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ENVIRONMENTAL HETEROGENEITY, GENETIC POLYMORPHISM,
AND REPRODUCTIVE STRATEGIES

The debate over the relationship between intrapopulation genetic variation and the degree of environmental heterogeneity is an enduring one (Valentine 1976; Templeton 1977; Powell and Wistrand 1978; Vrijenhoek 1978, 1979; Spieth 1979). Levins (1968), in a theoretical presentation, suggested that genetic variability would be higher in an unstable environment than in one that was more homogeneous. The hypothesis was that genetic variability would be required to accommodate variation in the environment. Modifications of this hypothesis have been presented as data on the genetics of populations has accumulated. For example, a great deal of variability has been found in populations of deep sea invertebrates (Ayala et al. 1974, 1975), where one would expect a relatively stable environment and hence, little intrapopulation variation. To account for the high variation, a relationship was suggested between trophic resource stability and population genetic variability that would allow specialists to subdivide the resource. Genic variation in populations has also been related to the size and mobility of the organisms; large, motile animals would pass over many microhabitats and would adapt as generalists (Selander and Kaufman 1973). Rigorous proof of a positive correlation between environmental heterogeneity and intrapopulation genetic variation is, however, still lacking. This is largely because of the difficulty of identifying and measuring variant environmental parameters, and the lack of comparisons of conspecific populations.

In addition, the relationship between environmental variability and reproductive strategies has received much attention. Classically, reproductive strategies have been interpreted in relation to r - and K -selection theory, which predicts that in stable environments the best strategy is to produce few young with high energy content (K -strategy) while the opposite strategy (r -strategy) would be optimum in a more variable environment. Recently, however, many examples have been given which do not conform to the classical r - and K -selection theory. Other theories to account for these variations have been published and are reviewed by Stearns (1976, 1977) and Calow (1973). Giesel (1976) indicates that little attention has been paid to the relationship between reproductive strategies and genetic variability.

For primarily inbreeding species, classical theory suggests a simple, highly structured genetic makeup. Each population consists of a number of inbred, monomorphic lines with most of the heterozygotes being found in the occasional hybrids between different monomorphic lines (Allard 1970; Hutchinson 1965). Experimental support for this theory has recently been found in both plants and animals (Rick and Fobes 1975; Selander and Hudson 1976). This report provides data on the relationship between environmental heterogeneity, genetic polymorphism, and reproductive strategies, for the freshwater clam *Musculium partumeium*.

TABLE 1
 ALLELIC FREQUENCIES FOR EACH POLYMORPHIC LOCUS IN TWO
 POPULATIONS OF *Musculium partumeium*

Locus	Allele	DW	AM
<i>PEP-3</i>	<i>a</i>	.26	...
	<i>b</i>	.72	1.00
	<i>c</i>	.02	...
<i>PEP-4</i>	<i>a</i>	.31	...
	<i>b</i>	.66	1.00
	<i>c</i>	.03	...
<i>EST-8</i>	<i>b</i>	.77	1.00
	<i>c</i>	.23	...
<i>PGI-1</i>	<i>d</i>	.98	1.00
	<i>e</i>	.02	...
<i>PGI-3</i>	<i>b</i>	.45	...
	<i>c</i>	.55	1.00

Sphaeriid clams (including the genus *Musculium*) are ovoviviparous and simultaneous hermaphrodites. It is known that these clams are capable of self-fertilization (Thomas 1959; Heard 1965) but the degree to which self-fertilization occurs in nature is not known. Self-fertilization potentially permits a single individual to establish a new population after passive dispersal by waterfowl and/or aquatic insects (Rees 1965; Mackie 1979). However, dispersal mechanisms provide a potential means of genetic input to the population on a continuing basis. Recently, in a study of the related genus *Sphaerium*, inbreeding with occasional outcrossing was suggested as the major mode of reproduction (Hornbach et al. 1980a).

Individuals of *Musculium partumeium* were collected from two locations in west-central Ohio. The first site was an ephemeral pond located on a virgin stand woodlot (Drew Woods=DW). The second site was a permanent (remaining full on a seasonal basis) pond formed approximately 20 yr ago by damming a stream which drained a marsh (Aullwood Marsh=AM). Care was taken to collect individuals from a large area at each site to minimize the possibility of sampling a single genetic cohort. Standard techniques of horizontal starch gel electrophoresis and histochemical staining were employed (Selander et al. 1971; Ayala et al. 1972).

Ten enzyme systems (isocitrate dehydrogenase, phosphoglucomutase, acid phosphatase, xanthine dehydrogenase, glutamate oxaloacetate transaminase, catalase, peptidase (PEP), phosphoglucose isomerase (PGI), esterase (EST), and nonspecific protein) encoding 22 presumptive genetic loci were consistently resolved. If several forms of the same enzyme were present and each was controlled by a separate gene locus, a hyphenated numeral was added to the abbreviation for the enzyme. The enzyme with the greatest anodal migration was called 1, the next 2, and so on. When allelic variation occurred, the allele with the greatest anodal migration was called *a*, the next *b*, and so on. Five loci (*Pep-3*, *Pep-4*, *Est-8*, *Pgi-1*, *Pgi-3*) were polymorphic in samples from the ephemeral pond. The collection from the permanent pond, however, was completely monomorphic at every locus. The allelic frequencies at each of the polymorphic loci are given in table 1.

