

Chapter 19

The Microevolution of Feeding Behavior

Stevan J. Arnold

What we require is the study of comparative variations in species whose life history and ecological niche in the community are well understood and easily studied. (Lewontin, 1967)

The genetic basis of behavioral factors involved in determining the niche of organisms has hardly been touched. (Ehrman and Parsons, 1976, p. 347)

An evolutionary response to natural selection depends on three conditions (Lewontin, 1970). First, there must be phenotypic variability within the population. Second, there must be phenotypic resemblance among relatives; the variation must be heritable. Third, there must be a correlation between phenotype and reproductive success; that is, there must be selection according to phenotype. There may be no evolutionary change even if all three conditions are satisfied, but there will certainly be no progressive change if any one condition is not satisfied. These three necessary conditions are easily translated into behavioral terms. In order for feeding behaviors to evolve by natural selection, there must be behavioral alternatives within populations, this behavioral variation must be heritable, and some behavioral phenotypes must confer greater reproductive success than others. Thus an evolu-

This research was supported by NSF Grants BNS76-00619 and DEB78-12560 and by the Spencer Foundation.

tionary perspective on feeding behavior raises the following fundamental question which will be the first major subject of this chapter: *What is the nature of variation in feeding behavior in natural populations?* Of all the evolutionary questions we can ask about feeding behavior, this one is the most basic. Any concrete discussion of the evolution of feeding behavior must begin with the answer to this question.

Small steps in the evolution of feeding behavior can be detected within species. A widely distributed species will encounter geographic differences in the selective pressures that mold the evolution of feeding behavior. As conspecific populations respond to such geographic differences in selection, their feeding behaviors may diverge. Such divergence or differentiation of conspecific populations is termed *microevolution* (in contrast to macroevolution, the divergence of species or higher taxa). Microevolution is the process that yields *geographic variation* (geographic differences between conspecific populations). Geographic variation is the smallest amount of evolution that can be detected in nature unless populations are followed through time. It is bound to be more subtle than the more familiar differences between species and will be of a statistical nature. The second major objective of this chapter will be to describe geographic variation in feeding behavior, the hallmark of microevolution.

Feeding behaviors are particularly favorable traits for evolutionary study because it is possible to identify the selective pressures responsible for their microevolution. To make an especially trustworthy identification, we must demonstrate that geographic variation in behavior coincides with geographic differences in plausible selective pressures. For example, if we can detect geographic variation in the tendency to attack particular prey, we can immediately ask whether this variation coincides with a spatial pattern in the availability of that prey. Such a coincidence is a strong case for adaptive evolutionary change. Thus the third major objective of this chapter will be to compare geographic differences in prey availability with geographic variation in feeding behavior in order to identify the selective pressures, responsible for behavioral microevolution.

In this chapter I will first define some technical terms used to describe behavioral variation. I will then present the results of a case study of the microevolution of feeding behavior in garter snakes. I begin with a discussion of the phylogenetic, ecological, and physiological significance of behaviors that have been studied

in the laboratory. These behaviors are of two types: feeding response to actual prey and chemoreceptive response to prey odors. Three major issues are then addressed: (1) geographic differences in prey availability and diet, (2) the nature of behavioral variation within populations, and (3) the nature of geographic variation. Genetic analysis has proceeded only to calculations of resemblance among relatives, and behavioral inheritance in crosses has not yet been analyzed. Finally, microevolution of behavior is analyzed by computer simulation to suggest the time scale for population divergence, and the results are discussed in relation to the empirical and theoretical literature.

The Concept of Innate Behavior

The term "innate" carries a diversity of connotations. For this reason I abandon the term in the following discussions and recognize three separate aspects of "innate" behavior: *congenital*, *heritable*, and *ontogenetically stable*. It is important to distinguish among these three aspects since they may vary independently (e.g., congenital behaviors need not be heritable). These components of innate behavior are defined and discussed below.

The Analysis of Behavioral Variation within a Species

A complete description of behavioral variation within a species involves partitioning variation at various levels (e.g., populations, families, individuals) as well as tracing ontogenetic change in individuals. Table 19-1 shows a hierarchy of levels which will be useful in succeeding discussions, as well as the major causal factors contributing to variation at particular levels. This table supposes that a particular behavior has been measured at the same point in ontogeny in all individuals, so that ontogenetic change does not contribute to the differences between groups of individuals. Once this source of variation has been removed, the component of variation unique to a particular level can be estimated with an analysis of variance (Snedecor, 1956; Sokal and Rolf, 1969).

The statistical estimation of a particular observational component of variation enables us to isolate the contribution of one or a few causal factors (Falconer, 1960). Genetic differences between populations and additive genetic variance (heritable variation) within populations are the two causal components of major inter-

Table 19-1. The Observational Components of Behavioral Variation within a Species and Contributing Causal Factors. For example, the Observed Component of Variance among Sets of Full Sibs Estimates $\frac{1}{2} V_A + \frac{1}{4} V_D + V_{E_c}$. (Symbols follow Falconer, 1960)

Observational Components of Variance	Causal Components of Variance*
1. Geographic Variation (variance between populations)	genetic differences between populations; geographic differences in environment
2. Intrapopulation Variation (total variance within populations)	$V_P = (V_A + V_D + V_{E_c} + V_{E_w} + V_{E_i})$
3. Individual Variation (variance between individuals)	$(V_A + V_D + V_{E_c} + V_{E_w})$
Variance Between Families (e.g., between sets of full sibs)	genotypic variance ($\frac{1}{2} V_A + \frac{1}{4} V_D$); differences in common family environment (V_{E_c})
Variance within Families (e.g., within sets of full sibs)	genotypic variance ($\frac{1}{2} V_A + \frac{1}{4} V_D$); individual differences in environment and developmental accidents (V_{E_w})
4. Variation within Individuals	motivation and uncontrolled, temporal fluctuations in environment (V_{E_i})

*Key to symbols:

V_P = phenotypic variance = $(V_G + V_E)$;

V_G = genotypic variance = $(V_A + V_D)$; V_A = additive genetic variance (heritable variation), V_D = dominance variance;

V_E = environmental variance = $(V_{E_c} + V_{E_w} + V_{E_i})$; V_{E_c} = variance due to a common family environment, V_{E_w} = individual environmental variance, V_{E_i} = special environmental variance.

est. We see in Table 19-1, however, that both genetic and environmental factors contribute to the observed behavioral variation at each of these levels. We can, however, carefully control the environment in the laboratory, so that all individuals experience a uniform environment, and in this way eliminate or greatly reduce the contribution of environmental factors. To the extent that we have eliminated environmental contributions, we can attribute behavioral differences to genetic causes. A detailed example will be given later, but the reader should consult Falconer (1960) for further clarification.

Ideally the partitioning of behavioral variation within a population should be repeated at a variety of ages or ontogenetic stages. The benefits of making repeated measurements on the same set of individuals throughout ontogeny are described and stressed by Cock (1966). I will not analyze such an ideal data set here. Instead I will look for behavioral differences in newborn animals (partition congenital variation) and then determine whether these differences can be swamped by subsequent experience in a separate experiment.

Since data analysis will stress congenital, heritable, and ontogenetic variation, the relationships between these three kinds of variation deserve special comment.

Congenital variation is simply variation that is present at birth. Congenital does not mean genetic. Congenital variation may be a consequence of genetic differences, as in Down's syndrome in humans, or it may simply reflect environmental differences. For example, differences in birth weight are congenital by definition, but they may be due to differences in litter size or condition of the mother and not reflect any underlying genetic differences.

Heritability is a property of populations rather than individuals and may refer to a statistic or a parameter. As a parameter, heritability represents the proportion of phenotypic variance due to additive genetic variance (V_A/V_P). This parameter is estimated by heritability as a statistic. Estimation of parametric heritability is often accomplished by determining the degree of phenotypic resemblance among relatives. The estimation procedure derives from the theory of phenotypic resemblance on the supposition of Mendelian inheritance (Fisher, 1918), and, in principle, various replicated combinations of known relatives can be employed. Thus heritability is sometimes estimated from the regression of offspring behaviors on the behaviors of their parents. But heritability can also be estimated by analysis of behavioral variation

within and among other sets of relatives (e.g., within and among sets of sibs).

Heritability is not a property of a trait, but rather a property of a standardized phenotypic score in a particular Mendelian population existing in a specified environment. In other words, heritability will change with changes in relevant gene frequencies and can change with environment, or with maturation and experience, or with choice of trait measurement.

Heritability does not measure the genetic basis of a behavior in the ordinary sense. For example, a behavioral trait may be characteristic of a particular inbred strain and the trait may have an extensive genetic basis in the sense that many genetic loci contribute to the development and manifestation of the behavior. Nevertheless, heritability of the behavior is necessarily zero, if all individuals in the strain are genetically identical, as will commonly be the case in a highly inbred strain. Heritability is a summary statement about the genetics of behavioral differences, it is not a statement about the genetic basis of particular behaviors.

Nevertheless, heritability is of central importance in theories of phenotypic evolution, since response to selection is proportional to parametric heritability as well as to the intensity of selection (Falconer, 1960).

Ontogenetic variation is variation within individuals that arises during ontogeny. Ontogenetic variation in behavior may be a consequence of experience, sexual maturation, absolute age, or any other variable that changes during the individual's lifetime.

Ontogenetic change and heritability are separate issues. They represent two different axes of description. Thus heritability may change during ontogeny or it may remain constant. Imagine, for example, a cohort composed of only two genotypes and suppose that these genotypes show a congenital difference in behavior. If the genotypes respond differently to experience, so that their average behaviors diverge, then both parametric heritability and its statistical estimate will increase with time (even though the representation of genotypes in the population remains constant). Heritability changes with ontogeny in this case. Conversely, the behaviors of each genotype might change with time in parallel fashion such that the differences between the two genotypes remain constant. There is still ontogenetic change in each individual, but heritability will remain constant. Furthermore, two behavioral traits in the same population may differ dramatically in magnitude of ontogenetic change, yet they may have the same

heritabilities. Thus heritability says nothing about capacity for ontogenetic change. Heritability and ontogenetic change are separate issues for the simple reason that heritability is evaluated at a particular point in ontogeny. [These and other constraints on the utility of heritability estimates are discussed by Feldman and Lewontin (1975) and Cavalli-Sforza and Feldman (1978).]

