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THE LIMITS TO LIFE HISTORY EVOLUTION IN *DAPHNIA*

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Although evolutionary ecologists have studied variation within and between populations for some time, the variation reported in nearly all ecological investigations is restricted to the phenotypic level. In many cases this type of information is entirely adequate for solving ecological problems. However, because the phenotypic variance for characters can often be largely or even entirely attributed to environmental effects, a comparison of phenotypes is often an inappropriate evolutionary analysis. The concoction of evolutionary explanations from ecological data with little regard for genetic constraints has attracted some rather severe criticism (Gould and Lewontin, 1979) that is well supported on theoretical grounds (Lande, 1979, 1980, 1982; Templeton, 1981). If we are to understand the adaptiveness of morphological and behavioral characters and their potential for evolutionary change, it is imperative that we begin to evaluate the relative contribution of genetic effects to the variance of characters as well as the mechanistic and quantitative relations of characters to fitness and to each other via linkage disequilibrium and pleiotropy. Data of this type have been slow in com-

ing for natural populations (Istock et al., 1976; Derr, 1980; Giesel and Zettler, 1980; Arnold, 1981; Dingle and Hegmann, 1982) and, for practical reasons, may be nearly unattainable for many of the organisms upon which evolutionary ecologists have focused research.

One organism that is particularly suitable for genetic as well as ecological analysis and that may help shed some light on the limits to phenotypic evolution is the planktonic cladoceran, *Daphnia pulex*. This small (1-3 mm) crustacean reproduces by a non-recombinational mode of parthenogenesis during most of the year. *Daphnia* populations are often annually initiated by resting eggs produced sexually in previous years, and almost always consist of a multitude of genetically unique clones that differentially expand depending upon their fitness attributes. As parthenogenesis may proceed without disturbance for >10-25 generations and generation times are short (10-20 days), an excellent opportunity is provided for examining the operation of selection on a group of constant genotypes.

Here I examine the genetic basis of fitness characters in a *Daphnia pulex* population inhabiting an intermittent wood-

land pond (Busey Pond, Illinois). An analysis of the temporal dynamics of polygenic variation is used to derive minimal estimates of the intensity of natural selection operating on this population during the unisexual phase and to determine the potential phenotypic response to clonal selection. The analytical techniques that I employ are derived from standard quantitative genetics theory (Lande, 1977; Falconer, 1981; Lynch and Gabriel, 1983), although this appears to be their first detailed extension to unisexual populations.

Although all of the *Daphnia* in the study population are taxonomically referable to *Daphnia pulex* (Brooks, 1957; Dodson, 1981), electrophoretic data indicate that the population actually consists of three clonal groups that are nearly completely reproductively isolated (Lynch, 1983, 1984). Thus, while from an ecological perspective, all of the *Daphnia* in this population appear to be functionally similar and exposed to identical selection pressures, any interpretation of phenotypic evolution for a population with this type of structure necessitates the analysis of data at two levels of organization: the total population level and the clonal group level. Note that I use the word population in a liberal sense, as most zooplankton ecologists would, to refer to the total assemblage of *Daphnia pulex* in the pond without respect to genetic background.

Clonal group *A* contains obligate parthenogens only, nearly all of which are electrophoretically identical at 18 structural gene loci; its members never produce males and produce their resting eggs asexually. Groups *B* and *C* are cyclically parthenogenetic and probably consist of thousands of clones during most periods of clonal reproduction (Lynch, 1984); during periods of resting egg production, mating is approximately random within these groups (Lynch, 1983, 1984). Because the pond dried during each summer of this study, each year's population was initiated entirely from resting eggs. The minimum number of new clones hatching from the sediments

each spring is on the order of 10^5 (Lynch, 1984). Since all of these, with the exception of group *A* eggs, must be genetically unique, the potential for genetic variability in this population is quite high.

THEORY AND METHODS

The following derivations apply to any group of clones that maintain their genetic integrity between generations. Letting the phenotypic value of individual *i* be $z_i = (g_i + e_i + \alpha)$ where g_i is the genotypic value, e_i the environmental effect, and α the baseline value of the character, the total phenotypic variance (V_T) of a clonal population can be partitioned into three major components:

$$V_T = V_g + 2\text{Cov}_{ge} + V_e \quad (1)$$

V_g being the total expressed genetic variance, Cov_{ge} the genotype-environment covariance, and V_e the environmental effects variance (Falconer, 1981). In the absence of information on the allelic states of individual loci encoding for characters, the genetic variance within a unisexual population cannot be further partitioned into its additive, dominance and epistatic components. Cov_{ge} is also generally unmeasurable and treated as a contribution to V_e . The environmental variance, however, may be expressed as the sum of a within-clutch (V_c) and a residual environmental (V_r) component. V_c is the variance among individuals coming from the same clutch of the same mother, this being the minimum possible value of V_e . V_r accounts for the genotype-environment covariance as well as any maternal effects (including the transmission of environmental effects through lineages that have lived in different environments, and parental age effects).

Rearranging (1) the expressed genetic variance for a character is

$$V_g = V_T - V_c - V_r$$

so that heritability in the broad sense may be estimated by

$$H^2 = \frac{V_g}{V_T} = \frac{V_T - V_c - V_r}{V_T} \quad (2)$$

Although heritability is normally calculated as the ratio of additive genetic to total phenotypic variance in bisexual populations, the resemblance between relatives in a unisexual population is a function of the total expressed genetic variance because individuals are effectively linkage groups for the entire genotype.

To estimate the relative importance of the components of phenotypic variance and covariance of fitness characters in the Busey Pond *Daphnia* population, 50–200 gravid females were isolated in the laboratory on two occasions in 1980 and five times in 1981. These were maintained in an environmental chamber under pond light and temperature conditions, each individual being isolated in 40 ml of pond water with fresh water being substituted every other day. Upon the release of these clutches, one or more daughters of each female were then isolated from each other, treated as above, and as they matured, measured under a Wild M-8 dissecting microscope for size at maturity (B_k), age at first reproduction (k), size of the first two clutches (C_1 and C_2) and mean offspring size for the first two clutches (B_{01} and B_{02}). Those animals producing resting eggs were scored as having clutches of zero. An identical procedure was followed for offspring from the first clutches of each member of this laboratory generation. (A slightly different protocol was followed in 1980 when the second laboratory generation was established in all cases from clutches carried by mothers aged 24–25 days, and B_{02} was not measured.)

The raw data for sizes at birth and maturity (mm) and age at first reproduction (days) were generally normally distributed, but distributions of clutch size measures were often significantly skewed. The application of a square root transformation generally was successful in normalizing the distributions of C_1 and C_2 , and all analyses on these two variables involve square-root transforms.

Time constraints made it impossible to raise multiple sibs from all families to

TABLE 1. Within-clutch coefficients of variation (CV_c) and ratios of residual environmental to within-clutch variance (V_r/V_c) for five life history characters in the Busey Pond *Daphnia pulex* population. n_i and n_r are the total numbers of individuals and families used in the estimation of CV_c . CV_c^2 is the within-clutch variance on the natural logarithmic scale.

