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BEHAVIORAL VARIATION IN NATURAL POPULATIONS. I. PHENOTYPIC, GENETIC AND ENVIRONMENTAL CORRELATIONS BETWEEN CHEMORECEPTIVE RESPONSES TO PREY IN THE GARTER SNAKE, *THAMNOPHIS ELEGANS*

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A growing body of information indicates that many, perhaps most, of the characters that interest evolutionists, ecologists, physiologists and behaviorists are polygenic (Clausen et al., 1940; Clausen and Hiesey, 1958; Cavalli-Sforza and Bodmer, 1971; Ehrman and Parsons, 1976; Wright, 1978). These characters commonly show continuous frequency distributions that reflect segregation of genes at many loci. In a landmark paper, Fisher (1918) showed that an important summary parameter could be established for such polygenic characters by measuring and comparing the degree of phenotypic resemblance between various sets of relatives. This parameter, the additive genetic or genic variance, is the population property that is responsible for the phenotypic resemblance between parents and offspring (it is totally responsible for this resemblance in the absence of non-genetic causes of resemblance and if there is random mating). Because it predicts the expected phenotypic mean of the next generation from the phenotypes of parents, it is the key genetic parameter that permits prediction of response to selection in the laboratory, barnyard, garden and in nature (Fisher, 1930; Lush, 1945; Falconer, 1960; Crow and Kimura, 1970; Mather and Jinks, 1971; Lande, 1976*a*). Additive genetic variance is sometimes expressed as a ratio to the phenotypic variance, that is as heritability, h^2. This ratio represents the proportion of phenotypic variance that can be attributed to the additive effects of genes.

A second parameter, additive genetic or genic covariance, is the bivariate analog of genic variance. It reflects the degree of pleiotropy and linkage of genes underlying variation for two phenotypic characters. Pleiotropy is a more pervasive cause of genetic covariance than is linkage, particularly if selection is weak (Falconer, 1960; Nagylaki and Crow, 1974). The importance of genic covariance is that it permits prediction of correlated responses to selection; if selection acts directly only on character x, how much evolution will be induced in character y? (See DeFries and Hegmann, 1970; Hegmann and DeFries, 1970*a*; Hegmann et al., 1973; Hegmann and Boening, 1976; Pyle, 1978; Hegmann, 1979*a*, 1979*b*, for behavioral examples.) Thus genic covariance can constrain the direction of evolution, just as heritability can constrain its rate (Hazel, 1943; Crow and Nagylaki, 1976; Lande, 1979). Wright (1968) has argued that pleiotropy may be virtually universal: most genes probably affect more than one phenotypic character. Thus many characters may be genetically coupled and estimation of genic covariance provides a means of determining the magnitude of genetic constraints imposed by pleiotropy. Like genic variance, genic covariance is sometimes expressed as a ratio, the genetic correlation (the ratio of genic covariance to the geometric mean of genic variances). The genetic correlations describe correspondence or covariance in additive effects of genes on two different characters.

Despite the pivotal importance of heritability and genetic correlation there are remarkably few estimates of these parameters for natural populations. As Wright (1978, p. 323) put it, "there have been relatively few attempts at evaluation." In part this neglect is due to the difficulty of

estimation, but it may be largely due to oversight. Estimation procedures have been widely used in plant and animal breeding, because economics motivated application of the theory of quantitative inheritance. Unfortunately this somewhat difficult theory has been less popular with naturalists, although it applies to natural populations. Consequently estimates, or even demonstrations of heritability for traits in natural populations are rare. For behavioral traits in vertebrate populations, for example, estimates of heritability are almost nonexistent (Arnold, 1980). Estimates of genetic correlation are exceedingly rare. Consequently there is great need for additional estimates of genetic parameters in natural populations like those provided by Sumner (1918, 1923, 1932), Huestis (1925), McWhirter (1969), Murray and Clarke (1966), Clarke and Murray (1968), Smith and Zach (1979), Boag and Grant (1978), and Beatson (1976) for morphological traits and by Arnold (1980), Caldwell and Hegmann (1969) and Greenwood et al. (1979) for behavioral traits.

The magnitude of genetic parameters in natural populations is not the only unresolved issue. An outstanding problem is whether genetic parameters remain relatively constant in an evolving lineage. The application of the theory of quantitative genetics to evolutionary problems depends on this assumption (Falconer, 1960; Lande, 1976*a*, 1979, 1980). The expected phenotypic response to selection can be extrapolated over many generations only if heritabilities and genetic correlations remain relatively constant. Do heritabilities and genetic correlations fluctuate widely or equilibrate during evolution? One empirical approach to this question is taken up here, geographic comparison of genetic parameters in conspecific populations.

A recent study of chemoreceptive responses to prey odors by newborn, naive garter snakes (*Thamnophis elegans*) afforded an opportunity for estimation of genetic parameters (Arnold, 1980). Preparations of prey odors were made in a standardized way for a variety of natural prey taxa. The chemoreceptive responses of naive, newborn snakes to these prey odors were recorded under uniform, laboratory conditions. Responses were recorded for two natural populations in northern California: an inland population (representing the geographic race *T. e. vagrans*) and a coastal population (representing the geographic race *T. e. terrestris*). Heritabilities and genetic correlations were calculated for each population by comparing the behavioral variation within and between families (sets of full sibs). A whole array of genetic correlations was available for comparison in the two populations because chemoreceptive responses were recorded to ten different prey.

The ecologies of these two populations are strikingly different and have apparently caused microevolution of some feeding behaviors (Fitch, 1940; Fox, 1951; Arnold, 1980). The coastal snakes are terrestrial foragers that prey mainly on slugs, while inland snakes are prone to aquatic foraging and prey mainly on fish and amphibians. Furthermore the inland population is allopatric with slugs, the main prey of coastal snakes. These ecological differences apparently have been responsible for the evolution of different feeding behaviors. Thus although both populations are polymorphic for slug-eating tendency, a slug-eating morph predominates in the coastal population while a slug-refusing morph predominates in the inland population (Arnold, 1977). These behavioral differences are congenital and ontogenetically stable (Arnold, 1980). For example, the slug-refusing morph starves to death if only offered slugs (but readily eats other types of prey). Laboratory crosses between the two populations yield an F_1 with intermediate slug-eating scores (with a bias toward the inland mean) and no indication of maternal effects (Arnold, 1981). Naive snakes from these two populations also show a striking difference in chemoreceptive response to slug odor. Newborn coastal snakes show a much stronger response and the mean responses of the two populations differ by nearly two standard deviations (Arnold, 1980).