Ethologists have sometimes stressed the study of congenital behaviors that are ontogenetically stable for the wrong reasons. These two attributes have important implications, but they do not constitute evidence for genetic determination or heritability. First, genetics is the study of the inheritance of differences. The point of interest is whether there is congenital variation, not whether the behavior is perfectly expressed in newborn animals (i.e., simply congenital). Second, we require a comparison of behaviors in and among sets of known relatives in order to establish whether congenital differences are heritable. Third, ontogenetic stability of behavior is not only useful because it indicates immunity to modification by experience but also because it means that heritability may not change with ontogeny or its correlates.

The characterization of behavioral variation has special significance if the behavioral trait has important ecological ramifications. The evolution of the ecological niche, including its behavioral aspects, has been the subject of much theoretical work. But there has been surprisingly little empirical analysis of the genetics and microevolution of behavioral components of the niche. Mayr (1942), Lewontin (1967), Manning (1975), and Ehrman and Parsons (1976) have all stressed the need for such studies. The following case study is a response to these pleas.

The Microevolution of Feeding Behavior in Garter Snakes: A Case Study

The Ecology of Garter Snakes and Other Natricine Snakes

About 20 species of garter snakes (*Thamnophis*) are distributed throughout North and Middle America. The genus is part of an extensive radiation of natricine snakes (family Colubridae) of which garter snakes and water snakes (*Nerodia*) are the most familiar examples (Malnate, 1960; Mao and Dessauer, 1971; Rossman and Eberle, 1977; Ruthven, 1908). A common ecological denominator among the diverse natricine genera in the Old and New

Worlds is a riparian habit with predation of fish and frogs; this may represent the ancestral ecotype. Today natricines occupy a variety of habitats and exploit an unusual spectrum of prey (Fig. 19-1). Snake taxa are notorious for specialization on particular prey (Arnold, 1972), and natricines provide numerous examples: *Regina* are crayfish specialists, the monotypic genus *Tropido-*

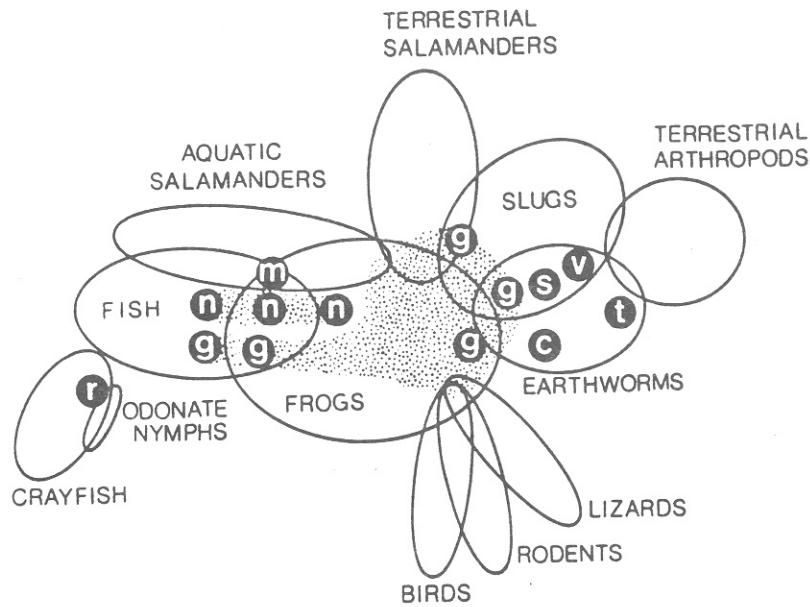


Figure 19-1. Diets of North American natricine snakes. The prey of these snakes are represented as a series of ellipses. Aquatic prey are on the left, terrestrial prey on the right. The diets of natricine genera are represented by the smaller, dark circles: *Regina* (r); *Nerodia*, formerly *Natrix* (n); *Seminatrix* (m); *Thamnophis* (g); *Storeria* (s); *Virginia* (v); *Tropidoclonion* (t); *Clonophis* (c). The area subsumed by each of these smaller circles accounts for about 80 percent of the diet; the remaining fraction of the diet can be deduced by doubling the diameter of each circle. Thus *Tropidoclonion* are mainly earthworm specialists that occasionally prey on soft-bodied arthropods. The diets of two speciose genera, *Nerodia* (n) and *Thamnophis* (g), are represented by stippled areas, while the diets of particular, representative species are designated by small circles. Thus, three species of water snakes are shown; from left to right they are *Nerodia cyclopion*, *N. sipedon*, and *N. erythrogaster*. Five groups of garter snakes are shown. Beginning from the extreme left and moving counter-clockwise, they are: *Thamnophis rufipunctatus*, *T. couchi* and *T. melanogaster*, *T. sirtalis*, *T. butleri*, and *T. ordinoides*. Information on the diet of *Regina* is from Godley (1979).

clonion is an earthworm specialist. Two speciose genera, *Nerodia* and *Thamnophis*, are less specialized but even they include species with restricted diets as well as species with catholic diets.

Thamnophis elegans, the subject of this chapter, is perhaps the most exceptional North American natricine in terms of dietary breadth. Its diet spans the entire range of prey taken by all other species of garter snakes (the lower stippled area in Fig. 19-1). In various parts of its range, *T. elegans* feeds on frogs, fish, rodents, leeches, slugs, lizards, birds, and salamanders. Sometimes it even forages in the intertidal zone and preys on crabs and gastropods (Arnold and Wassersug, 1978; Campbell, 1969; Fitch, 1940; Fox, 1951; Gregory, 1978; Tanner, 1949; White and Kolb, 1974). At any particular locality the diet is restricted to a subset of this prey inventory, and populations are sometimes quite specialized.

The tendency of some *T. elegans* populations to specialize on slugs will be a topic of major concern. Slug specialization has been a recurrent theme in the evolution of natricines (see Fig. 19-1) and it has independently evolved in other groups of snakes (e.g., *Conia*, *Duberria*, *Tropidodipsas*) (e.g., Zweifel, 1954). Slugs are a major prey of two natricine genera (*Storeria* and *Virginia*) and some species of *Thamnophis* (e.g., *T. ordinoides* and *T. butleri*). Presumably the ancestor of such a slug specialist first preyed on slugs in only a portion of its geographic range. Adaptations for slug predation were probably enhanced in these populations, and eventually the entire species was transformed into an obligate slug specialist. *T. elegans* provides a model for the first stage in this process of specialization or niche contraction, since some populations never prey on slugs, while others specialize on this prey.

The Geographical Ecology and Systematics of *T. elegans*

The distribution of *T. elegans* is centered in the Great Basin of western North America, but it ranges west to the Pacific Ocean, east to the Black Hills of South Dakota, far north in British Columbia and it follows the crest of the Sierra Madre Occidental south to Zacatecas, Mexico (Fitch, 1940; Stebbins, 1966; Webb, 1976). Throughout its range, *T. elegans* frequents riparian habitats. Isolated populations in the high mountain meadows of the San Bernardino Mountains of southern California and the Sierra San Pedro Matir of Baja California (Fig. 19-2) suggest that this species was more widely distributed when western North America had a moister climate during the Pleistocene. In California, for example, it is largely restricted to regions with an annual rainfall of 20

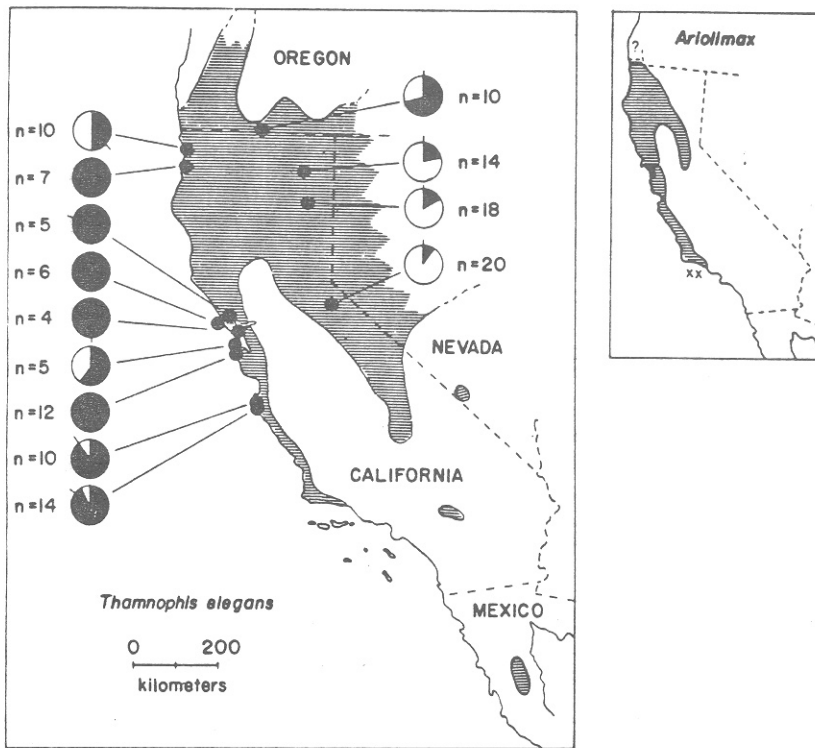


Figure 19-2. The geographic distribution of slug-feeding tendency in wild-caught *T. elegans*. The geographic distribution of *T. elegans* in California and adjoining regions is shown with cross hatching. The responses of 135 wild-caught snakes from 13 populations are shown; *n* indicates the number of snakes in each sample. The snakes were offered the slug *Ariolimax* on two dates. The black sectors of each pie diagram indicate the proportion of snakes that attacked and ate slugs on the date with the highest score (generally first date), and the score on the other date is indicated with a tic mark. Four inland populations are outside the range of *Ariolimax*, the distribution of which is shown in the map on the right (after Meade, 1943).

inches or more. During the late Pleistocene it probably inhabited lake shores in the Great Basin and invaded California from the northeast; this inference will prove useful in a later computer simulation of its behavioral microevolution.

In northern California I have studied the ecology and diet of this species at two principal study sites: a coastal site in Humboldt County and an inland site (Eagle Lake) in Lassen County. These

two sites were also the source of gravid females whose newborn progeny were used in laboratory tests of feeding behavior. Coastal California, including the coastal study site, is inhabited by a geographic race (*T. e. terrestris*) that differs markedly from inland races in coloration, scalation, body proportions, and foraging habits (Fox, 1951). The inland study site lies at the junction of two inland races (*T. e. elegans* and *T. e. vagrans*), but snakes at this site most closely resemble *T. e. vagrans*, the race characteristic of the Great Basin.