Trait	Within-clutch variance			Residual environmental variance
	n_i	n_r	CV_c	V_r/V_c
B_{01}	359	147	.0418	.177
B_{02}	217	81	.0436	.350
B_k	538	182	.0450	.301
k	531	182	.0825	.175
$\sqrt{C_1}$	498	177	.1722	.154
$\sqrt{C_2}$	431	161	.1516	.287

estimate V_c . Instead, the within-clutch variance was measured for 3–44 families during each experiment, each family consisting of 2–12 sibs from the same clutch all maintained in separate beakers. A subsequent analysis of variance on each character revealed that the within-clutch coefficient of variation ($CV_c = V_c^{1/2}/\bar{z}$) was homogeneous with respect to time and clonal group. Therefore, the family data from the entire study were pooled, natural log-transformed, and subjected to an analysis of variance with family as a factor. The square root of the error mean square was then used as an estimate of CV_c on the normal scale of measurement (Wright, 1968), and the within-clutch variances for each character/experiment were estimated by

$$V_c = (\bar{z} \cdot CV_c)^2.$$

The estimates of CV_c appear in Table 1.

Estimation of the residual environmental component of variance is difficult as it requires an experimental design in which the individual clones are replicated into sublimes (Lynch, unpubl.). In the following I rely on estimates of the ratio V_r/V_c determined for a Busey Pond *A* clone using such an analysis (Lynch, unpubl.). The values of V_r/V_c for the six life history traits in this study fall within the narrow range of .15–.35 (Table 1).

Such consistently low values for V_r/V_c suggest that although maternal effects may be modifying the expression of characters in this population, they do not greatly influence the phenotypic variance and hence will not significantly influence a quantitative genetics analysis. A similar conclusion can be derived from early work on the daphnid *Simocephalus vetulus*. Agar (1913) discovered that maternal effects are transmissible for up to three generations in this species. Yet, using an experimental protocol similar to the one employed here, he found, for sizes at both birth and maturity, that the correlation coefficients from regressions of offspring phenotype on parental, grandparental, great-grandparental, and great-great-grandparental phenotype were all virtually identical (Agar, 1914). If maternal effects exerted through maternal body size were an important source of parent-offspring resemblance (as they often are in vertebrates, Falconer, 1981), Agar should have noted a decline in the correlation coefficient as the number of generations separating relatives increased.

Thus, it does not appear that the following analyses would have been greatly affected if V_r had been ignored. Nevertheless, it is possible that V_r in a mixed clonal population will exceed that for a single clone, in which case my use of the ratios in Table 1 to calculate V_r resulted in underestimates of the environmental component of variance. Therefore, to be on the conservative side, the genetic variance estimates reported here are best viewed as upper limits.

Finally, some attention needs to be given to the estimation of V_T . Because individuals in a given experiment were never all born on the same day, but over a period of 2–8 days depending on the temperature, they were potentially subjected to slightly different temperature and food schedules. Under these conditions, pooling the data from all individuals from a generation would overestimate the phenotypic variance expected for a cohort of individuals all subjected

to identical conditions. To counter this problem, the total data set for each generation/experiment was subjected to a one-way analysis of variance with date at birth as a factor, and the error mean square was used as an estimate of V_T . This procedure has the effect of adjusting the data to provide estimates of V_T that would be expected for a cohort of synchronized individuals living in a realistically temporally variable environment. Such an analytical protocol is essential for most natural populations because the sudden transition to rigidly controlled temperature and food conditions could result in the selective elimination of some genotypes.

By electrophoretically assaying all of the clones in this study at five diagnostic loci (Lynch, 1983, 1984), it was possible to assign them to their respective clonal groups and to subsequently determine the proportion of phenotypic variance attributable to differences between groups. The quantity,

$$H_B^2 = \frac{V_B}{V_T},$$

where V_B is the between-clonal group variance, is a measure of population heritability. For each generation/experiment nested analyses of variance were performed with date and clonal group within date as factors. V_B was calculated from the ANOVA table by the standard procedure,

$$V_B = \frac{MS_B - MS_E}{n},$$

where MS_B and MS_E are the mean square between-group and error terms, and n is the number of measures/clonal group (see Snedecor and Cochran, 1967, for derivation and details).

Originally, I included two generations in the experimental design in anticipation that V_T of the parents would exceed that of the offspring generation because of the potential for parental age effects and greater background variation in the maternal environment in the first generation. In retrospect, however, this was

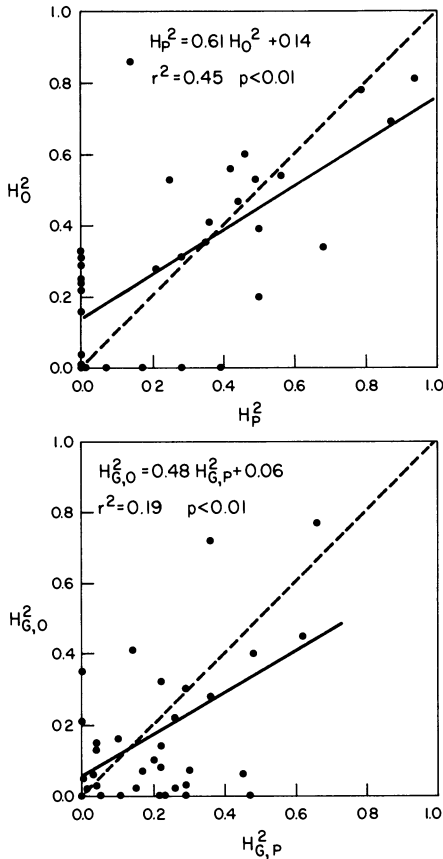


FIG. 1. *Top panel:* The relation between heritability estimates for parent (p) and offspring (o) generations of individual clonal groups. Only pairs of data for which parent and offspring sample sizes both exceeded 20 were included in the analysis. The dashed reference line is the expected pattern under perfect parent-offspring correspondence. *Lower panel:* The relation between estimates of population heritability, H_G^2 , for parent and offspring generations.

not found to be the case. Since there was no systematic bias in the estimates of H^2 or H_B^2 between generations (Fig. 1), the heritabilities reported below are the weighted averages of parent and offspring estimates. Of all the H^2 estimates resulting from the application of the above procedures and equation (2), one negative value was obtained for B_k , k , and $\sqrt{C_1}$ at the total population level. A few additional negative estimates of H^2 were obtained at the clonal group level, pre-

sumably because of smaller sample sizes. None of the H_B^2 estimates were negative. All $H^2 < 0$ were assumed to be equal to zero.