The main focus in geographic compar-

ison of genetic correlations in chemoreceptive response will be to compare the overall covariance structure in the two populations. By this I mean the structure deduced by principal component or factor analysis of matrices of genetic correlations (Bailey, 1956; Yap Potter et al., 1968; Hashiguchi and Morishima, 1969; Hegmann and DeFries, 1970*a*; Leamy, 1977). There are three reasons for focusing on overall structure rather than on pairwise comparisons of particular correlations. First, because of sampling errors, pairwise comparisons could easily lead to erroneous conclusions. Second, because 66 genetic correlations were estimated for each population, it is useful to collapse each set of correlations as much as possible in order to simplify geographic comparison. This is best accomplished by factor analysis. A further advantage is that sampling errors in individual estimates of correlation may cancel during factoring so that the picture of overall structure is more accurate than any individual estimate of correlation. Finally, the structure of genetic correlations in chemoreceptive response to prey may have a straightforward physiological meaning. For example, suppose that a particular molecule is present on the surface of many different frog species and is used by garter snakes to recognize frogs as prey. If there is genetic variation in the tendency of garter snakes to respond to this molecule, then genetic correlation between chemoreceptive responses to any two species of frogs can be expected as a matter of course. Thus by examining the structure of correlations between responses to a variety of prey taxa, we can glimpse the chemical taxonomy of the predatory garter snake and perhaps deduce certain general features of the chemosensory code.

Materials and Methods

The newborn snakes used in chemoreception tests were the progeny of gravid females collected at two study areas in northern California, 285 km apart. The inland area was at Eagle Lake, Lassen Co.; 19 gravid females were collected at this site. Ten gravid females were collected at two sites, 35 km apart, in coastal Humboldt Co.: 3 females from 124°05′19″W × 41°12′56″N and 7 females from 124°07′30″W × 39°57′00″N. Test scores of progeny from these two coastal sites were pooled for statistical analysis, since analyses of variance of litter means showed no differentiation in any of the behavioral scores. In addition, field work indicated that habitats and prey availabilities were similar at these sites and that *T. elegans* was continuously distributed between them. Accordingly, these two coastal sites will be considered a single, Mendelian population.

Gravid females were collected in July and shipped by air back to the laboratory within 14 days of capture. All snakes used in the tests were born in the laboratory under uniform conditions (211 young from the inland population and 102 from the coastal population). Newborn snakes were separated from their mothers within 18 h of birth and were then housed in individual containers. Each snake was weighed the day after it was born and each mother (dam) was weighed and measured on this day as well. Dams were measured by stretching them along a measuring tape and recording the length from the tip of the snout to the vent (body size). Newborn snakes were not fed prior to chemoreception tests: they were completely naive at the time of the tests. Details of housing are given in Arnold (1977, 1980).

Behavioral Tests

Prey species used in chemoreception tests were chosen to represent a balanced selection of prey actually encountered in nature. All but one of the test prey (*Poecilia*) were congeners or actual prey species eaten by one or both populations. Anurans are represented by two species in two families (Hylidae and Bufonidae) and by two developmental stages (premetamorphic tadpoles and postmetamorphic frogs). Salamanders are represented by four species in three families (plethodontids by *Batrachoseps* and *Aneides*; ambystomatids by *Ambystoma*; and salamandrids by *Taricha*). One salamander, *Taricha,* possesses the potent neurotoxin,

tetrodotoxin (Mosher et al., 1964). Both populations of *T. elegans* are susceptible to this toxin and do not eat transformed, toxic *Taricha* in nature. Fish, molluscs and annelids are each represented by one species. These four prey taxa (amphibians, molluscs, annelids and fish) constitute more than 95% of the natural diet in each of the populations (Arnold, 1980). No satisfactory chemical stimulus could be devised for the remaining classes of prey: birds, mammals and lizards. Some of these prey seemed to be recognized visually rather than by chemoreception.

All newborn snakes were subjected to the same sequence of chemoreception tests at age 14–15 days. At these ages chemoreceptive responses to ten prey odors and two controls were recorded in the sequence: *Ariolimax californicus, Aneides lugubris, Taricha torosa, Bufo boreas* tadpoles, *Poecilia reticulata,* distilled water (Control 1), *Erpobdella punctata, Batrachoseps attenuatus, Ambystoma tigrinum* larvae, *Hyla regilla* tadpoles, transformed *Hyla regilla,* and distilled water (Control 2). During a test a cotton-tipped swab, laden with prey odor, was held stationary in front of the snake. The number of tongue flicks that contacted the cotton-tip during a 1-min interval constituted the snake's chemoreception score. Preparation of test swabs and details of the testing procedure are described in Arnold (1977, 1980). Screening tests for feeding response to the slug, *Ariolimax californicus,* were conducted for a 10-day period (age 16–25 days) after the chemoreception tests and the results are reported by Arnold (1980).

All chemoreception scores (tongue flicks/min) were transformed by taking natural logarithms. This transformation made variances homogeneous and produced nearly normal distributions in each population. All statistical analyses were conducted on transformed scores.

Calculation of Phenotypic, Genetic and Environmental Correlations

Heritability estimates were based on analysis of variance within and among sets of full sibs (litters) and consequently they probably overestimate parametric heritabilities (Arnold, 1980). This overestimation occurred because twice the component of variance among full sib families estimates the genic variance plus half the dominance variance (Fisher, 1918; Falconer, 1960). So if dominance was present, heritabilities were overestimated. The magnitude of overestimation depends on gene frequencies and the degree of dominance, but it is unlikely to be very large. Partial dominance does not lead to serious overestimates and even with complete dominance the overestimate will be less than 25% unless the recessive allele is rare ($P < .5$) (Wright, 1952). For these reasons, estimates of heritability based on full sib families should be viewed as upper limits on the magnitude of parametric heritability (Falconer, 1960). Common family environment can also inflate estimates of heritability (and genetic correlation), but this was not a confounding problem with the present data (see Discussion).

Phenotypic correlations, r_P, between chemoreception scores in each population were calculated in the familiar way. Product moment correlation coefficients were calculated using the scores of individual snakes as data points.

Genetic correlations were calculated by the following formula (Falconer, 1960):

$$r_A = \frac{\mathrm{COV}_a}{\sqrt{\sigma^2_{ax}\sigma^2_{ay}}}, \qquad (1)$$

where COV_a is the among family component of covariance between two variables and σ^2_{ax} and σ^2_{ay} are the among family components of variance for the two variables. This expression is usually applied to data on paternal half sib families, for in this case the among sire components of variance and covariance estimate one quarter of the genic variance and covariance, respectively (Falconer, 1960, p. 317). In the present application, however, components of variance and covariance among families of full sibs were used. Thus the numerator in expression (1) will estimate half the genic covariance plus one quarter of the dominance covariance and

portions of epistatic covariance (Mode and Robinson, 1959). Portions of dominance variance will also occur in the denominator, and expression (1) will be an unbiased estimate of genetic correlation only in the absence of dominance. This expression also assumes random mating and no correlation or interaction between genotype and environment. Due to sampling errors, two variables showed negative among litter components of variance (Control 1 in the inland population and Control 2 in the coastal population). In order to calculate genetic correlations with these two variables, the arithmetic mean, rather than the geometric mean, of variance components was used in the denominator of the above formula (Reeve, 1955).

Environmental correlations, r_E, between each pair of variables were calculated using the following formula (Hazel, 1943; Falconer, 1960):

$$r_P = h_x h_y r_A + e_x e_y r_E, \qquad (2)$$

where h_x^2 and h_y^2 are the heritabilities of the two variables and $e^2 = 1 - h^2$.