Although the morphological differentiation of populations of *T. elegans* in California is impressive, it is clear that we are dealing with a single polytypic species. Fox (1951) demonstrated clines in characters that distinguish inland and coastal races in northern California. The morphological pattern is one of smooth intergradation. Furthermore, I have had no difficulty crossing snakes from my inland and coastal sites in the laboratory. The F_1 is as viable as crosses within populations and is intermediate in morphology.

At the inland site *T. elegans* is markedly aquatic and commonly forages underwater. In contrast, the coastal snakes are terrestrial foragers that seldom enter water to capture prey even though they frequent riparian habitats. This geographic difference in foraging habits is reflected in the diets of inland and coastal populations.

In California, *T. elegans* shows pronounced geographic variation in diet (Table 19-2). The prevalence of slugs in the diet is one of the most striking geographic differences. Slugs (*Ariolimax*, *Deroceras* and *Prophysion*) are the dominant prey of coastal populations, while inland populations prey principally upon anurans (Arnold and Wassersug, 1978), fish, and leeches. This geographic pattern reflects the distribution of slugs in California. Slugs are abundant in moist coastal habitats, characterized by high rainfall and marine fog during the summer, but they are absent or rare at arid inland sites. For example, I failed to find a single slug during five summers of rock and log turning at the inland site of Eagle Lake.

We can predict geographic variation in feeding reactions on the supposition that feeding behavior evolves in response to prey availabilities. The availability of prey taxa at the inland and coastal sites is summarized in Table 19-3. This table lists all prey taxa used in laboratory tests of feeding and chemoreceptive responses, as well as some related taxa. Of these prey, slugs and

Table 19-2. Geographic Variation in the Diet of *Thamnophis elegans* in California.^a

Prey Taxa	Coastal populations (<i>T. e. terrestris</i>)			Inland populations (<i>T. e. vagrans</i> and <i>T. e. elegans</i>)		
	Little Sur River, Monterey County	Garrapata Crk., Monterey County	Arcata, Humboldt County	Eagle Lake, Lassen County ^b	Mahogany Lake, Lassen County ^c	Gardner Meadows, Tuolumne County ^c
	% items (n = 127)	% stomachs (n = 18)	% items (n = 128)	% stomachs (n = 9)	% items (n = 137)	% stomachs (n = 70)
Slugs	87	67	99	89	93	94
Lagomorphs and rodents	3	22	0	0	6	4
Anurans	6	6	0	0	0	0
Salamanders	2	6	0	0	0	0
Lizards	1	6	0	0	1	1
Insects	1	6	0	0	0	0
Earthworms	0	0	1	11	0	0
	100%		100%		100%	

^aColumns labeled "% stomachs" include only stomachs that contained prey. Since some stomachs had more than one type of prey, these columns do not always sum to 100%.

^b*T. e. vagrans*.

^c*T. e. elegans*.

Table 19-3. The Occurrence of Prey Taxa at the Two Study Sites. (Presence in Diet Denoted as Follows: Present in Diet, Solid Underline; Suspected in Diet, Dashed Underline; Absent from Diet, No Underline.)

	Coastal (Humboldt Co., Calif.)	Inland (Lassen Co., Calif.)
Slugs		
<i>Ariolimax</i>		
<i>Deroceras</i>	<u>Present</u>	Absent ^a
<i>Prophysion</i>		
Anurans		
<i>Hyla regilla</i>	<u>Present</u>	<u>Present</u>
<i>Bufo boreas</i>		
Salamanders		
Plethodontidae		
<i>Batrachoseps</i>		
<i>Aneides</i>	<u>Present</u>	Absent ^b
<i>Ensatina</i>		
Ambystomatidae		
<i>Ambystoma</i>	<u>Present</u> ^c	<u>Present</u> ^c
Salamandridae		
<i>Taricha</i>	Present ^d	Absent ^d
Fish	Present ^e	<u>Present</u>
Annelids		
leeches	Present ^e	<u>Present</u>
earthworms	Present	Present

^aAbsent at inland site; absent or rare at other inland sites.

^bPresent at inland sites 70 km to SW.

^c*A. gracile* present at coastal site; *A. macrodactylum* occurs at a locality only 6 km from inland site.

^dPresent 70 km SW of inland site; this salamander is highly toxic to *T. elegans*.

^eAlthough present at the coastal site, these prey are seldom, if ever, encountered by *T. elegans* due to terrestrial foraging habits.

plethodontid salamanders are abundant at the coastal site, but absent at the inland site. We might expect geographic variation in predatory responses to these taxa. Likewise we might expect geographic differences in responses to fish and leeches. These prey are available at both sites, but in the field they are eaten only by inland snakes (see Table 19-2). We do not expect geographic

variation in reactions to other prey (anurans, *Ambystoma* and *Taricha*) since these prey are either present at both sites or absent from both coastal and inland diets.

Stimulus Control of Prey Attack in Natricine Snakes

A behavioral study stands or falls on the traits that are selected for study. Feeding responses to dead prey and chemoreceptive (tongue flicking) responses to prey odor are stressed in the following sections, and in order to develop the rationale for this choice of traits, I will briefly review the literature on stimulus control of prey attack in natricine snakes. The overriding point is that odors emanating either from dead prey or from odoriferous swabs are often sufficient to elicit prey attack in natricines.

Chemoreception via the Jacobson's organ is a major sensory modality governing prey attack in natricine snakes, but nasal olfaction, vision, and tactual contact with the snake's body may also play important roles (Arnold, 1978; Burghardt and Pruitt, 1975; Czaplicki and Porter, 1974; Drummond, 1979; Kubie and Halpern, 1976). Chemicals from the environment are apparently transported to the apertures of the Jacobson's organ in the roof of the mouth by the tips of the bifurcate tongue (Fig. 19-3). The flicking tongue samples the chemical environment and transports odoriferous particles to the chemosensory epithelium of the Jacobson's Organ (an apparent homologue of the mammalian vomero-nasal organ). Garter snakes begin tongue flicking immediately after birth, even while still inside the amnion, and show bouts of tongue flicking throughout life whenever there are sudden changes in the environment. Field observations show that tongue flicking is employed underwater, as well as on land, during prey search and predatory encounter.

Prey odor alone is sufficient to elicit prey attack in naive, newborn natricine snakes (Burghardt, 1967; Burghardt and Pruitt, 1975). This important fact can permit meaningful ecological interpretation of laboratory results, but some precautions are in order. Numerous studies of chemoreceptive response to prey odors have revealed congenital biases in the perceptual abilities of naive natricines; the odors of some prey elicit much stronger responses than the odors of other prey. The ecological significance of such biases is unclear, however, since it is difficult or impossible to say whether a stronger chemoreceptive response to one prey means that the snake is more prone to attack that prey in nature. Al-

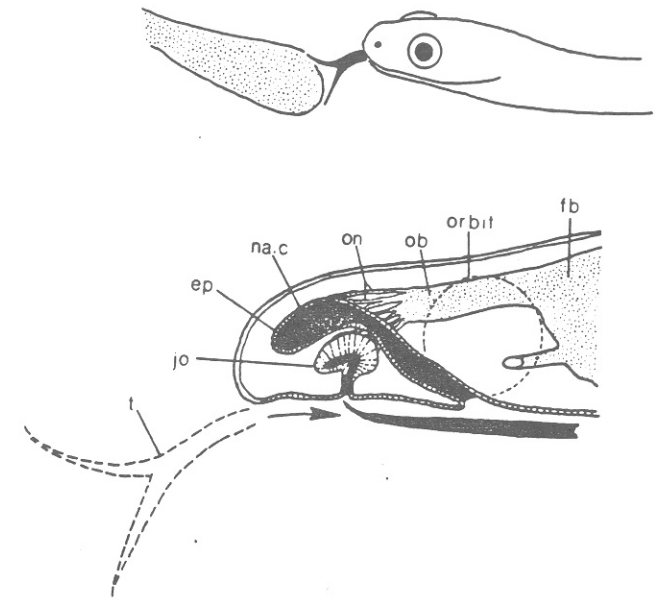


Figure 19-3. The chemoreception mechanism of snakes. Chemoreceptive response to an odoriferous swab is shown above. During maximum tongue protrusion just the tongue tips contact the odor source. The snake's head is shown in parasagittal section in the lower figure (after Smith, 1969): Jacobson's organ (jo); olfactory chamber of the nasal sac (na.c); olfactory epithelium (ep); olfactory nerves (on) dorsal to the vomero-nasal nerves from the Jacobson's organ; olfactory bulb (ob); forebrain (fb); orbit of the eye (orbit); tongue (t). The path of the tongue during retraction is shown by the arrow. The apertures of the Jacobson's organ lie just above the tips of the retracted tongue.

though such biases within a single snake population are difficult to interpret, a comparison of reactions of different populations or species of snakes to the same prey odor can be very informative. For example, congenital differences between snake species sometimes correspond with major dietary differences. The naive young of crayfish specialists (*Regina septemvittata* and *R. grahami*) show dramatic responses to crayfish odor, but the young of a non-crayfish predator (*Nerodia sipedon*) do not (Burghardt, 1968). Thus the comparative study of chemoreceptive response to particular odors can detect an important class of ecological adaptations, namely differential ability to recognize particular prey by chemoreception.

Chemoreception is probably the major sensory modality governing slug predation by coastal populations of *T. elegans*. When newborn coastal snakes were presented with their first live slug, they did not respond to the slowly moving object. Instead they showed an active tongue flicking response to the slug's mucus trail, followed and periodically attacked the trail as the unperturbed slug crawled along some distance away. Eventually the slug itself was attacked and eaten when the snake reached the end of the trail. I have observed coastal snakes as they foraged for slugs in nature. Again chemoreception seemed to be the major channel of detection, since the snakes probed and lunged at slugs hidden under the margins of large rocks.

Laboratory Tests of Wild-Caught Snakes

When *T. elegans* are brought into the laboratory from nature, they show stable, geographic differences in the propensity to eat slugs. Figure 19-2 summarizes the results of slug feeding trials with 135 snakes collected from various localities in California and Oregon. The snakes were offered a standard sized piece of dead slug (*Ariolimax californicus*) on two dates, five weeks apart. Prior to the tests the snakes were fed a standard food (fish) and, with the exception of five snakes from one coastal locality, none of the snakes had encountered slugs for at least six months. Coastal snakes showed a marked tendency to eat slugs in both trials, while inland snakes tended to refuse slugs. Allopatry with *Ariolimax* (four inland populations) versus sympatry (nine coastal populations) provided a nonarbitrary classification of populations. The feeding difference between inland and coastal populations was highly significant on both dates (chi square = 42.1 and 95.5, d.f. = 1, $p < .005$). This geographic difference in the propensity to attack slugs might be attributed to experience, but in any case, the difference persisted despite six months of uniform experience in the laboratory. The obvious next step was to rear snakes in the laboratory and control experience from birth.