The constraints on life history expression in this population were further evaluated by considering the correlations between characters. The phenotypic correlation is simply based upon the covariance of characters (x and y) within individuals, $Cov_{T,xy}$:

$$r_{T,xy} = \frac{Cov_{T,xy}}{(V_{T,x} \cdot V_{T,y})^{1/2}},$$

where $V_{T,x}$ and $V_{T,y}$ are the phenotypic variances for characters x and y . The phenotypic covariances within each generation/experiment were taken from the error mean square matrix for a multivariate analysis of variance after factoring out date at birth (as described above for the univariate case). The parent and offspring phenotypic correlation coefficients were then pooled to give a single estimate of r_T following Snedecor and Cochran (1967).

r_T may be further partitioned into two components measuring the correlation due to genetic effects (pleiotropy and linkage disequilibrium), r_g , and to environmental effects, r_e . For a clonal population, the covariance between characters within a sib-group can only be due to environmental effects. Thus, the environmental correlation between characters can be estimated by

$$r_{c,xy} = \frac{Cov_{c,xy}}{(V_{c,x} \cdot V_{c,y})^{1/2}}$$

where $Cov_{c,xy}$ is the covariance of characters x and y within individuals of the same clone. I assumed that r_e is time-independent and calculated $r_{c,xy}$ for each clonal group from the error mean square matrix for a multivariate analysis of variance on the multiple-sib data set described above (with family as the single factor as in the univariate case).

Finally, under the assumption that $r_e = r_c$, a derivation similar to that provided by Falconer (1981) for bisexual populations gives the genetic correlation,

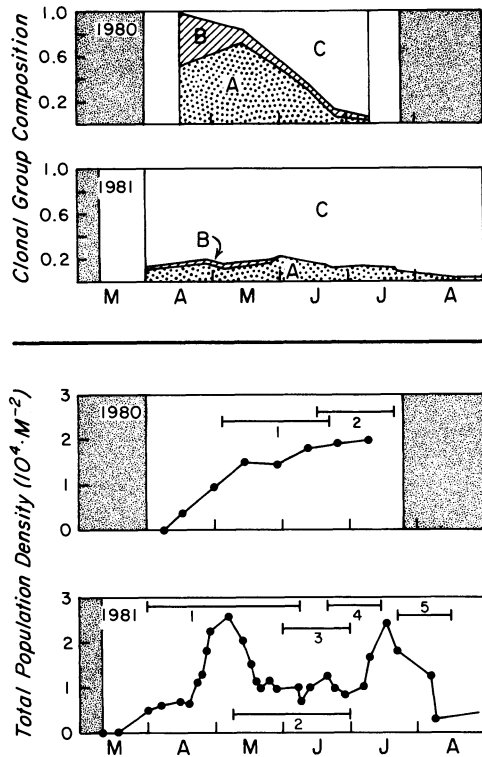


FIG. 2. *Top panel:* Clonal group composition (A, B and C) of the Busey Pond *Daphnia pulex* population in 1980 and 1981. Shaded areas represent periods when the pond was dry. *Lower panel:* Total population density (m⁻²) plotted as sliding three point averages to smooth the data. Dates for the start and completion of the two (1, 2) 1980 and five (1-5) 1981 experiments are also given.

$$r_{g.xy} = \frac{r_{T.xy} - r_{c.xy}[(1 - H_x^2)(1 - H_y^2)]^{1/2}}{H_x \cdot H_y}$$

where H_x^2 and H_y^2 are the broad-sense heritabilities of the two traits.

RESULTS

Components of Phenotypic Variance.—The starting and ending dates for the seven experiments and the total population densities and clonal group compositions associated with them are given in Figure 2. The temporal sequence of events in the population differed greatly between years. In 1980, as in previous years (Lynch, 1983), there was a seasonal succession from group A to group C, and

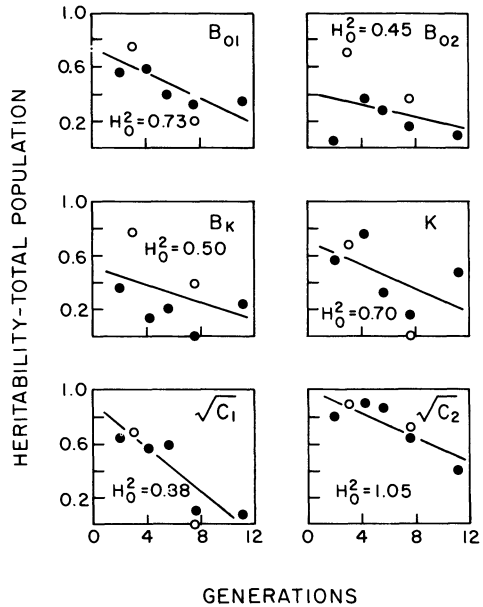


FIG. 3. Estimated values of H^2 measured at the total population level as a function of the approximate number of previous generations of uninterrupted clonal growth. Open circles are for the two 1980 measures, closed circles for the 1981 measures. The six characters are: B_{01} , B_{02} —mean sizes of offspring in the first and second clutches, B_k —size at maturity, k —age at first reproduction, $\sqrt{C_1}$, $\sqrt{C_2}$ —sizes of the first two clutches (square root transformation). H_0^2 , the estimated heritability at the onset of the growing season, is the intercept of the linear regression of H^2 on generation number. The correlation coefficients for the regressions are: B_{01} , $-.76$ ($P < .05$); B_{02} , $-.38$ (NS); B_k , $-.41$ (NS); k , $-.51$ (NS); $\sqrt{C_1}$, $-.86$ ($P < .01$); and $\sqrt{C_2}$, $-.87$ ($P < .01$).

the population size continuously increased until the pond dried. In 1981 group C dominated the population throughout the year, and population growth was oscillatory with early and late summer depressions.

Despite this dichotomy of events, several generalities emerge from an analysis at the total population level. Table 2 summarizes the phenotypic means and components of variance for the six characters, and Figure 3 illustrates the patterns of temporal change for the heritabilities. It is not surprising that there is considerable temporal variation in the

TABLE 2. Components of phenotypic variance for the analysis at the total population level, *Daphnia pulex*, Busey Pond. Subscripts *p* and *o* refer to parent and offspring generations. Significance of H_B^2 determined from the *F*-ratio; * and ** indicate $P < .05$ and $P < .01$, respectively.