Standard errors of genetic correlations were calculated using the following expression (Robertson, 1959*b*; Falconer, 1960):

$$\sigma_{r_A} = \frac{1 - r_A^2}{\sqrt{2}} \sqrt{\frac{\sigma h_x^2 \sigma h_y^2}{h_x^2 h_y^2}}, \qquad (3)$$

where σ represents standard error.

Two variables showed negative heritabilities, as already mentioned: $-.05 \pm .07$ for Control 2 in the coastal population and $-.05 \pm .05$ for Control 1 in the inland population. These two heritabilities were given positive signs for the purposes of calculating standard errors of genetic correlations and environmental correlations.

Principal Factor Analysis of Phenotypic, Genetic and Environmental Structure

The same computational procedures were used for principal factor analysis of phenotypic, litter mean and environmental correlations. Computations were done using the SPSS computer program (Nie et al., 1975). The estimates of communalities placed in the main diagonal were determined by iteration. Orthogonal factors were extracted and rotated to simple structure by the Varimax procedure.

The structure of the final solution can vary considerably depending on how many factors are extracted (Gould and Garwood, 1969; Leamy, 1977). In order to facilitate comparisons, four factors were extracted in all analyses. In initial computer runs successive factors were extracted until later factors accounted for less than the total variance in any single variable. On this criterion four factors were sufficient to describe the phenotypic and litter mean correlations for the inland population, but only three factors were required for the same two matrices in the coastal population. In order to make solutions for the two populations comparable, four factor solutions were made for the coastal population.

Matrices of genetic correlations usually cannot be factored by classical procedures because sampling errors in the estimates of components of variance and covariance often yield some genetic correlations that exceed one (Hashiguchi and Morishima, 1969; Leamy, 1977). This was the case for the genetic correlation matrices in both populations. To surmount this problem, the correlations between weighted litter means were factored. These correlations will often approximate closely genetic correlations, as can be seen by comparing expression (1) with the following expression for the correlation of weighted litter means,

$$r_M = \frac{(\mathrm{COV}_w/n_o) + \mathrm{COV}_a}{\sqrt{[(\sigma^2_{wx}/n_o) + \sigma^2_{ax}][(\sigma^2_{wy}/n_o) + \sigma^2_{ay}]}}, \qquad (4)$$

where σ^2_w and COV_w are, respectively, components of variance and covariance within litters, σ^2_w/n_o are the sampling variances of litter means, COV_w/n_o is the error covariance of the covariances between litter means and n_o is the average number of animals per litter corrected for differences in litter size (Sokal and Rohlf, 1969, p. 207). Since the variance-covari-

ance multiplier, n_0, was 10 for the coastal population and 11 for the inland population, the sampling variances and error covariances in the above expression were relatively small, and so the correlations of litter means gave reasonable estimates of the genetic correlations (see Blizard and Bailey, 1979, for an empirical example). This approximation can also be justified on more theoretical grounds. Genetic correlations represent correlations between breeding values (Falconer, 1960). Since average litter sizes were 10 or more in both populations, correlations of litter means gave reasonable estimates of correlations in breeding values. Although the breeding value of a dam is twice the mean deviation of her progeny from the population mean (Falconer, 1960), this scaling does not affect the correlation of litter means, which will be the same as the correlation in breeding values in the absence of dominance.

The major point of concern was the overall structure of genetic covariances rather than the particular values of r_A as approximated by r_M. Consequently the matrix of correlations of litter means was factored with the aim of approximating the structure of genetic covariances. This was accomplished by constructing a data set in which the vector of mean chemoreceptive responses for each litter was represented in proportion to litter size. Thus if there were 10 progeny in the first litter, the first 10 rows in the data set were 10 copies of the means for that litter. The correlations resulting from these data are the desired correlations of weighted litter means. Principal factors were then calculated for this data set using the SPSS program as already described.

Results

Phenotypic, Environmental and Genetic Correlations

Phenotypic correlations are generally positive in both populations and in the moderate range, 0–.52 (Tables 1–2). Genetic correlations tend to be higher and there are many negative correlations, although most are positive (Tables 3–4). Standard errors for genetic correlations are moderately large, particularly in the coastal population where correlations are based on data from only 10 families. Sampling errors in the coastal population also lead to a number of estimates of genetic correlation that exceed one. Environmental correlations are generally lower than phenotypic and genetic correlations (Tables 3–4).

Correlations between litter means are generally in the moderate to high range and tend to be greater than corresponding phenotypic correlations (Tables 1–2).

There is a reasonable correspondence between genetic correlations and correlations between litter means. (This correspondence would increase with larger family sizes, as already discussed.) The correspondence between matrices of genetic correlation (r_A) and litter mean correlations (r_M) can be measured by the operation of matrix substraction, such that the deviation in elements is $r_{A_{ij}} - r_{M_{ij}}$. In the inland population the average deviation is only 0.05 and in the coastal population it is 0.18, indicating rather good correspondence. There seems to be no bias in the pattern of deviations in the inland population, but in the coastal population negative deviations appear to be concentrated in correlations involving both *Taricha* and Control 1, suggesting that litter mean correlations overestimated genetic correlations with these variables and underestimated genetic correlations with other variables. In general, however, with average family sizes of 10–11, litter mean correlations satisfactorily approximate genetic correlations.

Generally, there were no significant correlations between chemoreceptive responses to prey and the covariates: birth weight, litter size and size of dam. In the inland population, however, there was a tendency for responses to the two controls to be positively correlated with these nonbehavioral covariates. The biological significance of these correlations is not apparent. In initial calculations these three covariates were included in factor analysis

TABLE 1. *Phenotypic correlations (above diagonal) and correlations between weighted litter means (below diagonal) in the coastal population of* Thamnophis elegans. *Correlations between chemoreceptive responses to prey odors are shown for naive, newborn snakes* (n = *102 individuals).*

Prey taxa		1	2	3	4	5	6	7	8	9	10	11	12
Anurans	1. Hyla tads		.45	.23	.30	.41	.26	.02	−.09	.09	.20	.26	.17
	2. Hyla frogs	.63		.24	.34	.44	.21	.14	.11	.19	.13	.39	.41
	3. Bufo tads	.11	.46		.14	.24	.14	.11	.14	.14	.19	.13	.25
Salamanders	4. Batrachoseps	.68	.77	.55		.52	.26	.12	.15	.23	.19	.20	.18
	5. Ambystoma	.81	.82	.37	.90		.38	.09	.10	.24	.30	.38	.33
	6. Aneides	.66	.61	.22	.79	.70		.36	.20	−.02	.31	.25	.21
	7. Taricha	−.46	−.07	.31	.09	−.21	.17		.25	.00	.26	.05	.13
Controls	8. Control 1	−.11	.05	.27	.36	.12	.42	.88		.15	.12	−.04	−.17
	9. Control 2	.49	.67	.40	.67	.59	.75	.43	.43		.19	.07	.08
Fish	10. Poecilia	.41	.15	.49	.53	.35	.30	.18	.44	.40		.10	.06
Slug	11. Ariolimax	.45	.64	.69	.74	.73	.36	−.23	−.09	.16	.29		.45
Leech	12. Erpobdella	.46	.80	.78	.67	.59	.39	−.00	−.01	.57	.45	.68	

of weighted litter means. In the coastal population they loaded on separate factors from behavioral responses and in the inland population dam size and litter size loaded one factor along with controls. Consequently, since these three covariates explained so little of the behavioral variation, they were not included in the final factor analyses.