Laboratory Tests with Naive, Newborn Snakes

FEEDING TRIALS. Naive, newborn snakes also show geographic variation in slug-eating tendency. Arnold (1977) compared the response of naive, 14-day old *T. elegans* from coastal localities ($n = 293$

snakes) and inland localities ($n = 101$) and found that 73 percent of the coastal snakes attacked and ate slugs, while only 35 percent of inland snakes attacked this prey. This difference persisted in three subsequent trials, again suggesting that the geographic difference in behavior was ontogenetically stable. The difference could not be attributed to differences in hunger, since control feeding trials with anurans after each slug trial showed no geographic difference. The results of these slug-feeding trials, as well as subsequent trials with naive snakes are displayed in Figure 19-4. The results are in remarkable agreement with tests of experienced, wild-caught snakes. Naive coastal snakes from localities sympatric with slugs are prone to attack these prey, while inland snakes from allopatric localities tend to refuse them.

In order to study frequency distributions of feeding tendency we have applied a simple screening procedure to relatively large samples of naive snakes from various populations. The screening technique consists of offering a small, standard-sized piece of prey on each of ten successive days (Arnold, 1977). The resultant feeding score ranges from 0 (consistent refusal) to 10 (consistent attack and feeding). The pieces of prey are small enough to avoid satiation. They are also motionless, so that chemoreception is probably the dominant modality mediating attack. The screening tests are executed at a standard age after birth in the laboratory and represent the first exposure to prey or any food. In other words, they provide a test for congenital variation in behavior.

Congenital feeding scores show bimodal distributions within snake populations. For example, when population samples were screened for slug-eating propensity, most snakes either consistently ate or consistently ignored slugs (Fig. 19-5). The rarity of snakes with intermediate scores produces an extreme departure from binomial expectations and permits a simple classification of snakes as belonging to either a slug-eating morph (feeding score 5-10) or a slug-refusing morph (score 0-4) (Arnold, 1977). The proportion of slug-eating morphs varies geographically in relation to the distribution of slugs. The significance of this spatial pattern will be discussed in subsequent sections, since it implies a response to natural selection. For the moment, our focus is on the form of feeding morph distributions. We have applied screening tests to over 1500 naive young of *T. sirtalis*, as well as *T. elegans*, using a variety of prey (fish, anuran tadpoles, slugs, earthworms) and always obtained the same result. Feeding scores were always bimodally distributed within populations with one or the other modal

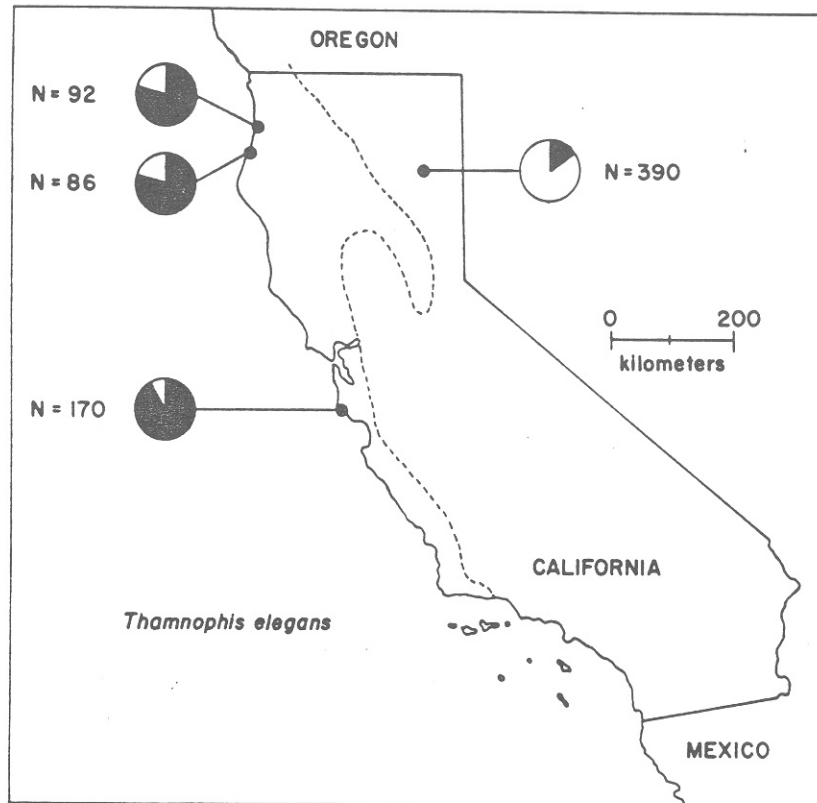


Figure 19-4. The geographic distribution of slug-feeding morphs in samples of naive, newborn snakes. The black sectors represent the proportion of snakes that consistently attacked and ate slugs, *Ariolimax*; N indicates the number of snakes in each population sample. The inland distribution limit of the slug *Ariolimax* is shown with a dashed line.

class predominating in the sample. The minority morph (either prey refusers or prey eaters, depending on the snakes species, population and prey) generally constituted less than 15 percent of the sample. These minority morphs have attracted our attention, despite their relative rarity, because they often refuse prey that are important in the natural economy of their parental population. Our working hypothesis is that genetic segregation in natural snake populations produces maladaptive feeding morphs in each generation.

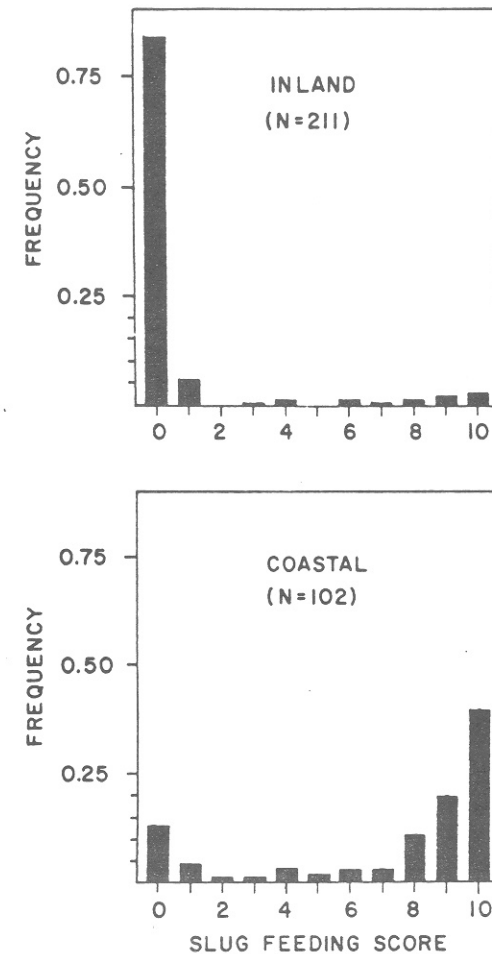


Figure 19-5. Frequency distributions of slug feeding scores in an inland and a coastal sample of naive, newborn snakes.

Prey-refusers refuse to eat only particular prey taxa, and they will persist in such refusal until they starve to death unless alternative prey are offered. Specificity of prey refusal is characteristic of both species that have received most attention in the laboratory—*T. elegans* and *T. sirtalis*. Thus fish-refusing morphs in a population of *T. sirtalis* readily ate anurans (Arnold, 1978), the slug-refusing morphs in *T. elegans* refused two genera of unrelated slugs but readily attacked anurans (Arnold, 1977). Subsequently

we obtained the same general result by screening for tendency to eat one prey for 10 trials and then immediately screening for 10 additional trials with a second prey type. Such tests revealed independence between the two batteries of trials. Thus prey-refusing morphs are not afflicted with a general anosmia for prey recognition or a general lack of interest in food; they simply fail to react to specific classes of prey.

Feeding morphs are remarkably stable. In a recent experiment, we reared a sample of inland *T. elegans* ($n = 41$ Eagle Lake snakes) for one year in the laboratory after screening for slug-feeding responses when the snakes were naive and newborn. When the snakes were retested for slug-feeding responses after 12 months of maintenance on a fish diet, polymorphism for slug predation proved to be very stable (Table 19-4). Not only was the distribution of responses still bimodal, the probabilities of remaining the same morph were .90 or greater. This suggests that congenital differences in tendency for slug predation are maintained throughout life.

I have speculated (Arnold, 1977) that failure to attack slugs by some individual *T. elegans* might be a consequence of initial experience with slugs during screening tests. Perhaps slug-refusal is

Table 19-4. Ontogenetic Stability of a Feeding Response in *T. elegans*. Forty-one Inland *T. elegans*, Representing 12 Litters from Eagle Lake, were Screened for Slug Feeding Tendency in 10-trial Feeding Tests at Two Ages. Transition Probabilities are Shown in Parentheses.

		Slug feeding score at age one year		
		Consistent refusal (score 0-4)	Consistent acceptance (score 5-10)	
Slug feeding score at age 16-25 days	Consistent refusal (score 0-4)	27 (.90)	3 (.10)	30
	Consistent acceptance (score 5-10)	1 (.09)	10 (.91)	11
		28	13	$\Sigma = 41$ snakes

chi-square = 24.33**, d.f. = 1

a consequence of an initial negative experience with slugs (slugs are sticky, difficult prey), rather than being strictly congenital. Handling difficulty during the first attempt at slug predation might be a wholly random event and it might cause the snake to refuse all subsequent slugs. Recently we videotaped naive *T. elegans* during their first slug presentation and found that slug-refusing morphs failed to even respond to their first slug. Thus, prey-refusal appears to be strictly congenital as well as specific.

Congenital differences in the tendency to attack particular prey also appear to be heritable and hence vulnerable to natural selection. Thus, Arnold (1977) reported significant heterogeneity in proportions of slug-refusing morphs among litters from a *T. elegans* population. In order to conduct a stronger test for heritability of feeding scores, we will need to rear and breed test subjects in the laboratory so that we have naive test scores for both parents and offspring. These studies are now underway. In the meantime, we have tested for the heritability of a behavioral trait correlated with feeding score—the chemoreceptive response of naive snakes to prey odor. This trait has the statistical virtue of being unimodally distributed (rather than bimodal) and so permits a classical partitioning of variance among families and conventional estimates of heritability. These analyses confirm the suspicion of genetical variation underlying feeding responses.