Trait	Exp.	Sample size		Mean phenotype		Genetic variance		Environmental variance		Heritability	
		N_p	N_o	\bar{z}_p	\bar{z}_o	V_{gp}	V_{go}	V_{ep}	V_{eo}	H^2	H_B^2
B_{01}	1,1980	36	32	.645	.627	.00268	.00239	.00085	.00081	.754	.507**
	2,1980	38	29	.586	.615	.00021	.00012	.00070	.00078	.188	.103
	1,1981	98	51	.601	.596	.00092	.00110	.00074	.00073	.570	.070
	2,1981	50	29	.602	.592	.00119	.00086	.00074	.00072	.591	.292
	3,1981	91	81	.603	.602	.00078	.00032	.00075	.00074	.411	.023
	4,1981	117	101	.598	.603	.00047	.00027	.00073	.00075	.333	.169
	5,1981	114	93	.600	.604	.00038	.00041	.00074	.00075	.347	.090
	B_{02}	1,1980	34	—	.656	—	.00265	—	.00111	—	.706
2,1980		27	—	.612	—	.00057	—	.00096	—	.371	.336**
1,1981		68	27	.614	.601	.00000	.00021	.00097	.00093	.053	.179
2,1981		31	22	.605	.572	.00028	.00112	.00094	.00084	.371	.552*
3,1981		70	69	.583	.602	.00034	.00040	.00087	.00093	.289	.146
4,1981		105	82	.596	.601	.00013	.00020	.00091	.00093	.147	.126
5,1981		109	84	.598	.634	.00016	.00000	.00092	.00103	.084	.150
B_k		1,1980	82	22	1.707	1.726	.02472	.04535	.00769	.00783	.782
	2,1980	94	40	1.570	1.559	.00833	.00020	.00650	.00641	.403	.151
	1,1981	112	82	1.622	1.554	.00826	.00085	.00694	.00637	.363	.164
	2,1981	59	34	1.601	1.497	.00000	.00364	.00676	.00591	.139	.191
	3,1981	110	84	1.546	1.483	.00021	.00473	.00631	.00580	.213	.086*
	4,1981	117	108	1.581	1.573	.00000	.00000	.00659	.00653	.000	.268**
	5,1981	114	93	1.566	1.591	.00220	.00225	.00647	.00668	.253	.284**
	k	1,1980	82	22	11.951	10.409	3.8716	.5343	1.1411	.8657	.689
2,1980		94	39	10.479	7.400	.0000	.0000	.8773	.4375	.000	.037
1,1981		112	82	16.830	16.341	2.9046	2.9729	2.2630	2.1334	.571	.014
2,1981		59	34	22.805	15.294	14.7604	5.4735	4.1551	1.8688	.767	.000
3,1981		110	84	12.873	10.905	.4997	.6335	.3240	.9501	.329	.044
4,1981		117	108	9.235	7.981	.0000	.2798	.6814	.5089	.170	.237**
5,1981		114	93	8.482	8.220	.6744	.4077	.5748	.5398	.491	.055
$\sqrt{C_1}$		1,1980	82	22	1.510	2.452	.5420	.0000	.0780	.2056	.689
	2,1980	94	40	2.575	2.315	.0000	.0000	.2268	.1833	.000	.065
	1,1981	112	82	1.876	1.772	.3557	.1143	.1204	.1074	.649	.203
	2,1981	59	34	1.374	1.516	.1899	.0332	.0646	.0786	.582	.178
	3,1981	110	84	1.609	1.620	.1916	.0984	.0885	.0898	.614	.094
	4,1981	117	108	2.297	2.112	.0000	.0471	.1805	.1526	.113	.165
	5,1981	114	93	2.052	2.359	.0243	.0000	.1440	.1903	.079	.034
	$\sqrt{C_2}$	1,1980	82	22	1.529	2.132	1.0751	.4337	.0692	.1345	.903
2,1980		94	34	2.776	2.295	.6041	.4091	.2280	.1558	.726	.215**
1,1981		112	82	2.464	1.476	.5410	.4827	.1796	.0645	.806	.284
2,1981		59	34	1.020	1.333	.5812	.3046	.0308	.0526	.914	.126
3,1981		110	84	1.367	1.919	.6312	.4405	.0553	.1090	.868	.125*
4,1981		116	108	2.660	2.034	.3177	.2535	.2093	.1224	.637	.320**
5,1981		114	93	2.421	2.914	.0944	.2131	.1734	.2512	.400	.182

mean phenotypic value of all the fitness traits examined, since all are dependent on temperature and food availability (Bottrell et al., 1976) both of which were allowed to vary naturally in the experiments. However, irrespective of the direction of change in the mean pheno-

types, the genetic variance and heritability of each character exhibit a decline within both years. Moreover, the seasonal erosion of expressed genetic variance in 1980 does not appear to be reflected in the level of genetic variance at the onset of the following growing season. Despite the

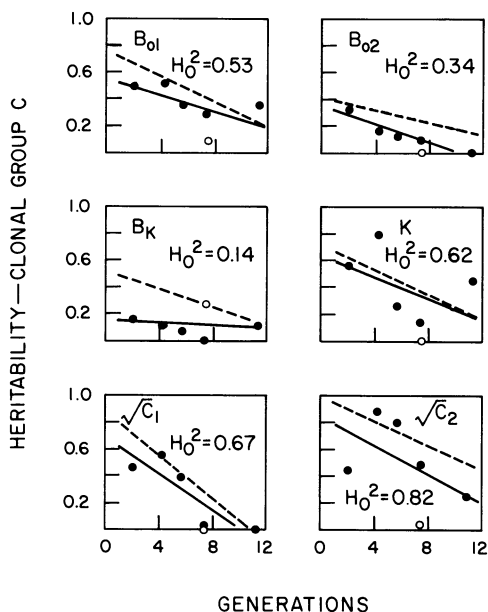


FIG. 4. Heritability estimates for clonal group C as a function of the approximate number of previous generations of uninterrupted clonal growth, as in Figure 3. For reference, the total population regressions from Figure 3 are given as dashed lines. The correlation coefficients for the group C regressions are: B_{01} , $-.58$ (NS); B_{02} , $-.91$ ($P < .01$); B_K , $-.09$ (NS); k , $-.44$ (NS); $\sqrt{C_1}$, $-.85$ ($P < .05$); $\sqrt{C_2}$, $-.53$ (NS).

small sample sizes, three of the six linear regressions of H^2 on generation number in Figure 3 are significant at the .05 level, and as a group, they suggest that 45–100% of the phenotypic variance for fitness characters is heritable at the onset of the growing season. These are extremely high heritability levels for characters related to fitness (Falconer, 1981).

The dynamics of genetic variance in this population are not simply a consequence of temporal changes in clonal group composition since both it (Fig. 2) and the between-group component of phenotypic variance (Table 2) were relatively constant in 1981. Moreover, the seasonal trends in the group C heritabilities are essentially the same as those for the total population except that the latter are somewhat higher because of their in-

corporation of phenotypic differences between clonal groups (Fig. 4).

Comparison of Clonal Groups.—A significant proportion of the phenotypic variance in this population is accounted for by differences between groups (Table 2). Members of clonal group A consistently mature at a larger size and later age and produce smaller clutches of larger progeny than those of clonal groups B and C (Table 3). Similar results were obtained in earlier work (Lynch, 1983).

Unlike the seasonal erosion of heritability measured at the individual level, the relative proportion of between-group variance did not exhibit a general decline within years (Table 2). Significant declines in H_B^2 were observed in 1980 when a major shift in clonal group composition occurred, but the ratio appeared to be temporally stable in 1981. With the possible exception of B_{01} , there is a general tendency for the mean phenotypes of clonal groups A and C to exhibit temporal changes in the same direction (compare exps. 1, 2, and 3, 1981, Table 3), but the changes cannot be described as convergent.

Although several of the sample sizes for clonal group A are small, the data set in Table 3 provides an exceptional opportunity to test the frequent assumption that the evolutionary rate of obligate parthenogens is severely constrained relative to that of bisexual organisms because of a restricted reservoir of genetic variance. Of the 24 heritability estimates for obligately parthenogenetic group A, 15 were higher than those obtained for the coexisting cyclically parthenogenetic race ($\chi^2 = 1.500$, NS). These results are inconsistent with the notion that obligate unisexuality is an evolutionary dead end (Darlington, 1939; Mayr, 1970; Uzzell, 1970; White, 1973; Maynard Smith, 1978).