Principal Factor Analysis of Phenotypic, Environmental and Litter Mean Correlations

In Tables 5–10 the squares of the indicated factor loadings represent the proportion of variance in each variable explained by a particular factor. For example, in Table 5, 24% = (100 × .49²) of the variance in chemoreceptive response to *Hyla* tadpoles is associated with factor I, and all factors together accounted for 43% of the variance in this variable. The following discussions focus on associations with factors that accounted for more than 20% of the variance in particular variables (factor loadings > .45).

Principal factor analysis of phenotypic correlations yielded factors relating response variation to taxonomically related groups of prey (Tables 5–6). Furthermore, both populations showed similar phenotypic structure. Thus an anuran factor can be recognized in both populations: factor II in the inland population and factor I in

TABLE 2. *Phenotypic correlations (above diagonal) and correlations between weighted litter means (below diagonal) in the inland population of* T. elegans. *Correlations between chemoreceptive responses to prey odors are shown for naive, newborn snakes* (n = *211 individuals).*

Prey taxa		1	2	3	4	5	6	7	8	9	10	11	12
Anurans	1. Hyla tads		.35	.42	.23	.16	.02	−.09	.11	−.04	.12	.14	.09
	2. Hyla frogs	.50		.35	.23	.26	−.04	−.01	.05	−.04	.22	.02	.08
	3. Bufo tads	.59	.43		.20	.20	.04	.06	.03	−.13	.20	.03	.08
Sala-	4. Batrachoseps	.47	.52	.43		.35	.12	.02	.08	.13	.15	.20	.22
manders	5. Ambystoma	−.00	.11	.14	.43		.19	−.00	.06	.14	.24	.09	.19
	6. Aneides	−.07	−.29	.15	.25	.08		.36	.16	.18	.10	.19	.14
	7. Taricha	−.30	−.22	−.04	.26	−.16	.42		.34	.33	.23	.15	.17
Controls	8. Control 1	−.16	.03	−.23	.29	−.09	.03	.53		.18	.22	.05	.18
	9. Control 2	−.30	−.13	−.34	.43	.41	.37	.50	.51		.21	.13	.08
Fish	10. Poecilia	.12	.54	.45	.62	.30	−.15	.15	.21	.23		.11	.13
Slug	11. Ariolimax	.63	−.01	.45	.37	.22	.30	−.26	−.33	−.10	−.02		.33
Leech	12. Erpobdella	.45	.07	.28	.50	.36	.47	.08	.04	.16	−.12	.62	

TABLE 3. *Genetic and environmental correlations in the coastal population of* T. elegans. *Genetic correlations are shown above the main diagonal and environmental correlations are shown below the main diagonal. The correlations are between chemoreceptive responses to prey odors by naive, newborn snakes. Standard errors of genetic correlations are shown in parentheses. Heritability estimates* (h^2) *for each of the behavioral responses are shown on the last line.*

Prey taxa		1	2	3	4	5	6	7	8	9	10	11	12
Anurans	1. Hyla tads		.74 (.19)	.05 (.36)	.95 (.05)	.97 (.02)	1.17 (.22)	−.83 (.15)	−.14 (.52)	.30 (.56)	.67 (.33)	.62 (.31)	.60 (.22)
	2. Hyla frogs	.29		.58 (.25)	1.10 (.10)	1.01 (.01)	1.14 (.20)	−.24 (.47)	−.01 (.56)	.60 (.42)	.18 (.60)	.88 (.12)	1.01 (.01)
	3. Bufo tads	.40	.01		.80 (.15)	.80 (.15)	.32 (.49)	1.60 (.67)	.39 (.41)	.17 (.54)	.83 (.16)	1.14 (.14)	.98 (.01)
Salamanders	4. Batrachoseps	−.00	.04	−.26		1.14 (.10)	1.54 (.95)	.07 (.54)	.96 (.06)	.38 (.60)	1.00 (.00)	1.34 (.43)	.98 (.02)
	5. Ambystoma	−.41	−.22	−.11	.02		1.09 (.09)	−.37 (.31)	.15 (.40)	.15 (.46)	.45 (.36)	1.03 (.02)	.67 (.15)
	6. Aneides	.03	.00	.10	.01	.14		−.09 (.71)	.79 (.30)	1.33 (.73)	.28 (.82)	.55 (.54)	.61 (.33)
	7. Taricha	.39	.28	−.74	.14	.67	.45		1.64 (1.06)	.45 (.58)	.09 (.69)	−.55 (.44)	−.08 (.41)
Controls	8. Control 1	−.08	.14	.05	.04	.12	.11	−.07		1.83 (1.93)	.96 (.06)	−.15 (.67)	.11 (.46)
	9. Control 2	.06	.14	.17	.23	.50	−.13	−.06	−.02		.51 (.67)	.13 (.77)	.21 (.51)
Fish	10. Poecilia	.08	.12	−.02	.03	.41	.32	.29	−.00	.16		.59 (.49)	.84 (.16)
Slug	11. Ariolimax	.14	.24	−.35	−.10	−.02	.20	.19	−.02	.06	.03		.89 (.09)
Leech	12. Erpobdella	−.24	−.05	−.71	−.36	−.50	.10	.28	−.35	.07	−.25	.29	
	h^2	.39	.32	.54	.25	.82	.11	.22	.15	−.05	.11	.17	.59

TABLE 4. *Genetic and environmental correlations in the inland population of* T. elegans. *Genetic correlations are shown above the main diagonal and environmental correlations are shown below the main diagonal. The correlations are between chemoreceptive responses to prey odors by naive, newborn snakes. Standard errors of genetic correlations are shown in parentheses. Heritabilities (h^2) for each of the behavioral responses are shown on the last line.*