CHEMORECEPTIVE RESPONSES TO PREY ODORS BY NAIVE SNAKES. The following experiment was designed to test for geographic variation in chemoreception and to estimate heritabilities of chemoreceptive responses. Nineteen gravid females from the inland site and 10 gravid females from the coastal site were captured in July and shipped back to Chicago by air. These females subsequently gave birth to a total of 313 progeny in the laboratory. In order to eliminate, or at least minimize, the four major categories of environmental variance in behavior detailed in Table 19-1, all newborn snakes were kept and tested under identical conditions in the laboratory. In particular, all newborn snakes were separated from their mother immediately after birth and each snake was housed in its own container in a special attempt to reduce the possibility of a common family environment (see Arnold, 1977, 1978 for additional details of maintenance). In addition, none of the snakes were fed prior to the tests; all of the snakes were completely naive.

Chemoreception test procedures. Prey odors were presented to naive, newborn snakes on cotton-tipped swabs (single cotton

tipped applicators, 15 cm, Chesebrough-Ponds, Inc., 5-5405) (Fig. 19-6). These test swabs were prepared either by rubbing the cotton tips directly on prey (i.e., the slug *Ariolimax*), or by swirling the swabs among recently thawed, dead prey (amphibians and leeches), or among live prey (fish) in standard, weight-specific volumes of distilled water (5 cc water at 27°C per g prey). In order to insure

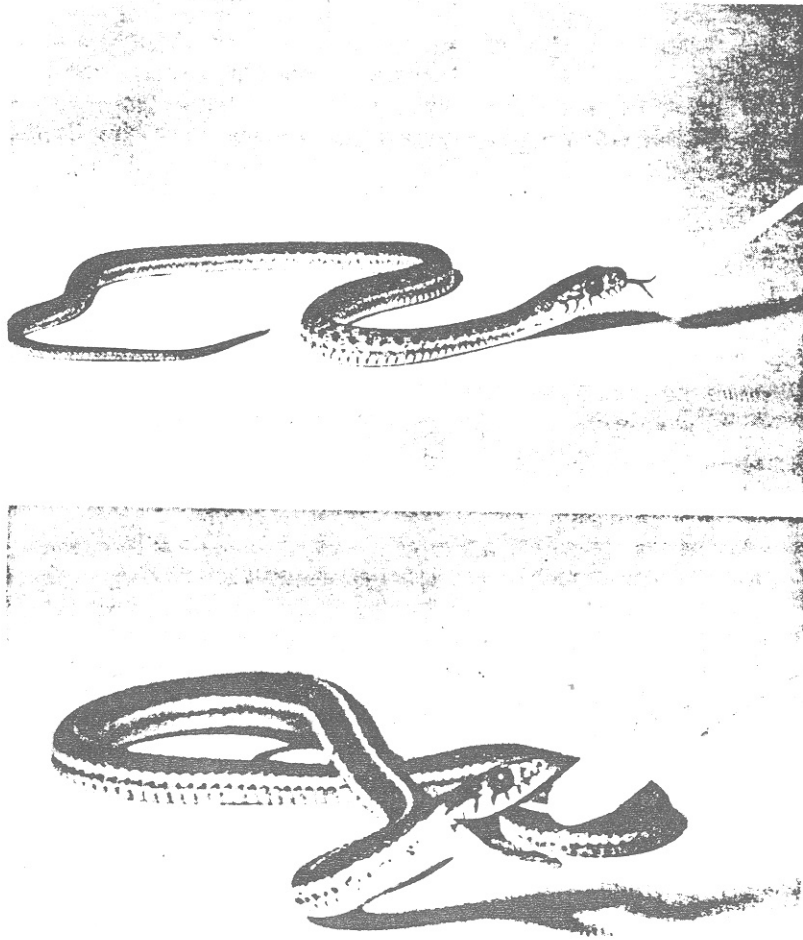


Figure 19-6. Chemoreceptive (above) and attack response (below) to odoriferous test swabs by naive, newborn garter snakes.

uniformity of a particular swab type, all the swabs required for the experiment were made at one time in a single batch and kept frozen until needed. Control swabs were similarly prepared by dipping the cotton tips in distilled water and freezing them in a batch. The aim of this preparation procedure was to produce swabs that simulated the gross chemistry of prey surfaces as closely as possible. All swabs were visually identical. Consequently differences in response to different swab types could be attributed to chemical rather than visual differences.

The snakes were tested with the odors of natural prey species that are sympatric with *T. elegans* in some portion of its range; the one exception was the common guppy (*Poecilia reticulata*), a neotropical fish. Many of the test species (Table 19-5) occurred in the natural diets of inland and/or coastal populations of *T. elegans* (see Table 19-3).

Prey odors were presented in a standard sequence to all snakes (Table 19-5). At each presentation the odoriferous cotton tip of the swab was held 1 cm in front of the snake. The number of tongue flicks that contacted the swab tip during a 1 min. interval constituted the snake's raw chemoreception score (see Arnold, 1978 for details of the scoring procedure). The natural logarithm of these tongue flick rates was taken in order to assure uniform variances for statistical tests. The presentations were grouped in two sequences of 5 prey odors and a control. The first sequence was presented at 14 days of age and the second sequence was presented the next day. A standard interval of 40 min. elapsed between tests in each sequence. The day after the completion of the chemoreception tests, both populations were screened for slug feeding responses during a 10-day presentation sequence, as previously described.

General results of chemoreception tests. Snakes from both populations showed dramatic responses to prey odors (Table 19-5). While the modal response to the distilled water control was one tongue flick (Fig. 19-7), prey odors elicited responses that were higher by 2-30 fold.

Chemoreception scores (log_e of tongue flick rates) were continuously distributed within populations, in marked contrast to the bimodal distributions of feeding scores (Figs. 19-5, 19-8, 19-9). Normal probability plots indicated a reasonable approach to normality, especially when the mean response fell midway on the scale (e.g., Fig. 19-9). The contrast between continuously distributed chemoreception scores and discontinuously distributed feeding

Table 19-5. A Comparison of Chemoreceptive Responses to Prey Odors by Naive, Newborn *T. elegans* from a Coastal Population (n = 102) and an Inland Population (n = 211).

Prey Species	Prey Taxon	Mean (Tongue Flick Rate)		Standard Deviation (log _e TFR)	Divergence ¹ (in standard deviations)	Analysis of Variance of Litter Means (F _{1,27}) ²
		Coastal	Inland			
First Presentation Sequence (age 14 days)						
<i>Ariolimax californicus</i>	slug	30.9	4.3	1.1406	1.1464	85.71**
<i>Aneides lugubris</i>	salamander	9.4	4.5	1.3579	1.0705	11.30**
<i>Taricha torosa</i>	salamander	3.0	2.4	1.2068	.9378	1.54ns
<i>Bufo boreas</i> tadpoles	anuran	25.9	30.3	1.1957	.7605	2.09ns
<i>Poecilia reticulata</i>	fish	2.1	3.2	1.0115	.9577	9.11**
distilled water	control	1.3	1.6	.5407	.5825	7.76**
Second Presentation Sequence (age 15 days)						
<i>Erpobdella punctata</i>	leech	11.8	2.5	1.5536	.9487	19.40**
<i>Batrachoseps attenuatus</i>	salamander	14.0	12.7	1.4331	1.3478	.04ns
<i>Ambystoma tigrinum</i> larvae	salamander	9.4	10.2	1.4830	1.1132	.37ns
<i>Hyla regilla</i> tadpoles	anuran	28.2	21.2	1.1641	.9858	1.65ns
<i>Hyla regilla</i> transformed frogs	anuran	37.6	25.8	.8724	1.0273	3.01ns
distilled water	control	1.4	1.5	.5024	.5951	.68ns

¹The difference between population means (log_e TFR) divided by the average standard deviation.

²Analysis of variance performed on log_e TFR; ** indicates significance at the .01 level, ns indicates p > .05.

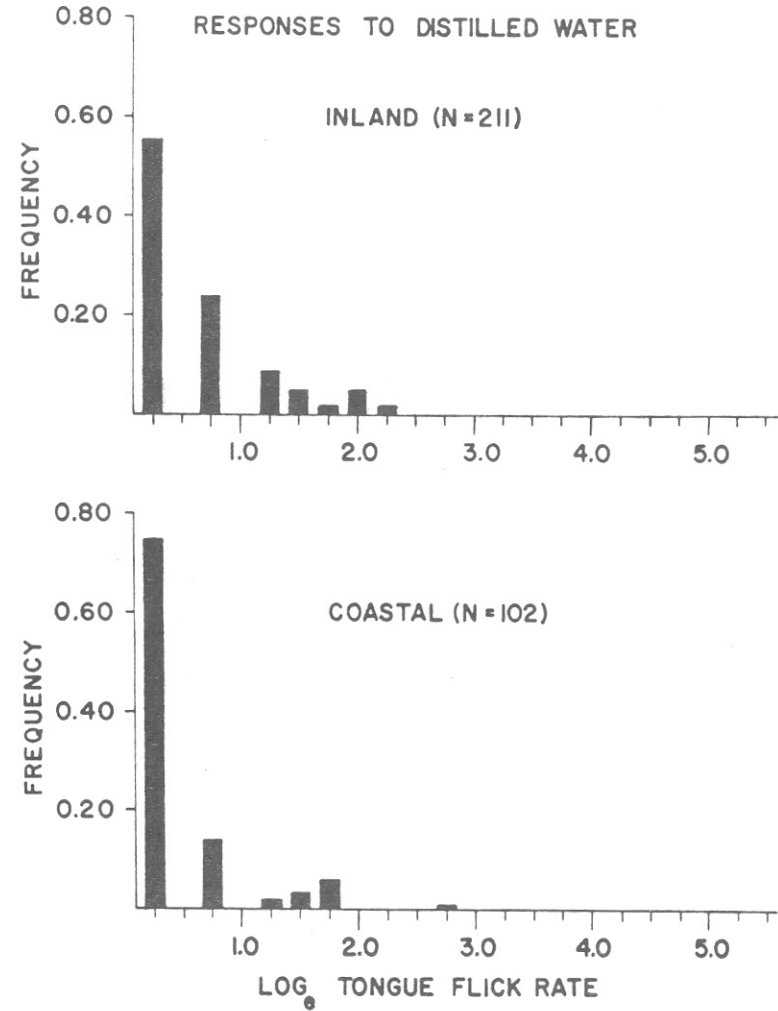


Figure 19-7. Distributions of chemoreceptive response to distilled water (first control presentation) by naive, newborn *T. elegans* from inland and coastal populations.

scores will be discussed after we consider the conspicuous geographic differences in chemoreception response.