Correlations Between Characters.—The existence of genetic variance is not a sufficient condition for the evolution of a character even if it is exposed to intense selection. Negative genetic covariance of two traits that are each positively cor-

TABLE 3. Phenotypic means (\bar{z}), coefficients of variation (CV_T), and heritabilities (H^2) determined as weighted means for parent and offspring generations for individual *Daphnia pulex* clonal groups, Busey Pond. N is the total of the parent and offspring sample size. The cyclical parthenogen is group B in exp. 1, 1980 and group C in all other experiments.

Trait	Exp	Obligately unisexual group A				Cyclically parthenogenetic group			
		N	\bar{z}	CV_T	H^2	N	\bar{z}	CV_T	H^2
B_{01}	1,1980	30	.677	.063	.41	24	.592	.042	.00
	3,1981	32	.612	.069	.56	132	.600	.058	.35
	4,1981	15	.639	.034	.00	191	.597	.054	.28
	5,1981	15	.636	.063	.32	169	.598	.056	.34
B_{02}	1,1980	13	.722	.049	.00	19	.608	.069	.45
	3,1981	19	.614	.072	.44	115	.590	.054	.12
	4,1981	9	.641	.045	.00	169	.624	.047	.08
	5,1981	7	.653	.100	.74	162	.620	.042	.00
B_k	1,1980	57	1.853	.041	.09	40	1.505	.068	.62
	3,1981	41	1.580	.073	.65	145	1.503	.034	.30
	4,1981	16	1.664	.046	.34	197	1.572	.042	.14
	5,1981	15	1.745	.095	.80	169	1.562	.051	.27
k	1,1980	57	12.816	.104	.43	40	9.900	.105	.58
	3,1981	41	12.339	.131	.63	145	11.907	.097	.38
	4,1981	16	9.312	.067	.13	197	8.602	.088	.24
	5,1981	15	9.300	.134	.49	169	8.509	.121	.61
$\sqrt{C_1}$	1,1980	57	1.604	.587	.70	40	1.855	.162	.00
	3,1981	41	1.494	.446	.80	145	1.641	.236	.36
	4,1981	16	2.070	.117	.00	197	2.221	.175	.00
	5,1981	15	2.329	.273	.41	169	2.195	.177	.00
$\sqrt{C_2}$	1,1980	57	1.234	.771	.87	40	2.252	.258	.45
	3,1981	41	1.154	.781	.93	145	1.752	.399	.75
	4,1981	16	1.498	.803	.94	197	2.407	.241	.37
	5,1981	15	2.270	.379	.52	169	2.666	.198	.09

related with fitness can prevent both of them from responding to selection, as is amply demonstrated by the repeated observation of animal breeders that after characters have reached their selection limit, considerable genetic variation generally remains for the underlying components (Lande, 1982). Thus, any attempt to elucidate the limits to selection for an organism must consider the nature of the constraints between important fitness parameters.

For clonal groups A and C only two of the possible 126 comparisons for temporal changes in the phenotypic correlation coefficients exhibited significant sign changes. Therefore, a simple examination of the weighted, pooled coefficients (Snedecor and Cochran, 1967) taken over the entire study suffices to illustrate the general constraints on the

expression of life history characters in the different clonal groups (Table 4). The complete data set is available from the author. Sample sizes for clonal group B were not sufficient for the estimation of correlations between characters.

At the phenotypic level, both clonal groups exhibit significantly positive correlations between the sizes of offspring produced in the first two clutches, and between size at maturity and size of offspring in the first clutch but not the second clutch. The phenotypic association between these three body size measures is primarily a product of the environmental component of covariance. Moreover, this environmental correlation is much more pronounced in group A than in group C ; r_e for B_{02} and B_k is nearly 1.0 in group A but close to 0 in group C . In general the genetic constraints between

TABLE 4. Pooled phenotypic, environmental, and genetic correlation coefficients for life history traits in clonal groups *A* and *C*, *Daphnia pulex*, Buscy Pond. Significance levels are denoted by * ($P < .05$) and ** ($P < .01$).

Traits	Group A				Group C			
	<i>d.f.</i>	r_e	r_g	SE	<i>d.f.</i>	r_e	r_g	SE
$B_{01}; B_{02}$	29	.642**	.775*	.177	89	.254**	.282**	.092
$B_{01}; B_k$	80	.562**	.472**	.155	143	.485**	.211*	.361
$B_{01}; k$	80	.208	.650**	.314	143	.340**	-.060	.416
$B_{01}; C_1$	80	.196	.381*	.124	143	-.122**	-.097	.174
$B_{01}; C_2$	80	-.041	.285	.161	136	.018	-.036	.380
$B_{02}; B_k$	36	-.015	.927**	.239	100	.062	.019	.149
$B_{02}; k$	36	-.362*	.062	.313	100	-.041	.138	.222
$B_{02}; C_1$	36	-.187	.254	.235	100	-.067	.105	.299
$B_{02}; C_2$	36	-.428**	-.562	.253	100	-.264**	-.022	.100
$B_k; k$	117	.559**	.502**	.109	198	.411**	.489**	.118
$B_k; C_1$	117	.118	.190	.309	190	.407**	.259*	.187
$B_k; C_2$	117	-.223*	-.170	.340	190	.027	-.037	.264
$k; C_1$	117	-.161	.026	.268	190	.203**	.218**	.520
$k; C_2$	117	-.358**	-.090	.256	190	-.032	-.061	.273
$C_1; C_2$	117	.265**	.109	.092	190	.120**	-.072	.433

B_{01} , B_{02} , and B_k appear to be small, but there is a very strong positive genetic correlation between B_{02} and B_k in group *C*.

The expression of clutch size is also clearly related to other aspects of the phenotype. Both clonal groups exhibit a positive phenotypic correlation between the sizes of the first two clutches, largely as a consequence of the genetic component of covariance. Three of the four comparisons between size and number of progeny within clutches indicate a significant tradeoff at the phenotypic level due to both environmental and genetic effects; but a positive association between the environmental effects on B_{01} and $\sqrt{C_1}$ in group *A* results in their positive phenotypic association.

A positive correlation between B_k and k in both clonal groups results from positive genetic and environmental covariances. A positive phenotypic correlation also exists between B_{01} and k , but for substantially different reasons in each group. While there is no significant genetic correlation between these traits in group *A*, r_g is approximately 1.0 in group *C*. On the other hand, a significantly positive environmental correlation exists between B_{01} and k in group *A*, while it is nearly zero in group *C*. To add to the complexity, the phenotypic correlation between B_{02} and k tends to be negative largely because of a strong negative genetic covariance.

Another major difference between the clonal groups is the relation between k and $\sqrt{C_2}$. In both groups the environmental correlation is close to zero, but a significantly negative genetic covariance in group *A* results in their negative phenotypic association. The two traits are independently expressed in group *C* because the genetic covariance is essentially zero. On the other hand, k and $\sqrt{C_1}$ are uncorrelated in group *A*, but a significant positive association between the two traits exists in group *C* as a result of environmental covariance.