Prey taxa		1	2	3	4	5	6	7	8	9	10	11	12
Anurans	1. Hyla tads		.59 (.20)	.69 (.16)	.68 (.20)	−.11 (.31)	.60 (.18)	−.51 (.28)	−.23 (.43)	−.46 (.24)	.13 (.39)	1.03 (.02)	.66 (.17)
	2. Hyla frogs	.23		.49 (.25)	.81 (.13)	−.01 (.34)	−.86 (.17)	−.45 (.33)	−.00 (.49)	−.19 (.32)	.89 (.09)	−.03 (.38)	.07 (.32)
	3. Bufo tads	.30	.29		.65 (.22)	.11 (.33)	.41 (.55)	−.13 (.40)	−.39 (.41)	−.49 (.25)	.72 (.20)	.81 (.13)	.41 (.26)
Salamanders	4. Batrachoseps	.09	.07	.08		.51 (.30)	.65 (.45)	.57 (.33)	.30 (.53)	.72 (.19)	1.27 (.31)	.56 (.31)	.77 (.16)
	5. Ambystoma	.27	.36	.23	.32		−.12 (.68)	−.34 (.38)	−.15 (.50)	.61 (.21)	.38 (.38)	.35 (.35)	.48 (.26)
	6. Aneides	.00	.07	−.01	.06	.23		.65 (.48)	−.71 (.49)	.84 (.20)	−.88 (.19)	.63 (.47)	1.22 (.32)
	7. Taricha	.04	.10	.11	−.07	.08	.34		.56 (.42)	.68 (.23)	.02 (.53)	−.79 (.18)	−.01 (.40)
Controls	8. Control 1	.18	.06	.09	.06	.08	.20	.33		.84 (.14)	.04 (.63)	−.56 (.39)	−.12 (.47)
	9. Control 2	.15	.02	.02	−.03	−.03	.11	.25	.10		.26 (.39)	−.30 (.35)	.20 (.31)
Fish	10. Poecilia	.12	.07	.09	−.04	.22	.18	.27	.24	.21		−.19 (.47)	−.38 (.35)
Slug	11. Ariolimax	−.15	.03	−.20	.12	.02	.15	.32	.12	.25	.17		.89 (.08)
Leech	12. Erpobdella	−.20	.09	−.06	.06	.08	.01	.23	.17	.03	.26	.16	
	h^2	.36	.28	.29	.16	.25	.04	.14	−.05	.28	.12	.17	.31

TABLE 5. *Phenotypic structure in the coastal population of* T. elegans. *Four factors were extracted from the phenotypic correlations between chemoreceptive responses to prey by naive, newborn snakes.*

Prey taxa		Factors I	II	III	IV	Percent of variation
Anurans	Hyla tads	.69	.10	.02	.01	48
	Hyla frogs	.49	.36	.10	.24	43
	Bufo tads	.20	.19	.15	.22	15
Salamanders	Batrachoseps	.45	.09	.17	.34	35
	Ambystoma	.63	.23	.20	.31	59
	Aneides	.36	.13	.66	−.12	59
	Taricha	−.02	.10	.58	.04	35
Controls	Control 1	−.07	−.16	.41	.36	33
	Control 2	.13	.04	−.00	.51	28
Fish	Poecilia	.24	.01	.36	.17	22
Slug	Ariolimax	.36	.42	.07	.02	32
Leech	Erpobdella	.13	.96	.05	.02	94
	Percent of variation	57.0	20.4	13.6	8.9	
	Cumulative percent	57.0	77.5	91.1	100.0	

the coastal population. Inland factor II shows high loadings for all three anuran variables (*Hyla* frogs, *Hyla* tadpoles and *Bufo* tadpoles) and insubstantial loadings for all other variables. Coastal factor I is a salamander factor as well as an anuran factor. A slug/leech factor can also be recognized in both populations: inland factor IV and coastal factor II. Responses to the poisonous salamander *Taricha* are associated with inland factor I and coastal factor III. Responses to the controls show moderate loadings on this factor (I) in the inland population and responses to *Aneides* are associated with responses to *Taricha* on coastal factor III. Thus three out of four factors are comparable in the two populations.

The remaining pair of phenotypic factors are not similar in composition. Inland factor III is associated with responses to the salamanders *Ambystoma* and *Batra-*

TABLE 6. *Phenotypic structure in the inland population of* T. elegans. *Four factors were extracted from the phenotypic correlations between chemoreceptive responses to prey by naive, newborn snakes.*

Prey taxa		Factors I	II	III	IV	Percent of variation
Anurans	Hyla tads	−.05	.61	.08	.17	40
	Hyla frogs	.02	.53	.24	−.02	34
	Bufo tads	.05	.68	.07	.02	46
Salamanders	Batrachoseps	.07	.24	.41	.26	30
	Ambystoma	.10	.19	.70	.08	54
	Aneides	.37	−.03	.12	.20	19
	Taricha	.84	−.02	−.13	.09	74
Controls	Control 1	.42	.09	.03	.05	19
	Control 2	.42	−.16	.20	.10	25
Fish	Poecilia	.35	.23	.24	.04	23
Slug	Ariolimax	.11	.04	.03	.70	51
Leech	Erpobdella	.17	.08	.16	.41	23
	Percent of variation	45.2	29.8	13.8	11.1	
	Cumulative percent	45.2	75.1	88.9	100.0	

TABLE 7. *Genetic structure in the coastal population of* T. elegans. *Four factors were extracted from the weighted litter mean correlations between chemoreceptive responses to prey by naive, newborn snakes.*

Prey taxa		Factors I	II	III	IV	Percent of variation
Anurans	Hyla tads	.82	.11	−.34	.29	89
	Hyla frogs	.75	.57	−.02	−.24	95
	Bufo tads	.04	.88	.27	.23	90
Salamanders	Batrachoseps	.75	.49	.14	.33	94
	Ambystoma	.83	.40	−.14	.19	90
	Aneides	.84	.09	.26	.12	79
	Taricha	−.11	.06	.98	−.02	98
Controls	Control 1	.19	−.04	.90	.31	94
	Control 2	.71	.23	.51	.00	81
Fish	Poecilia	.23	.29	.23	.62	58
Slug	Ariolimax	.34	.74	−.25	.21	77
Leech	Erpobdella	.40	.82	.01	.03	84
	Percent of variation	58.3	23.4	12.5	5.8	
	Cumulative percent	58.3	81.7	94.2	100.0	

choseps, whereas these variables cluster with anuran responses in the inland population. This factor is associated with responses to the distilled water controls.

Covariance between responses to distilled water controls and responses to prey odors is of particular interest. Some individuals might have been less timid, or more generally responsive to the test situation and so might have shown higher responses to all test stimuli, including controls. Apparently this did not occur. There is no indication that a general responsiveness factor accounted for significant variation in responses to prey odors. Thus in the coastal population, the controls showed insignificant loadings on the two major prey odor factors (I and II). And in the inland population the controls showed insignificant loadings on the three major prey odor factors (II, III, IV). Responses to controls tend to form a separate factor (IV) in the coastal population and to be associated with responses to the toxic salamander *Taricha* in both populations.

The structure of correlations between litter means can be taken as an approximation of genetic covariance structure (Tables 7–8). Genetic structures are very similar in the two populations and parallel the results from phenotypic structure. An amphibian factor, which includes responses to both anurans and salamanders, can easily be recognized in both populations (factor I in both). Likewise, a slug/leech factor is apparent in both populations (factor II in both). Finally, a factor associated with responses to controls and *Taricha* is evident (factor III in both). These three factors (amphibian, slug/leech and control/*Taricha*) are remarkably similar to major factors extracted from phenotypic correlations.

Despite the striking similarity of genetic covariance structure in the two populations, there are some notable differences. In the coastal population responses to *Bufo* tadpoles are associated with the slug/leech factor (II) rather than with the amphibian factor, as in the inland population. Responses to fish constitute a nearly unique factor in the coastal population (IV) but are associated with the amphibian factor in the inland population. Finally, responses to the salamander *Ambystoma* and to Control 2 constitute a separate factor (IV) in the inland population, but responses to *Ambystoma* are associated with the amphibian factor (I) in the coastal population.