Geographic variation in behavior. Coastal snakes showed a much stronger chemoreceptive response to slug odor than inland snakes. This geographic difference was apparent in a comparison of mean chemoreceptive scores (see Table 19-5) and also in comparison of attack responses to the slug test swabs; 59 percent of the

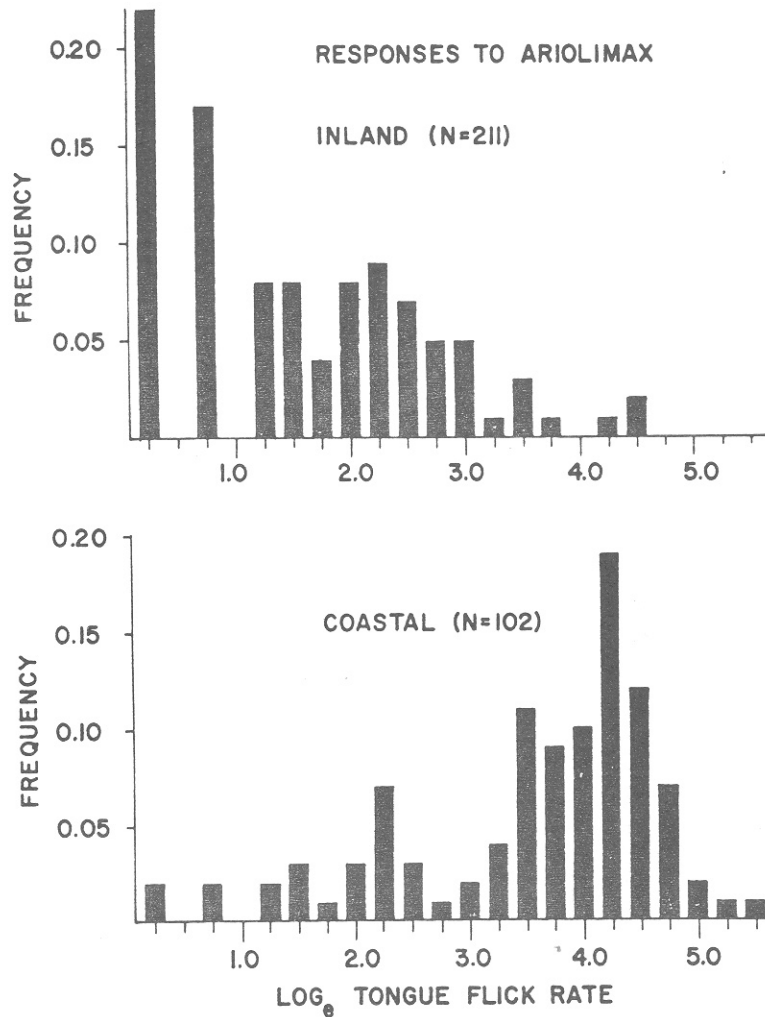


Figure 19-8. Distributions of chemoreceptive response to the odor of the slug *Ariolimax californicus* by naive, newborn *T. elegans*, from inland and coastal populations.

coastal snakes attacked the slug swabs, while only 4 percent of the inland snakes attacked these swabs. (The difference was not simply a consequence of the fact that slug odor was the first test in the sequence. The same geographic difference in chemoreceptive recognition of slugs also occurred in two other experiments, independent of presentation order.) When the two population samples

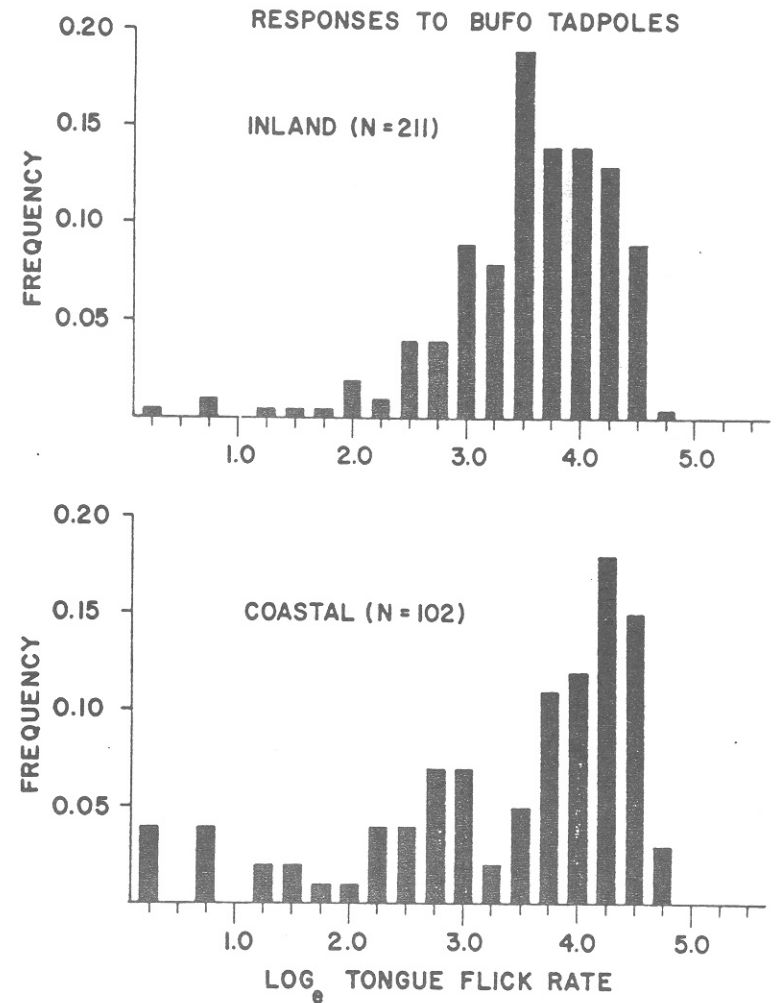


Figure 19-9. Distributions of chemoreceptive response to the odor of toad tadpoles (*Bufo boreas*) by naive, newborn *T. elegans*, from inland and coastal populations.

were screened for feeding responses to slugs immediately after the chemoreception tests, coastal snakes showed a greater predilection for slug feeding, as expected (Fig. 19-5). Thus, naive coastal snakes whose parental population exploits slugs in nature, showed a greater chemoreceptive response to slug odor and also a greater tendency to actually feed on slugs.

Coastal snakes also showed a stronger chemoreceptive response to leech odor, but geographic differences in reaction to other prey odors were either slight or nonexistent. For example, there was no indication of geographic variation in chemoreceptive recognition of anurans (Fig. 19-9). Some small differences were nevertheless statistically significant: the inland population showed a stronger response to fish odor and the coastal population showed a stronger response to the salamander *Aneides lugubris*. Both of these geographic differences may be adaptive responses to selection since only coastal populations are likely to encounter plethodontid salamanders like *Aneides*, and only inland populations prey on fish in nature. However, these interpretations should be viewed with caution, since the differences are so slight (the average inland snake gave only one more tongue flick to fish odor than the average coastal snake). Finally, the stronger response of coastal snakes to leech odor was most surprising. Inland snakes prey on leeches in nature, but they are unknown in the diet of coastal snakes and even related terrestrial annelids (earthworms) are rare in coastal diets (see Table 19-2). It turned out that leech responses and slug responses were correlated traits, perhaps as a consequence of shared surface chemicals. The relevant analyses of phenotypic and genetic covariation will be taken up later.

The nature of behavioral variation within populations. Heritabilities were calculated by partitioning the total variance within populations into within and among litter components. The ratio of the among litter component of variance to the sum of these two components is known as the intraclass correlation coefficient, r_i , and, when corrected for the degree of relationship within families (litters), it provides an estimate of heritability (Falconer, 1960). In the present case, littermates were full sibs (Blanchard, 1943, Devine, 1975), so heritability was estimated as twice the intraclass correlation.

Such estimates simply place an upper bound on the magnitude of heritability. We desire an estimate of the ratio (V_A/V_P) , but twice the full sib intraclass correlation estimates $([V_A + \frac{1}{2} V_D + 2 V_{Ec}]/V_P)$; (see Table 19-1). Thus the present estimates of heritability necessarily include a portion of dominance variance (V_D) of unknown magnitude. Fortunately, however, nongenetic variance due to a common family environment (V_{Ec}) was undoubtedly eliminated by the experimental design: (1) littermates were separated immediately after birth and all snakes were kept and tested under identical conditions, (2) maternal diet has no effect on the chemore-

ceptive responses of progeny (Burghardt, 1971), and (3) birth weight, litter size, and dam size showed no correlation with litter differences in chemoreception. Hence the present calculations of heritability can be taken as estimates of $([V_A + \frac{1}{2} V_D]/V_P)$, and thus as upper limits for the magnitudes of heritability.

Chemoreceptive responses to many prey odors show heritable variation within populations (Table 19-6). Heritabilities of chemoreceptive response to prey odor ranged from .04 to .82 and averaged $.35 \pm .20$ in the coastal population and $.21 \pm .12$ in the inland population. In contrast, there was generally no heritable variation in responses to the distilled water controls; one anomalous exception can be seen in Table 19-6. Thus, heritable variation in chemoreceptive responses to prey odor cannot be attributed to simple heritable differences in tendency to flick the tongue. In several instances, responses that showed no geographic differentiation, nevertheless showed heritable variation within populations (e.g., responses to the odors of anurans and the salamanders, *Batrachoseps* and *Taricha*). This suggests that geographic differentiation would not fail for lack of variation vulnerable to selection within populations. But both traits that showed pronounced geographic variation (responses to slug and leech odors) also showed

Table 19-6. Heritability Estimates for Chemoreceptive Responses to Prey Odors by Naive, newborn *T. elegans*.