Attention could be called to other features of the covariance structure of these two clonal groups, but the central point

should be clear by now. Although there are similarities in the environmental and genetic constraints on life history expression in the two groups, there are also many striking dissimilarities. Therefore, the two groups cannot be expected to respond to selection in the same way.

The Intensity of Selection and the Short-term Limits to Phenotypic Evolution.—A progressive seasonal decline in genetic variance from a population that contains millions of individuals can only be accounted for by natural selection. Theoretical work suggests that selection on cladoceran life history traits will generally be of a stabilizing nature with a temporally variable optimum (Lynch 1977, 1980a, 1980b). This has been empirically supported by data on body size in the Busey population (Lynch, unpubl.). Conflicting selective pressures of vertebrate and invertebrate predators that respectively prefer large and small prey as well as size-related energetic constraints contribute to the shifting balance. Even where specific selective forces would seem to suggest that selection is of a purely directional nature, mutual constraints between size and age at maturity and offspring size and number and their relation to fitness will almost always result in intermediate optima for individual life history characters (Lynch, 1980b; Lande, 1982).

Selection of this nature is best approximated by a Gaussian fitness function with a variable optimum. Such a function has the property that, when applied to a population, it reduces the variance and/or alters the mean without influencing the normality of the distribution as is often observed in natural populations for characters measured on an appropriate scale. Except in cases of frequency-dependent selection, the mean multivariate phenotype in a population will always evolve in the direction of the local optimum (Lande, 1976b). Other forms of selection functions are possible, but in general they do not share the biologically realistic properties of the Gaussian, and in some cases, such as the pure exponential mod-

el, selection has no influence on the genetic variance of a population. Clearly that is not the case with the Busey Pond *Daphnia*.

Under Gaussian selection the dynamics of expressed genetic variance are dependent on the width (V_w) but independent of the optimum (θ) of the fitness function, and for unisexual populations are defined by

$$V_g(t+1) = V_g(t) + V_m - \frac{V_g^2(t)}{V_T(t) + V_w} \quad (3)$$

(Lynch and Gabriel, 1983), where V_m is the input of total genetic variance for the character per generation by mutation. Since V_w is directly related to the proportional selective mortality, S , in a population by

$$S = 1 - \left\{ \frac{V_w}{V_T(t) + V_w} \right\}^{1/2} \exp \left\{ - \frac{[\theta - \bar{z}(t)]}{2[V_T(t) + V_w]} \right\} \quad (4)$$

(Lynch and Gabriel, 1983), which is a minimum when $\theta = \bar{z}$, the solution of equation (3) for V_w can be used to estimate the minimum intensity of selection that is operating on a unisexual population. The impact of the selective load on the dynamics of a population depends on the effective fecundity of the population. If the product of mean progeny production of surviving individuals and the proportion of individuals surviving both selective and nonselective events is less than one, the population must decline.

Ideally, equation (3) should be solved in its multivariate form for the various V_w , since a decrease in the genetic variance of a character can result from selection acting directly on the character and/or indirectly on correlated characters. While the univariate solution of equation (3) will provide information on the total selection intensity on a character, it will

not discriminate the sources of selection. It is clear that all six of the fitness characters measured in this study are genetically correlated in one way or another, but the large standard errors for most of the genetic correlation coefficients (Table 4) preclude a precise assessment of the genetic covariance structure for this suite of characters. Moreover, it is likely that selection operates on other unmeasured traits in this population, which would thwart any multivariate analysis.

With the above in mind, I have opted to use the univariate form of equation (3) to gain some information on the intensity of selection required to account for the seasonal erosion in genetic variance observed in this study. While in theory the annual decline in genetic variance from a cyclically parthenogenetic population should follow an exponential approach to the equilibrium level expected for obligate parthenogenesis (Lynch and Gabriel, 1983), the initial decline will be approximately linear. Therefore, in order to calculate V_w for each character, I relied on heritability estimates for the 0th and 5th generations derived from the fitted regressions in Figures 3 and 4. Although the exact value of V_m is not known for any of the characters, it is almost definitely on the order of $10^{-3} V_e$ (Lande, 1977; Lynch, unpubl.), and could safely be ignored without significantly influencing the solution of equation (3) over a five generation period. After setting V_e equal to its value on the natural log scale (the square of CV_c in Table 1) to stabilize the variance, equation (3) was solved by iteration to give the value of V_w that accounts for the observed 5-generation decline in genetic variance.

The estimated values of V_w and their associated selective mortality rates are given for the total population and clonal group *C* in Table 5. With few exceptions, all of the observed reductions of V_g require a selective removal of 10–20% of the population per generation for the case in which the mean phenotype is at the optimum and selection is simply removing the excess variance around the mean.

TABLE 5. Estimated values of the width of the selection function, V_w , for six life history characters at the total population and clonal group *C* levels measured on the natural logarithmic scale. The percent selective mortalities that these values of V_w would cause in generations 0 and 5 are given for $|\theta - \bar{z}| = 0$ and $\sqrt{V_e}$. Because the heritability estimate for $\sqrt{C_2}$, total population, was >1.0 at generation 0, V_w is based on the change in V_g from generations 2 to 7; all other estimates are based on generations 0 to 5 as described in the text.

Trait	V_w	% Selective mortality			
		$ \theta - \bar{z} = 0$		$ \theta - \bar{z} = \sqrt{V_e}$	
		Gen. 0	Gen. 5	Gen. 0	Gen. 5
Total population					
B_{01}	.012	19	12	74	77
B_{02}	.009	15	13	85	86
B_k	.008	18	15	87	89
k	.043	19	12	57	58
$\sqrt{C_1}$.120	43	17	55	49
$\sqrt{C_2}$.281	—	16	—	30
Clonal Group <i>C</i>					
B_{01}	.011	14	11	79	80
B_{02}	.001	49	45	>99	>99
B_k	.009	11	11	88	88
k	.040	17	12	59	60
$\sqrt{C_1}$.070	34	22	61	63
$\sqrt{C_2}$.178	24	12	40	37

Since it is unlikely that \bar{z} is ever precisely equal to θ , the actual selective load on the population must exceed these minimum estimates, but without precise information on θ it is impossible to calculate the true selective load. If, however, the deviations between means and optima averaged as little as one environmental standard deviation (a few percent on the normal scale of measurement; Table 1) throughout the year, the selective mortality would be on the order of 70% of the population per generation (Table 5).

DISCUSSION

The dynamics of genetic variance observed in this population are qualitatively in agreement with theoretical expectations for cyclical parthenogens (Lynch and Gabriel, 1983). During a prolonged period of parthenogenesis, the expressed genetic variance of a population will be

TABLE 6. Estimated equilibrium levels of expressed genetic variance (\hat{V}_g) and heritability (\hat{H}^2) for group C life history characters expected under prolonged parthenogenesis; the minimum estimates of the factor, $V_g/(V_g + V_e + V_w)$, that determines the response to selection; the observed levels of expressed genetic variance at generation 5 ($V_{g,5}$) taken from Figure 4; and the estimated limits to the hidden genetic variance present at generation 5 (V_{gh}).

