, an unusually large invertebrate that is highly mobile both in developmental stages and as an adult, has an unusually low level of heterozygosity; and the very small fish (*Astyanax*) is more heterozygous than other, larger vertebrates. Apparently there is a threshold in size beyond which heterozygosity does not decrease, for men are no less polymorphic than mice.

Our discussion has been limited to animals, because reliable estimates of genic heterozygosity based on surveys of randomly selected loci are not presently available for plants. The balance of factors influencing genetic variability may be very different in plant populations for several reasons, including a stronger tendency for gametes and seeds to be dispersed randomly with respect to patch types in the environment (19), increased phenotypic flexibility (20), and greater diversity of breeding systems (21). Available data suggest that some species of plants have heterozygosity levels similar to those of the smaller animals. The work of R. W. Allard and his associates (22) has demonstrated extensive variability in the esterases, phosphatases, and leucine aminopeptidases of several grasses, including some predominantly self-fertilizing species. For two predominantly outcrossing species of *Lupinus* (Leguminosae) and two species of *Hymenopappus* (Compositae) assayed at seven loci, Babbel and Selander (in preparation) found an average heterozygosity of 0.216 (range, 0.10–0.36).

In conclusion, Levins' theory of adaptive strategies is supported by observed average differences in genic variability in populations of large-sized and small-sized animals. Inasmuch as an adaptive basis for monomorphism and polymorphism is the essence of Levins' theory, the correspondence of the data
to theoretical expectations argues indirectly that at least a major proportion of the allozymic variation in natural populations is maintained by natural selection.

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