Prey Species	Prey Taxon	Coastal ($h^2 \pm \text{std. error}$)	Inland ($h^2 \pm \text{std. error}$)
<i>Ariolimax californicus</i>	slug	.17 ± .16	.17 ± .11*
<i>Aneides lugubris</i>	salamander	.11 ± .14	.04 ± .07
<i>Taricha torosa</i>	salamander	.22 ± .17*	.14 ± .10*
<i>Bufo boreas</i> tadpoles	anuran	.54 ± .25**	.29 ± .13**
<i>Poecilia reticulata</i>	fish	.11 ± .14	.12 ± .10*
distilled water	control	.15 ± .15	-.05 ± .05
<i>Erpobdella punctata</i>	leech	.59 ± .26**	.31 ± .14**
<i>Batrachoseps attenuatus</i>	salamander	.25 ± .18*	.16 ± .11*
<i>Ambystoma tigrinum</i> larvae	salamander	.82 ± .27**	.25 ± .12**
<i>Hyla regilla</i> tadpoles	anuran	.39 ± .22**	.36 ± .15**
<i>Hyla regilla</i> transformed frogs	anuran	.32 ± .20**	.28 ± .13**
distilled water	control	-.05 ± .07	.28 ± .13**
Average of Responses to Prey Odors		.35 ± .20	.21 ± .12
Average of Responses to Controls		.05 ± .11	.12 ± .09

*Tests of statistical significance were conducted by analysis of variance among and within litters; ** indicates significance at the .01 level, * significance at the .05 level.

heritable variation within one or both populations. Chemoreceptive response to slug odor is of particular interest. This trait showed heritabilities of .17 in both populations, but only the inland sample was large enough to demonstrate statistical significance.

Feeding Response as a Threshold Character and its Microevolution.

Consider the proposition that feeding response is a threshold character. We can test this presumption by asking whether chemoreceptive response to slug odor is correlated with subsequent feeding responses to slugs. This was the case in both the coastal and inland populations. In both populations, snakes that showed strong chemoreceptive responses to slugs also showed high slug feeding scores. The relationship between these two variables is graphed in Figure 19-10, for the pooled sample. Notice that the relationship is initially level, then rises sharply and finally levels again; a straight line would produce a poor fit to the data. Thus,

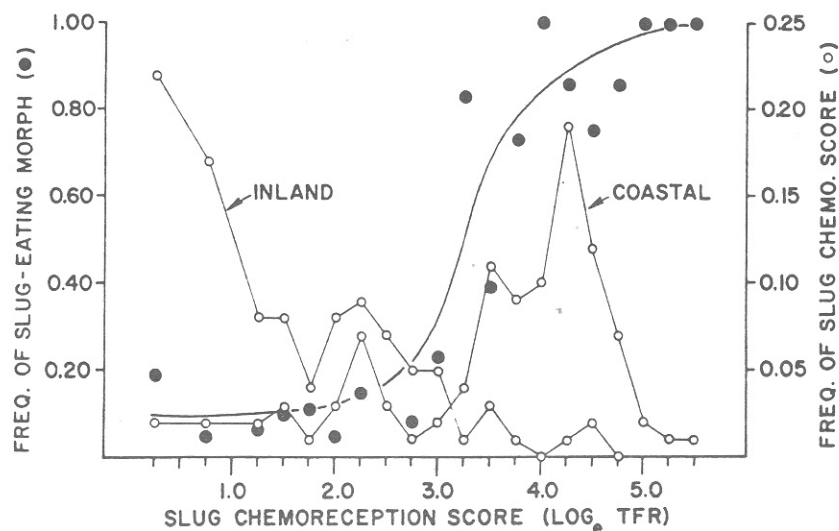


Figure 19-10. The slug attack threshold in *T. elegans*. Open circles show the frequency distributions of chemoreception scores for inland ($n = 211$) and coastal populations ($n = 102$). Solid circles show the frequency of slug-eating morphs as a function of chemoreception score in a preceding test.

feeding response is a *threshold* trait in relation to chemoreceptive score. The point on the chemoreception scale where the probability of attack suddenly increases will be termed the *attack threshold*. Snakes whose capacity for chemoreceptive recognition of slugs falls below the attack threshold become slug-refusers, while snakes whose capacity exceeds this same threshold become slug-eaters. Consequently, feeding scores showed bimodal distributions (see Fig. 19-5), even though distributions of chemoreceptive scores were essentially unimodal and continuous. These observations have several important implications.

Feeding responses may also show a threshold relationship to underlying genetic variation. We have already demonstrated heritable variation in chemoreceptive response to slug odor. Furthermore, the marked divergence of chemoreceptive scores between the two populations (see Fig. 19-8) carries the strong implication of genetic divergence. Thus we can reasonably expect that differences in position along the chemoreception scale in Figure 19-10 represent, in part, differences on a genetic scale. In this view, there appears to be a threshold on the genetic scale that lies about midway on the correlated phenotypic scale of chemoreceptive score. Genotypes that fall below this threshold tend to be slug-refusers, while those falling above it tend to be slug-eaters.

The nature of this imagined genetic threshold depends on our conception of the genetic variation along the scale. If we imagine that polygenic variation underlies chemoreception, then some critical number or combination of alleles enhancing chemoreceptive recognition of slugs must be accumulated in the genotype in order to yield a slug-attacking phenotype. In this view, the two ends of the chemoreception scale would represent extreme genotypes, perhaps homozygous for alternative alleles at many loci. However, we could equally well imagine that slug-eating is a simple Mendelian trait, rather than a polygenic one. For example, one homozygote might tend toward slug-eating (and high chemoreception scores), while the other homozygote and heterozygotes tend toward slug-refusal (and low chemoreception scores). Dispersion about the mean chemoreception score in each population is, of course, interpretable under both the simple Mendelian and polygenic hypotheses as nongenetic variation, and so provides no basis for deciding between them. We could decide between the two extreme hypotheses only by observing segregation of behavior in the F_2 or backcross progenies derived from a cross between the two populations or between two phenotypes in one of them. We have

begun to make crosses of both kinds, but the results are not in. For the sake of present discussion, let us assume polygenic inheritance, since this is a common mode of inheritance for behaviors as well as morphological characters, although by no means the absolute rule. Note that we are quibbling about the nature of our genetic threshold; the existence of the threshold is less equivocal. Let us apply our results in a discussion of the process of niche evolution and assume polygenic inheritance.

When a population of *T. elegans* extends its geographic range into sympatry with slugs, we expect the distribution of chemoreception scores to respond in time to directional selection for slug predation. The probable nature of this selection can be inferred from the relationship between the companion traits of chemoreceptive response and feeding response. From the standpoint of selection, actual feeding response to slugs is the more important variable; differences in chemoreceptive response are irrelevant, as long as two phenotypes both fail to feed on slugs. Consequently, the general form of the relation between fitness and chemoreception score can be deduced from Figure 19-10. Two phenotypes that fall below the threshold for slug attack are likely to have the same fitness with respect to the slug resource, and this fitness is bound to be lower than for phenotypes that fall above the threshold. The magnitude of this difference in fitness is, of course, unknown, but it may be considerable since slugs constitute a major portion of the diet in coastal populations (see Table 19-2). The probable relation between fitness and chemoreception is shown diagrammatically in Figure 19-11. For populations in sympatry with slugs, the relation probably rises dramatically at the slug attack threshold, as was just discussed. For populations allopatric with slugs, the relationship is likely to be a flat line, since, if slugs are never encountered, differences in chemoreceptive recognition of slugs are irrelevant. When a population of snakes extends its range into sympatry with slugs, we expect the fitness function to change from this flat form to a positive relationship that rises sharply at the attack threshold (Fig. 19-11a). A small tail of the chemoreception distribution may fall beyond this threshold. Consequently, these individuals may enjoy a small increment in reproductive success, since they alone are prone to eat slugs. To the extent that chemoreceptive response is heritable, this directional selection will shift the proportions of genotypes in the population, and cause a slight translation of the chemoreception distribution in the next few generations (Fig. 19-11b). Our calculations indicate a heritability of .17, therefore,

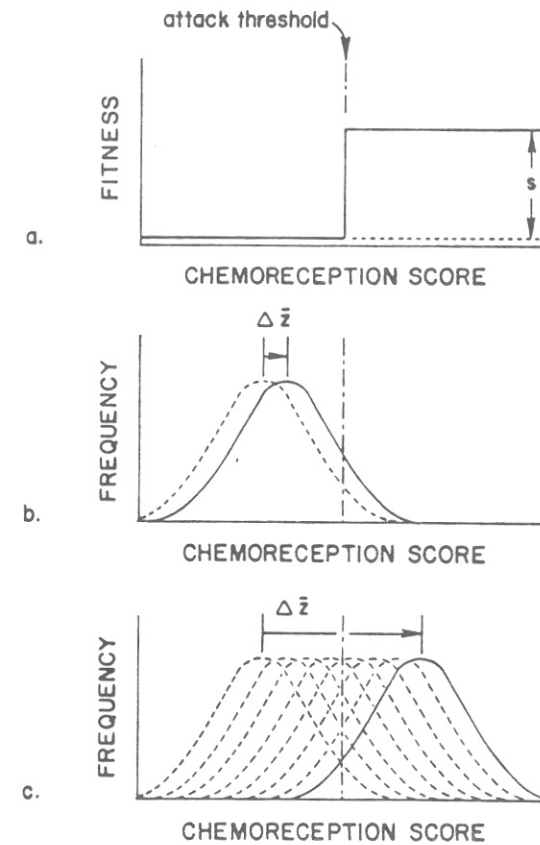


Figure 19-11. A diagrammatic model for the microevolution of behavior, e.g., chemoreception score: **a.** fitness as a function of chemoreception score. Fitness is a step-function (solid line) when the population is sympatric with the prey, but a flat-line (dashed line) when allopatric with prey. The selective advantage of eating the prey, s , accrues only to phenotypes with high chemoreception scores, because only these phenotypes are prone to attack the prey. **b.** response to selection, $\Delta\bar{z}$, after a few generations of directional selection (**a**) acting on a population in sympatry with the prey. **c.** response to selection, $\Delta\bar{z}$, after many generations of selection.

such a response to selection can reasonably be expected. We imagine that this process continues with each generation, so that the distribution continues to move and eventually lies to the right of the attack threshold (Fig. 19-11c). At this point, the majority of snakes in the population are slug-attackers and the distribution ceases its translation. Differences in fitness, with respect to the

slug resource, effectively vanish, except for the small tail of the distribution which still falls below the threshold. These individuals may represent purely phenotypic variants, the products of genetic segregation or mutation or an influx of migrants from populations allopatric with slugs.