Trait	\hat{V}_g	\hat{H}^2	$\hat{V}_g/(\hat{V}_g + V_e + w^2)$	$V_{g,5}$	V_{gh}
B_{01}	.000150	.08	.012	.00112	.00114-.00171
B_{02}	.000075	.04	.025	.00038	.00081-.00121
B_k	.000151	.07	.014	.00028	.00005-.00008
k	.000568	.08	.012	.00499	.00802-.01203
$\sqrt{C_1}$.001733	.06	.017	.01480	.05977-.08968
$\sqrt{C_2}$.002161	.09	.011	.02914	.09983-.14978

gradually eroded by selection until a point is reached at which the output due to selection is balanced by the input via mutation. At the same time, hidden genetic variance in the form of negative covariances between the additive effects of alleles and non-alleles will continually approach its biological limits. This will necessarily occur in a clonal population as polygenic mutations randomly arise and selection sorts individuals on the basis of their phenotypes rather than individual alleles. Depending upon the recombination rate between loci, an intervening generation of sexual reproduction will suddenly convert 50–75% of the hidden genetic variance to expressed genetic variance (Lynch and Gabriel, 1983). For that reason, cyclical parthenogens are expected to have exceptionally high heritabilities following a phase of sex, and, when the periodicity of sex is regular and the width of the fitness function roughly constant, to exhibit cycles of expressed and hidden genetic variance. The seasonal patterns of H^2 shown in Figure 4 for the dominant cyclical parthenogen in Busey Pond, clonal group C, are consistent with these predictions.

The minimum level of expressed genetic variance that can be expected for a well-established cyclical parthenogen is the same as the equilibrium level of expressed genetic variance under obligate parthenogenesis defined by equation (3),

$$\hat{V}_g = \frac{V_m + \{V_m[V_m + 4(V_e + V_w)]\}^{1/2}}{2} \tag{5}$$

Since the dynamic expression for the evolution of the mean of a normally distributed character in a unisexual population under Gaussian selection is

$$\bar{z}(t + 1) - \bar{z}(t) = \frac{V_g(t)[\theta - \bar{z}(t)]}{V_g(t) + V_e + V_w} \tag{6}$$

(Lynch and Gabriel, 1983), a knowledge of \hat{V}_g is very useful. Through the factor $\hat{V}_g/(\hat{V}_g + V_e + V_w)$, \hat{V}_g defines the minimum response of a character to stabilizing selection under the assumption that the character does not negatively covary with other fitness traits.

Measures of V_m/V_e for corn, mice, *Drosophila*, and *Daphnia* are consistently near 10^{-3} (Lande, 1976a; Lynch, unpubl.). Therefore, I used equation (5) to estimate \hat{V}_g on the natural logarithmic scale for group C by setting $V_m = 10^{-3}V_e$ and substituting the estimates of V_e from Table 1 (squares of CV_e) and V_w from Table 5. The resultant minimum heritability estimates for life history traits in this population fall within the narrow range of .04–.09 (Table 6). Thus, the intensity of selection operating on clonal group C is of a magnitude such that fewer than 25 generations of uninterrupted clonal growth are sufficient to reduce the expressed genetic variance to the univariate levels expected under obligate parthenogenesis (Fig. 4).

The estimated values of $\hat{V}_g/(\hat{V}_g + V_e + V_w)$ for group C also fall within a narrow range, .011–.024 (Table 6). Therefore, since genetic tradeoffs in fitness components exist in the group C *Daphnia*, it appears that after about 25 generations

of continuous clonal selection, clonal group C would be capable of per generation rates of phenotypic evolution of no more than 2% of $\theta - \bar{z}$. These results are not an artifact of using a Gaussian selection function, as essentially the same conclusions were reached by using directional selection functions with fitness increasing linearly and with the square and cube of the phenotype.

Since \hat{H}^2 is relatively insensitive to variation in V_w/V_e over the range 10^{-1} – 10^2 (Lande, 1976a; Lynch and Gabriel, 1983), the limits to selection estimated for clonal group C may be close to what can be expected for many cladoceran populations, if V_w/V_e is commonly within about an order of magnitude of the observed values (range: .5–7.7). Close studies of permanent lake populations, in particular, often reveal little if any evidence of sexual reproduction, and it may not be uncommon for parthenogenesis to go uninterrupted for several years or hundreds of generations in such environments. Such populations should, therefore, be close to the levels of expressed genetic variance defined by equation (5).

In the long term, values of $V_g/(V_g + V_e + V_w)$ as low as .01 can, of course, give rise to substantial evolutionary change if θ is relatively stable and if the population can bear the load of the selection event. However, as can be seen from equation (4) and Table 5, the selective load is quite high even when $(\theta - \bar{z})$ is as small as $\sqrt{V_e}$ (or a few percent of the mean). Values of $(\theta - \bar{z})$ of one to several $\sqrt{V_e}$ are probably not uncommon for cladoceran populations that are exposed to substantial temporal variation in predator and food types and densities and physical factors (Lynch, 1977, 1980a, 1980b). Thus, observed per generation changes in mean phenotypes during a phase of parthenogenesis in cladocerans that are in excess of 1–2% and that are not accompanied by a decline in population size will almost always be a result of phenotypic plasticity (a change in α , the baseline value of the character) and not clonal selection. This does not imply that seasonal fluctuations

in θ will not be reflected in clonal succession, but simply that there will always be a substantial lag between the mean genotypic value of a clonal group and the optimum phenotype.

These results provide an evolutionary/genetic explanation of why cyclomorphosis (inter-generational, environmentally-induced morphological change) is so widespread among cladocerans (Dodson, 1974). If the major morphological changes often demanded by seasonal shifts in ecological factors cannot be met by clonal selection, a premium would be placed on those clones that could make such a switch via physiological mechanisms since they would not be in direct competition with specialized clones that were genetically preadjusted to the new environment. The results also have important implications for understanding the extreme fragility of lake ecosystems in which cladocerans play a central ecological role as consumers of algae and forage for fish and invertebrate predators. Since prolonged parthenogenesis will lead to populations consisting of a narrow range of genotypic values, it is not surprising that permanent lake cladoceran populations are extremely vulnerable to novel perturbations such as predator or nutrient introductions (Brooks and Dodson, 1964; Wells, 1970; Goldman et al., 1979; Lynch, 1979, 1983).

Although continuous clonal selection can quickly depress the heritabilities for life history traits in a cyclical parthenogen to levels expected under obligate parthenogenesis, periodic phases of sex will replenish the genetic variance through the recombination of alleles whose individual additive effects had been concealed by the clonal selection process. Moreover, this release of hidden genetic variance is expected to result in heritabilities following sex that are greater than those that would be found under obligate bisexuality (Lynch and Gabriel, 1983).