The absence of high, negative loadings on any factors in either population is no-

TABLE 8. *Genetic structure in the inland population of* T. elegans. *Four factors were extracted from the weighted litter mean correlations between chemoreceptive responses to prey by naive, newborn snakes.*

Prey taxa		Factors I	II	III	IV	Percent of variation
Anurans	Hyla tads	.55	.54	−.31	−.19	73
	Hyla frogs	.80	−.05	−.12	.02	66
	Bufo tads	.58	.43	−.15	−.15	56
Salamanders	Batrachoseps	.70	.45	.38	.37	97
	Ambystoma	.15	.19	−.09	.78	67
	Aneides	−.26	.56	.39	.08	53
	Taricha	−.07	.06	.89	−.13	83
Controls	Control 1	.10	−.16	.64	.06	45
	Control 2	−.10	.02	.67	.63	86
Fish	Poecilia	.73	−.14	.22	.25	67
Slug	Ariolimax	.11	.81	−.30	.08	77
Leech	Erpobdella	.05	.79	.07	.20	67
	Percent of variation	38.7	29.9	20.1	11.2	
	Cumulative percent	38.7	68.7	88.8	100.0	

table. This is true of both phenotypic and genetic structures. This suggests that variation in responses to prey odors does not take the form of a tradeoff. There seems to be no tendency for inverse correlation in responses. This kind of pattern might have occurred if populations consisted, for example, of one morph that responded to amphibians but not to slugs and leeches and another that responded to slugs and leeches but not to amphibians. Instead the picture is one of independent dimensions of variation in chemoreceptive response. Bivariate scatterplots of phenotypic values and litter means both approximated bivariate, normal distributions in all cases, although some distributions were censored at low values.

Environmental structures are similar to phenotypic and genetic structures in both populations (Tables 9–10). However, these similarities are less striking than the correspondence between phenotypic and genetic structures in each population. Furthermore, the two populations show less similarity in environmental structures than in phenotypic or genetic structures. An anuran factor can be identified in both populations. Thus responses to both developmental stages of *Hyla* are associated with factor II in the inland population and with factor III in the coastal population. Responses to *Bufo* are associated with the anuran factor of the inland (II), but are not strongly associated with the comparable anuran factor (III) of the coastal population. Responses to salamanders constitute separate factors in both populations and are not strongly associated with responses to anurans. Thus factor III describes responses to *Batrachoseps* and *Ambystoma* in the inland population and factor II describes responses to *Ambystoma, Aneides, Taricha* and the fish *Poecilia* in the coastal population. The remaining environmental factors are not comparable in the two populations although some of them are similar to phenotypic or genetic factors in their respective populations. Thus factor I of the inland population has *Taricha* as its leading variable and is similar in loading pattern to factor I in Table 6 and to factor III of Table 8. In the coastal population responses to leech show a strong positive association with factor I and responses to *Bufo* show a strong negative association with this same factor. These same two variables are associated with genetic factor II (Table 7), but both signs are positive. Finally, the environmental results show a conspicuous difference from both

TABLE 9. *Environmental structure in the coastal population of* T. elegans. *Four factors were extracted from the environmental correlations between chemoreceptive responses to prey by naive, newborn snakes.*

Prey taxa		Factors I	II	III	IV	Percent of variation
Anurans	Hyla tads	−.14	.04	.73	−.03	55
	Hyla frogs	.08	.05	.53	.13	30
	Bufo tads	−.90	−.17	.21	−.15	90
Salamanders	Batrachoseps	.01	.02	.06	.46	21
	Ambystoma	−.11	.70	−.40	.47	88
	Aneides	.02	.56	.12	−.32	43
	Taricha	.54	.74	.24	.15	92
Controls	Control 1	−.23	.14	−.03	.04	08
	Control 2	−.12	.06	.04	.61	39
Fish	Poecilia	−.12	.54	.08	.12	33
Slug	Ariolimax	.37	.12	.26	−.03	22
Leech	Erpobdella	.82	−.19	−.06	−.34	82
	Percent of variation	36.3	31.5	20.0	12.2	
	Cumulative percent	36.3	67.8	87.8	100.0	

phenotypic and genetic results. Environmental structures show no indication of a slug/leech factor.

DISCUSSION

The Nature of Environmental and Genetic Variance in Behavior

Environmental variance and covariance might have taken several forms in this experiment. It is useful to recognize three levels of environmental effects (Falconer, 1960): special environmental effects due to temporary or localized circumstances (causing variance within individuals), general environmental effects due to permanent or widespread circumstances (causing variance between individuals) and effects due to a common family environment (causing non-genetic resemblance within families). Motivation and

TABLE 10. *Environmental structure in the inland population of* T. elegans. *Four factors were extracted from the environmental correlations between chemoreceptive responses to prey by naive, newborn snakes.*

Prey taxa		Factors I	II	III	IV	Percent of variation
Anurans	Hyla tads	.11	.59	.10	−.17	40
	Hyla frogs	.08	.35	.27	.10	21
	Bufo tads	.02	.57	.08	.02	33
Salamanders	Batrachoseps	−.01	.02	.38	.01	15
	Ambystoma	.10	.33	.83	.06	81
	Aneides	.41	−.02	.21	−.05	22
	Taricha	.69	.06	−.03	.16	51
Controls	Control 1	.40	.17	.01	.16	21
	Control 2	.42	.05	−.08	−.05	19
Fish	Poecilia	.40	.14	.08	.23	24
Slug	Ariolimax	.48	−.34	.13	.05	36
Leech	Erpobdella	.16	−.12	.07	.82	71
	Percent of variation	41.8	29.9	16.4	11.9	
	Cumulative percent	41.8	71.7	88.1	100.0	

habituation (waning in response upon repeated exposure to the same stimulus) fall into the first category. Habituation to the same molecules on different prey may have contributed to some environmental correlations. Variation in hunger, perhaps due to differences in birth weight, might have contributed to environmental variance and covariance among individuals. However, the general failure to find correlations between individual birth weight and behavioral responses rules out birth weight as a significant contribution to general environmental variance and covariance. Since repeated measurements were not made on individuals, these two sources of environmental variance and covariance, i.e., special and general, were not separable. Both contributed to the calculated environmental variances and correlations but were not confounded with genetic contributions in estimates of heritability and genetic correlation (here we make the reasonable assumption that genotype-environment interaction and correlation were eliminated by the experimental design).

In contrast, any effects exerted by a common family environment would have been confounded with genetic effects in estimates of heritability and genetic correlations, since these estimates were based on full sib families (Falconer, 1960). Common family environments were disrupted the day after birth and this lessened the opportunity for common effects. Although full sibs shared a common maternal environment before birth, there is no evidence that this can affect subsequent behavioral responses. In experimental studies, Burghardt (1971) was unable to influence chemoreceptive responses of newborn garter snakes by varying the dam's diet during gestation. Furthermore, Arnold (1981) found no indication of a maternal effect on feeding responses to slugs in reciprocal crosses between populations of *T. elegans*. Birth weight is another candidate for a common family effect, since in both populations there was little variation between littermates in birth weight; most of the variation was among litters. Thus in the coastal population 86% of the variance in birth weight was among litters and in the inland population 71% of the variance was among litters. Fortunately, however, there was no correlation between the average birth weights of litters and their chemoreceptive responses to prey. Thus it is unlikely that estimates of heritability and genetic correlation were inflated due to a common family environment.