TABLE 2
GENETIC VARIATION IN TWO POPULATIONS OF *Musculium*

	DW	AM
<i>n</i>	49	45
% heterozygosity	6.14	0
% polymorphism*	18.18	0
% polymorphism†	22.72	0

* Mean percentage of loci polymorphic per population where the most common allele has a frequency of .95 or less.

† Mean percentage of loci polymorphic per population where the most common allele has a frequency of .99 or less.

Percent heterozygosity (table 2) suggests that there is some outbreeding in the ephemeral site, although this is limited in its occurrence. Nei's (1972) standard genetic distance (an estimate of the number of electrophoretically detectable codon differences per locus) between the two populations is 0.0198.

In terms of the genetic structure of the two populations, the population from the ephemeral habitat is much more variable than the one from the permanent pond. Passive dispersal is undoubtedly a mechanism for genetic input into both ponds (Rees 1965; Mackie 1979). However, gene frequencies are probably not due to passive input, but instead the result of environmental pressures. Further, the percentage of polymorphic loci and heterozygosity indicate that several genetic lines exist in the ephemeral population. The low amount of heterozygosity, however, suggests that self-fertilization or inbreeding within lines is the rule and that outbreeding between lines occurs only rarely. This idea is further supported by the fact that genotypic frequencies for only one polymorphic locus (*Pgi-1*) are in Hardy-Weinberg equilibrium. That this one locus is in equilibrium is most easily explained as a chance event.

To relate the genetic data to reproductive strategies it is necessary to outline briefly the life histories of the two populations (see Hornbach et al. 1980*b*; and Way et al. 1980 for a more complete description). The ephemeral pond (DW: pond surface area 1,042 m²; maximum depth 0.9 m) usually has a single generation per year. Young are born in the spring and early summer (May–July), remain dormant as juveniles in the dry substrate (August–January), begin growth in March, reproduce, and then die when the pond dries in late summer.

The permanent pond (AM: pond surface area 396 m²; maximum depth 0.7 m) has two generations per year. The first generation is born between May and July (AM-SG). These individuals grow during August and September and then give birth between September and November. Some adults of the spring generation overwinter and contribute to the next spring generation. Young of the fall generation (AM-FG) overwinter as subadults and experience rapid growth and reproduction in the spring. Most of the fall generation die by the end of July, but some survive to contribute to the new fall generation.

Life-history parameters for these populations (from Hornbach et al. 1980*b*; Way et al. 1980; unpublished data) indicate that they do not support *r*- and *K*-se-

lection theory. The annual selection ratio (no. of young born per average adult) for the ephemeral pond, DW (25:1), is lower than for either generation from the permanent pond, AM (38:1 and 136:1 for AM-FG and AM-SG, respectively); however the energy content for newborns from DW (37.03 μgC) is greater than for newborns from AM (21.82 and 24.21 μgC for AM-FG and AM-SG, respectively). The intrinsic rate of increase (r) for DW (0.0084 day^{-1}) is lower than for AM (0.0115 day^{-1} and 0.0304 day^{-1} for AM-FG and AM-SG, respectively). In terms of productivity, the turnover time (time needed for the population to produce the average standing crop biomass) for DW (73 days) is greater than for AM (36 and 61 days for AM-FG and AM-SG, respectively) indicating that productivity is lowest in the temporary pond (DW). Two theories deal specifically with the effect of environmental stability on the evolution of life-history traits. One theory (a deterministic theory) proposes that populations inhabiting stable environments tend to have low intrinsic rates of increase, with few young of high energy content (K -strategy), whereas those populations which inhabit more variable environments tend to have higher intrinsic rates of increase, with more young of lower energy content (r -strategy). The other theory (a stochastic theory) holds that when juvenile mortality fluctuates more than adult mortality, the combination of life-history traits expected with the deterministic theory (r - and K -selection) will be reversed. The stochastic theory (not r - and K -selection) probably applies to the populations of *M. partumeium* at AM and DW. In the ephemeral pond, mortality for adults is probably less variable than for juveniles since the majority of adults die over a relatively short period of time (several weeks) as the pond dries, while juvenile mortality extends over many months. Thus, the ephemeral nature of the pond at DW probably results in mortality varying more for juveniles than adults and could reverse the reproductive tactic predicted by r - and K -selection theory. These findings support a bet-hedging strategy put forth by Stearns (1976, 1977) rather than r - and K -selection theory.

It would seem obvious, then, that the population in the ephemeral pond is adapted to its habitat on several levels. Genetically, the population supports a high amount of variability (relative to the AM population). This presumably allows the population to remain adapted to the harsh conditions and also possibly subdivide the habitat so that different monomorphic genetic lines become, in effect, specialists. Reproductively, the population opts for quality over quantity. By endowing the young with a high energy content, they are prepared to endure a harsh winter in a dry pond. It appears that this adaptation is, at least partly, on a phenotypic level. This is suggested by the fact that in the odd year when the pond at Drew Woods does not dry, a second generation can be produced in the fall. This pattern is like that for the population in the permanent pond (AM). However, only 19% of the spring-born clams at DW grew in late summer to produce the second generation in the fall of 1979 when the pond remained full.

The population from the permanent pond has exploited its environment by taking the opposite tactic. This population has introduced a highly productive second generation each year and has spread out the available reproductive energy to many young. Also, in view of the potential of continued genetic input through passive dispersal, the monomorphism exhibited by this population indicates that

the genetic composition has been streamlined by selection; the reproductive strategy of self-fertilization helps to maintain this genetic uniformity.

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