The importance of the release of hidden genetic variance even when sex occurs quite frequently is illustrated by the very high heritability levels in the Busey

population immediately following the hatching of resting eggs from previous years. The amount of hidden genetic variance in a population at the time of a recombinational event is

$$V_{gh} \approx \frac{2\Delta V_g}{1+r}, \quad (7)$$

where ΔV_g is the difference in expressed genetic variance between the sexual generation and that of its sexually produced progeny, and r is the recombination frequency with limits 0 and .5 (Lynch and Gabriel, 1983). Taking the average time of recombination to be about midway through the growing season (generation 5) and using the fitted values of V_g from Figure 4, I used equation (7) to calculate the limits to V_{gh} for clonal group C (Table 6). These estimates may be somewhat inflated if the pool of colonists each year derives from resting eggs produced in several preceding years. Nonetheless, with the exception of the values for B_k , all of the estimates of V_{gh} are larger than those of the expressed genetic variance during mid-season. Thus, to account for the sudden increase in heritability at the onset of the growing season, the amount of hidden genetic variance in this population must be of the same order of magnitude as the expressed genetic variance at the time of recombination.

Since the absolute amount of hidden genetic variance released by sex is proportional to the length of the phase of clonal selection (Lynch and Gabriel, 1983), other populations that engage in sex less frequently than the Busey population should occasionally exhibit heritabilities even higher than the H_o^2 values estimated in this study (Figs. 3 and 4). Based on these empirical results and the theoretical results of Lynch and Gabriel (1983), the heritabilities for life history traits of permanent lake populations following a rare phase of sex should be close to 1.0. Under conditions of intense selection on the progeny hatching from resting eggs, such high heritabilities can result in changes in \bar{z} of several phenotypic standard deviations in a single gen-

eration in large populations (Lynch and Gabriel, 1983). Thus, while populations of cladocerans in permanent lakes are expected to exhibit prolonged phases of evolutionary stability, on occasion they should also exhibit the most rapid rates of phenotypic evolution. In the long run more frequent release of genetic variance by sex is approximately balanced by a smaller reservoir of hidden genetic variance so that the potential long-term rate of phenotypic evolution is approximately independent of the periodicity of sex (Lynch and Gabriel, 1983).

Finally, this study has revealed that, in addition to selection within clonal groups, between-group selection provides a supplementary mechanism for phenotypic evolution in *Daphnia*. Indeed, considering the magnitude of phenotypic differences between clonal groups (Table 3) as well as the possible differences in their covariance structure (Table 4), the opportunity for clonal group selection greatly expands the evolutionary flexibility of *Daphnia* populations. The coexistence of multiple clonal groups is by no means unique to the Busey population. None of the six central Illinois *D. pulex* populations that we have now studied in detail consist of a single clonal group (Lynch, 1983, unpubl.; Weider, unpubl.), and several other detailed examinations of cladoceran genetics and/or morphology have revealed traditional taxonomic species to be complexes of cryptic species that in many cases coexist on a fine scale (Hebert, 1977; Manning et al., 1978; Dodson, 1981; Frey, 1982a).

Of special interest in the *D. pulex* complex is the existence of numerous obligately unisexual races, such as group A, which often coexist in the same pond with each other and/or with related cyclically parthenogenetic races (Hebert and Crease, 1980; Lynch, 1983). In theory, obligate unisexuals should contain much lower levels of genetic variance for polygenic characters than otherwise comparable cyclical parthenogens (Lynch and Gabriel, 1983). However, there is no evidence that obligately parthenogenetic

group *A* is exceptionally depauperate with respect to genetic variance for quantitative characters (Table 3). The mechanism responsible for generating the genetic variance in group *A* is not revealed at the electrophoretic level since almost all group *A* individuals are electrophoretically identical (Lynch, unpubl.). Polygenic mutation is undoubtedly involved. However, V_m would have to be significantly higher in group *A* than in cyclically parthenogenetic groups *B* and *C* to account for the relatively high level of expressed genetic variance in the obligate parthenogen unless the intensity of selection operating on group *A* is exceptionally low. Regardless of the variance generating mechanisms, the comparative data in Table 3 are important because they force us to re-evaluate the commonly held notion that obligate parthenogens are incapable of adaptive change. Moreover, if occasional backcrosses occur between obligately unisexual *Daphnia* and their cyclically parthenogenetic relatives as in most unisexual-bisexual complexes, the former may serve an important function as a reservoir of polygenic variance stored in the form of exceptionally high levels of hidden genetic variance.

SUMMARY

Using quantitative genetic techniques, the components of phenotypic variance and covariance for fitness traits were periodically determined for an intermittent population of *Daphnia pulex* and applied to phenotypic selection models to determine the limits to the response to selection. Levels of expressed genetic variance in this population are extremely high early in the year as a consequence of the release of hidden genetic variance via sex in the previous year. However, <25 generations of continuous clonal selection are required to depress the expressed genetic variance to levels expected under obligate parthenogenesis. A minimum of 10–20% selective mortality per generation is required to account for this erosion in genetic variance.

Since *Daphnia pulex* populations generally consist of several closely related clonal groups that are distinct with respect to both phenotypic means and genetic covariance structure, selection between groups supplements clonal selection within groups as a mechanism for phenotypic evolution. Of particular interest in the study population is the coexistence of an obligately unisexual race with two cyclically parthenogenetic clonal groups. Despite the fact that nearly all members of the obligately unisexual race are electrophoretically identical, it contains substantial genetic variance for polygenic characters and clearly does not constitute an evolutionary dead end.

The results of this study suggest that rates of phenotypic evolution in excess of ~2% of the mean phenotype/generation are unlikely to occur in most cladoceran populations, especially those that have foregone sex for more than a few generations, without a substantial reduction in population size. This rules out the possibility of close tracking of seasonal variation in optimal phenotypes by clonal selection, and provides an evolutionary genetic explanation for the widespread use of cyclomorphosis in cladocerans as well as for the extreme sensitivity of lake plankton communities to novel perturbations. On the other hand, it is argued that populations that exhibit the greatest degree of evolutionary stability because of a lack of sex will also experience the most dramatic responses to selection following a rare recombinational event because the amount of hidden genetic variance converted to expressed genetic variance is proportional to the time between sexual phases.

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FORTHCOMING MEETINGS

INTERNATIONAL *ARCHAEOPTERYX* CONFERENCE

Eichstätt, West Germany; September 11-15, 1984.

Correspondence: Dr. Gunter Viohl
Willibaldsburg, 8078 Eichstätt
West Germany

BASIC AND APPLIED ASPECTS OF POLLEN BIOLOGY

University of Massachusetts, Amherst; July 8-11, 1985.

Correspondence: David Mulcahy
Botany Department, Univ. of Mass.
Amherst, MA 01003

CHEMICAL SIGNALS IN VERTEBRATES IV

University of Wyoming, Laramie; July 27-29, 1985.

Correspondence: Dr. David Duvall
Department of Zoology and Physiology
University of Wyoming
Laramie, WY 82071

XIX INTERNATIONAL ORNITHOLOGICAL CONGRESS

Ottawa, Canada; June 22-29, 1986.

Correspondence: Dr. Henri Ouellet
National Museum of Natural Sciences
Ottawa, Ontario, Canada K1A 0M8

INTERNATIONAL ORGANIZATION OF PLANT BIOSYSTEMATISTS SYMPOSIUM: "Differentiation Patterns in Higher Plants"

Zürich, Switzerland; July 13-18, 1986.

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