Heritable variation in chemoreceptive response to a particular prey may reflect genetic differences in chemoreceptors or in neurons that process information from these receptors. In other words, there may be genetic variation in what information is perceived (perception) or in how the information is processed (sensation). For example, perceptual variation might be due to heritable, individual differences in kinds or numbers of chemoreceptors. Alternatively, each individual might have the same array of receptors, but there might be heritable differences in networks of interneurons that process chemosensory information. The present results do not distinguish between these two major possibilities, although they could be distinguished by neurophysiological studies.

Heritabilities for chemoreceptive response to prey are in the low to moderate range (20–35%). These are simply upper bounds since these full sib estimates include a portion of the dominance variance, if present (Weinberg, 1909), and portions of epistatic variance (Fisher, 1918; Falconer, 1960). (Heritability estimates were probably not inflated by common family environments; see above.) Although less ambiguous estimates of heritability would be desirable, the important point is that statistically significant components of variance among families were revealed in both populations. This strongly suggests that there is heritable (genic) variance for chemoreceptive responses to many prey in both populations. Such demonstrations for behavior in natural populations are exceedingly rare (Caldwell and Hegmann, 1969). Furthermore, since the estimates indicate that

many parametric heritabilities must be in the low range (0–.20), analysis of full and half sib families may be preferable to parent-offspring regression in obtaining more precise heritability estimates (Robertson, 1959*a*).

The magnitude of heritability for chemoreceptive response to prey by newborn, naive garter snakes gives no indication of whether these responses can be modified by experience (Arnold, 1980). Heritability merely expresses the degree of resemblance among relatives. It is not a statement about phenotypic plasticity or capacity for modification (Lewontin, 1974*a*). The potential for modification by experience can only be established by systematically varying experience and measuring the effect on the phenotypic trait. For example, chemoreceptive response to some prey is affected by feeding experience in the garter snake *T. sirtalis* (Fuchs and Burghardt, 1970), but responses to other prey are apparently unaffected by experience (Arnold, 1978). Although estimates of heritability describe an important genetic dimension, they are not a substitute for studies of learning and habituation. Ideally we would like estimates of heritability for a series of ontogenetic stages and as a function of experience. Heritability is not a solution to the nature-nurture controversy. The present results simply indicate that the chemoreceptive responses of naive, newborn snakes are vulnerable to evolution by natural selection.

The presence of genetic variance for important feeding responses within populations could have several explanations. 1) The variability in the response might not expose the population to selection. If all snakes will attack frogs on encounter, any modest variation in chemoreceptive response may be selectively neutral. In other words, the distribution of chemical responses may not straddle an attack threshold (Arnold, 1980). 2) The variation is exposed to selection but the polymorphism is transitory, not stable. Note that the behavioral variation revealed in this experiment is for samples of newborn snakes that have not yet been exposed to selection. Variation among adult snakes, after selection, may be far less than among newborn snakes. The polymorphisms might be transitory in evolutionary time as well. This is possible since the populations have apparently diverged recently (Lawson and Dessauer, 1979). Low heritabilities suggest that approach to equilibrium would be slow and may not have been achieved. 3) Selection is acting and the polymorphism is stable. There are several possibilities. First, migration from other geographic regions may be balanced by selection (Arnold, 1981). Second, selection itself may promote polymorphism if selection is frequency- and/or density-dependent. These are reasonable possibilities since similar predatory responses may often put individuals in competition for limited resources. Heterozygote superiority is also a possible mechanism, since the underlying genetics have not been dissected. Finally, a mutation-selection equilibrium is possible. Although in both populations the rarer morphs are at frequencies orders of magnitude greater than one locus mutation rate, the observed variation may represent a balance between polygenic mutation and selection (Lande, 1976*b*). Field measurement of selection differentials could rule out some of these possibilities. However, selection may be weaker than sample sizes can resolve (Haldane, 1964; Lewontin, 1974*b*). Thus it is no simple matter to demonstrate the mechanisms responsible for genetic polymorphism in this system or any other.

Geographic Comparisons of Genetic Parameters

Heritabilities show no or modest geographic variation. This observation supports the proposition that heritabilities may be relatively constant during microevolution. In a particularly striking case, chemoreceptive response to slugs, population means diverged more than 1.5 standard deviations. Although this divergence may have required hundreds to hundreds of thousands of generations (Arnold,

1980), both populations showed identical heritabilities for this trait.

On several counts, this cannot be considered a strong test for evolutionary constancy. 1) Systematic errors in estimates include non-additive genetic components of variance. An improved breeding design, which generates full and half sib families, is now being implemented. It should yield less ambiguous estimates. 2) Relatively small sample sizes (a total of 29 families) limit resolution and produce moderately large sampling errors. 3) Only two data points (populations) were available for each trait. Estimation for many populations or for many samples through time would be a formidable undertaking. It may be feasible for small organisms, like *Drosophila,* with short generations and large litters. The present results are suggestive, not definitive.

Nevertheless, the present results demonstrate the feasibility of estimating heritabilities in natural populations and the promise of geographic comparisons. Although there is a small, but growing list of heritability estimates for traits in natural populations (see references in introduction), I am unaware of any previous attempts to make geographic comparisons of heritabilities and genetic correlations. This kind of exploration has just begun. The importance of such results for theory is readily apparent.

Application of the theory of quantitative genetics to phenotypic evolution (Falconer, 1960; Lande, 1976*a,* 1979) assumes relative constancy of the key genetic parameters, heritability and genetic correlation. The theory could conceivably accommodate temporal change in these parameters, but empirical results have not demonstrated this necessity. Furthermore, equilibration of genetic parameters during evolution is a reasonable theoretical expectation. Recent theoretical work indicates that mutation is a substantial source of genetic variation for polygenic characters (Lande, 1976*b*). As a consequence, additive genetic variances might remain constant as losses to selection are balanced by mutational input and recombination. If selection is weak, so that genetic variance will be conserved, evolutionary response in one generation can be extrapolated to many generations (Lande, 1976*a*). Similar arguments apply to constancy of genetic correlations. Selection in nature may often be weak (Lewontin, 1974*b*). However the propositions of constancy in genetic variance and covariance are outstanding empirical problems. Thus geographic and temporal comparisons of genetic parameters may yield data vital to the use and development of evolutionary theory.

In order to make the best test for evolutionary stability of genetic parameters the estimates for two or more descendant populations should be based on analysis of variance among half sib families or on parent-offspring regressions (it is impractical to obtain data on more than two characters with selection experiments). Such data give estimates of genic parameters that are not confounded by dominance variance and covariance, and stability of genic variance and covariance is the key theoretical issue. However, even geographic comparisons of phenotypic variance-covariance matrices bear on the issue, since if heritabilities are high, phenotypic and genic covariance structures are likely to be similar (Lande, 1979). The estimates of genetic parameters in the present study certainly provide a better test for evolutionary stability than phenotypic data. Because of the experimental design the estimates were probably not inflated by a common family environment (see above). However, the estimates of genetic correlation do include portions of dominance and epistatic covariance, since they are based on analysis of full sib families (Mode and Robinson, 1959). Thus conclusions based on a geographic comparison of these estimates must be tempered by the realization that these are not the best data for a test of evolutionary stability.

Estimates of genetic correlation appear roughly comparable in the two populations, but sampling errors frustrate pairwise comparisons. In one remarkable

case, however, genetic correlations were identical despite considerable divergence in bivariate mean. This is the case of genetic correlation between chemoreceptive responses to slugs and to leeches. Despite modest phenotypic correlations (.33–.45) in both populations, genetic correlations were high and identical (.89 ± 0.08–0.09). Before turning to the other evidence for covariance constancy, the results of principal factor analysis, this particular case will be considered in detail.

A genetic correlation between chemoreceptive responses to slugs and leeches was an unexpected finding, but one with interesting consequences. Because of this genetic correlation, selection on chemoreceptive response to one of these prey, say leeches, will necessarily produce evolution in the response to the other prey, say slugs. The direction of selection on these behavioral traits probably differs in the two *T. elegans* populations. Leeches are probably hazardous prey for inland snakes (they remain alive in the snake's gut); these snakes are allopatric with slugs. Slugs, however, are the principal prey (90–99% of the diet) of coastal snakes; these terrestrial snakes never encounter leeches (Arnold, 1980). Thus the inland population has apparently responded to selection to avoid leeches and experienced a decreased reaction to slugs as a correlated response to selection. In contrast, the coastal population apparently responded to selection for slug attack and experienced a correlated response to selection, an increased reaction to leech odor. Since coastal snakes do not encounter leeches, this correlated response was not opposed by selection. Despite considerable divergence, genetic correlations between responses to slugs and leeches were identical in both populations.

Factor analysis of correlations revealed a consistent overall pattern in variation. In particular genetic covariance structure was very similar in the two populations. Chemoreceptive responses to prey form at least three distinct clusters: responses to amphibians; responses to slugs and to leeches; responses to a poisonous salamander (*Taricha*) and to controls. Geographic similarity in genetic covariance structure suggests that the structure was not perturbed since divergence from a common ancestor.

This study also revealed an overall similarity between environmental and genetic covariance structure. Such similarity has been reported in several other studies, mostly of morphological traits (Reeve and Robertson, 1953; Tantawy and Rakha, 1964; Hegmann and DeFries, 1970*b*; Bryant, 1977; Leamy, 1977). However, in some striking instances genetic and environmental correlations may differ in sign as well as magnitude (Falconer, 1960). The correspondence between genetic and environmental correlations revealed in the present study is particularly interesting since it is not due to common genetic and environmental effects mediated through growth.

The Physiological Significance of Genetic Correlation

Genetic correlations between chemoreceptive responses to different prey may have a straightforward physiological meaning. These correlations may represent a simple form of pleiotropy. Suppose garter snakes recognize frogs by means of a particular class of molecules in frog skin. Heritable variation in chemoreceptive response to a particular frog species might represent genetic differences in chemoreceptors that respond to this critical molecular class. If two frog species share these critical molecules, then snakes with a heritable tendency to respond to one frog species will also have a heritable tendency to respond to the other frog species. In other words, the presence of the same critical molecules on two prey species could result in a genetic correlation in chemoreceptive response.

The absence of genetic correlation in chemoreceptive responses to two different prey, but heritable variation in response to each prey, suggests that at least two groups of genes underlie chemoreception. Again we suppose that the heritable variation is at the level of chemoreceptors. If

two prey species do not share critical molecules, this could account for the absence of genetic correlation.

The present results indicate that at least three distinct groups of genes are responsible for chemoreceptive variation in garter snake populations (Tables 7–8). Thus on the supposition of variation in receptors, frogs and salamanders might share one class of critical molecules, slugs and leeches might share another molecular class and the poisonous salamander, *Taricha,* might possess yet a third critical molecule (perhaps this is tetrodotoxin). The sharing of molecules by groups of prey is, of course, a statement about which molecules elicit responses from the same receptors and not a statement about overall biochemical similarity.

The available results provide no indication of how many genes reside in each of these groups. In principle a minimum estimate could be made by crossing two geographic races or inbred lines and studying segregation of behavioral responses in the F_2 and backcross progenies (Wright, 1968).

Whether one imagines heritable variation in receptors (perception) or in central processing, the results still suggest at least three groups of genes. Thus individual snakes might all possess the same array of receptors, but might differ in neuronal connections between receptors and tongue-flicking response. In this case at least three groups of genes, affecting interneurons, are required to account for the genetic covariance structure.

A study of heritable variation and covariation in natural populations, combined with behavioral and neurophysiological assays, might be used to dissect the chemosensory code of garter snakes and other organisms. Because this sensory modality responds to stimuli that vary in many dimensions, its code has not been cracked. Sensory screening of families from natural populations might be a valuable alternative to the practice of isolating single locus, sensory mutants in laboratory strains (Kikuchi, 1973; Wysocki et al., 1977). Screening for genetic covariance in natural populations has two advantages: (1) it can collapse variation into a manageable number of dimensions, and (2) it can provide estimates of genetic parameters required to predict response to natural selection.

Summary

Naive newborn snakes showed active chemoreceptive responses to ten different prey odors. These responses were studied in two conspecific populations of *Thamnophis elegans,* representing a coastal and an inland geographic race. The phenotypic correlations between responses to different prey were partitioned into genetic and environmental parts by analyzing the variation and covariation within and among families (litters of full sibs).

Correlations between chemoreceptive responses to different prey species were studied by factor analysis. Taxonomic factors could be readily discerned in both phenotypic and genetic correlations. Factor analysis of genetic correlations (approximated by correlations between weighted litter means) suggests that at least three groups of genes underlie chemoreceptive responses to prey: one group of genes affecting responses to amphibians (anurans and salamanders), another group affecting responses to both slugs and leeches, and a third group affecting responses to the toxic salamander *Taricha.* Phenotypic correlations showed similar structure.

Genetic correlation between responses to different prey species is probably due to a simple form of pleiotropy: some genes affect chemoreceptive responses to particular molecules and these molecules are shared by certain, often by related, species of prey. These genetic correlations could place important genetic constraints on the evolution of the niche. Because of genetic correlation, selection to recognize or avoid one species of prey could affect predatory reactions to many other species of prey. For example, the genetic correlation between responses to slugs and leeches was extremely high (.89) and geographic variation in these responses confirmed the ex-

pectation of correlated response to selection.

Estimates of heritability and genetic correlation, although confounded by dominance variance and covariance, showed little or no geographic variation. This suggests that these genetic parameters were not perturbed during the evolutionary divergence of the two study populations. Although the data suggest evolutionary stability of genetic parameters, this conclusion must be tempered by the imprecision of the estimates. The application of quantitative genetic theory to evolution in nature depends on the assumption of constancy in heritability and genetic correlation. Geographic comparisons of conspecific populations can provide a direct test of this proposition.

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