How much time was required for the behavioral divergence we have observed between coastal and inland populations? The phenotypic divergence between the two populations in chemoreceptive response to slugs amounted to 1.72 standard deviations. The time required for such divergence will depend on (1) the intensity of selection for slug predation, and (2) the heritability of the trait. We can only guess at the magnitude of selection, but our observation that the trait has a heritability of .17 in both populations places an important constraint on estimates of divergence time. Lande (1978) derived a useful model for the phenotypic evolution of threshold characters, a topic also treated by Lush (1945), Falconer (1960), and Crow and Kimura (1970). In Lande's model, the change in mean phenotype in generation t ,

$$\Delta\bar{z}(t) = h^2 s p(T,t) \quad (1)$$

where h^2 is the heritability of a normally distributed trait, s is the selective advantage of slug eating in sympatry with slugs, and $p(T,t)$ is the height of the phenotypic distribution at the threshold in generation t . This formulation assumes weak selection, $s \leq .1$. Thus, the response to selection is a function of distance to the threshold as well as heritability and selection. As a consequence, response to selection will have the interesting dynamic property of accelerating as the distribution straddles the threshold and then decelerating as it passes beyond the threshold (Lande, 1978). From Figure 19-10 we can fix the position of the threshold at about 3.25 on the chemoreception scale or 1.56 standard deviations from the mean of the inland population. Using these parameters, Lande's model was simulated on a computer; the results are shown in Table 19-7. Thus, the populations could have taken as little as 780 years to diverge if slug-eating morphs experienced a 10 percent advantage ($s = .1$) and as long as 780,000 years if the advantage was only a hundredth of 1 percent ($s = .0001$).

This dynamic view of simple niche evolution is in accord with our data from extant populations of *T. elegans*, even though at present there is no way to check the time scale. In particular, notice that the distribution of chemoreception scores for an actual popu-

Table 19-7. Times for Behavioral Divergence Under a Simple Model for Directional Selection on a Threshold Character (Lande, 1978).^a

Magnitude of Selection (s)	Number of Generations (t)	Time (yrs) (2 yrs per generation)
.1	390	780
.01	3,889	7,778
.001	38,862	77,724
.0001	390,000 ^b	780,000 ^b

^aResults of computer simulations are shown using the parameter values: $h^2 = .1727$ for a normally distributed character with $\sigma = 1.1435$ and an initial mean 1.5626 standard deviations from the threshold. These parameters are derived from the statistics of the actual distributions shown in Figure 19-10. Calculations indicate the time required for a divergence of 1.7203 standard deviations.

^bThese values extrapolated from the three other calculated values.

lation in allopatry with slugs lies well below the threshold for slug attack; only a small tail of the distribution fell above the threshold and so only 8 percent of the sample were slug-attackers. In contrast, an actual coastal population lies above the threshold; 78 percent of this sample were slug attackers. This difference almost certainly represents a response to selection. However, the simple model just outlined neglected an important fact. Chemoreceptive response to slugs is not a simple trait, it is correlated with response to another prey, leeches. This raises the important issue of genetic correlation and the possibility of correlated responses to selection. For example, it may be impossible for selection to modify responses to slugs without simultaneously affecting responses to leeches.

Genetic Correlation and Correlated Response to Selection

There were significant phenotypic correlations between chemoreceptive responses to slugs and to leeches in both the coastal and inland populations. The phenotypic correlation, r_p , between individual scores for these two variables were .45 ($p < .01$) in the coastal population and .33 ($p < .01$) in the inland population. Such phenotypic correlation can arise from two theoretical causes: (1) genetic correlation (due mainly to the same genes affecting both characters, i.e., pleiotropy, and also due to linkage), and (2) environmental correlation (covariance of deviations due to environmental effects or of nonadditive genetic deviations) (Falconer,

1960). The relative contribution of these two sources of phenotypic correlation was estimated using the relationship

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

where h_x and h_y are the square roots of the heritabilities of the two traits, $e^2 = 1 - h^2$, r_A is the genetic correlation and r_E is the environmental correlation (Falconer, 1960). Genetic correlations were calculated from the among litter components of variance and covariance as described by Falconer (1960). Environmental correlations were then calculated by substitution into equation 2. These calculations indicated that genetic correlation made a significant contribution to phenotypic correlation in both populations (Table 19-8). The presence of genetic correlation can also be inferred from Figure 19-12, where the covariation of litter means is displayed for both populations. Genetic correlation raises the interesting possibility of a correlated response to selection, but first let us consider an interpretation of the observed correlations.

Genetic correlation of chemoreceptive responses may have a straightforward meaning. Such correlation would naturally arise if snakes were unable to distinguish prey odors and if there were genetic differences underlying chemoreceptive responses. Suppose, for example, that the same surface molecules eliciting chemoreceptive response to slugs are present on the surface of leeches. This seems an unlikely development since slugs and leeches are distantly related, indeed they are members of different phyla. Nevertheless, it appears that they share some surface molecules or that at least their surface chemistries are confused by *T. elegans*. As a consequence, alleles enhancing response to slug odor will necessarily enhance response to leech odor. A genetic correlation follows

Table 19-8. Phenotypic, Genetic, and Environmental Correlations between Chemoreceptive Responses to the Odors of Slugs and Leeches by Inland and Coastal Populations of *T. elegans*.

	Coastal	Inland
Phenotypic correlation, r_P	.4511	.3261
Genetic correlation, r_A	.8930	.8867
(\pm standard error)	($\pm .0960$)	($\pm .0793$)
Environmental correlation, r_E	.2865	.1606

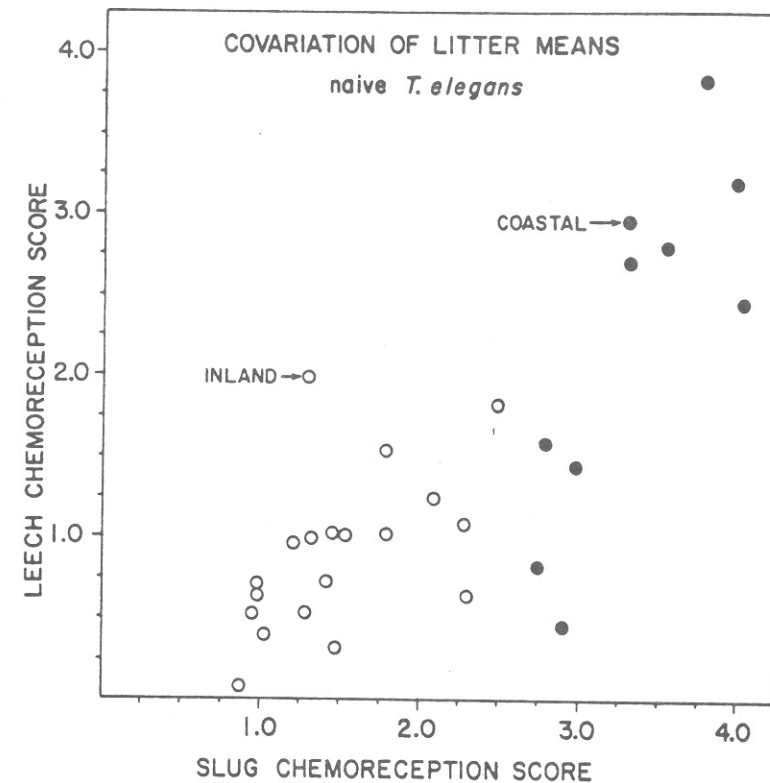


Figure 19-12. Covariation of litter means for coastal and inland populations of *T. elegans*. Mean chemoreceptive response to leech odor is shown as a function of mean chemoreceptive response to slug odor. Positive relationships in both populations indicate genetic correlation between these two responses.

naturally in any population with additive genetic variance for responses to the odors of either prey. In other words, the data suggest a simple form of pleiotropy (Wright, 1968) or that we are, in actuality, dealing with one trait (slug-leech response) rather than two traits. The important point is that selection cannot change responses to slug odor without simultaneously changing responses to leech odor. This prediction is confirmed by the results in Table 19-5. Thus we have uncovered a potentially important genetic constraint on niche evolution in *T. elegans*. In order to evaluate the importance of this constraint, we must first review the feeding ecology of this species.

Evolutionary divergence in chemoreceptive recognition of slugs between inland and coastal populations may be a consequence of selection for slug-predation in coastal populations and selection for leech avoidance in inland populations. The facts to be accounted for are the high responses of coastal snakes to both slug and leech odors and the low responses of inland snakes to both prey odors. The question that arises is whether this divergence represents evolution in response to the slug resource, the leech resource, or both. Since slugs dominate the diet of coastal populations while leeches have never been recorded, the high slug-leech response of these populations is undoubtedly an adaptation for slug predation. The significance of the low slug-leech response of the inland population is less apparent. There are two classes of explanation: (1) variations in slug-leech response might be selectively neutral in inland populations, or (2) low slug-leech responses might be favored by selection. Recent observations recommend the latter interpretation. We have found that leeches can remain alive in the guts of wild-caught snakes for several hours, in fact for as long as six hours. They may damage the snake's gut before finally succumbing to digestive processes, since blood is sometimes regurgitated along with the store of live leeches. These observations suggest that leeches may be hazardous prey for *T. elegans*. Consequently, avoidance of leeches may be a selective pressure maintaining low slug-leech responses in inland populations. Slug predation probably plays no role in the process due to the extreme rarity of slugs in the range of inland populations, but the low frequency of slug-eating morphs in these populations might be a consequence of gene flow from coastal populations.

Finally, we must account for the troublesome fact that leeches are a significant fraction of the diet of some inland populations. The preceding discussion was based on our laboratory and field results for our principle inland population at Eagle Lake. At this site, fish and anurans are the main source of nutrition, while leeches are only a minor component of the diet. In contrast, leeches dominate the diet of *T. elegans* at Mahogany Lake, a site only four kilometers from Eagle Lake (see Table 19-2). This dietary difference is not simply a consequence of greater leech abundance at Mahogany Lake, since, if anything, leeches are more abundant at Eagle Lake. In fact, their scarcity in the diet of Eagle Lake is remarkable, since leeches are commonly seen in the open and are slow moving. The principle environmental difference between the two lakes is not leeches, but rather the extremely limited spectrum

of prey at Mahogany Lake; leeches and tree frogs are the only available prey. Thus, snakes at Mahogany Lake may be forced into leech predation, despite its presumed hazards, due to lack of alternatives. I cannot say whether these environmental differences have promoted behavioral divergence in prey recognition. The rarity of gravid females at Mahogany Lake has thwarted a comparison of the predatory responses of newborn snakes.

Summary of Results

Recent research on garter snake feeding behavior suggests the following perspective on behavioral variability within populations. Feeding polymorphisms are common in populations. This behavioral variation is innate in the sense that it is congenital, ontogenetically stable, and heritable. It is not known whether such behavioral polymorphisms are actively maintained within populations, e.g., by density- or frequency-dependent selection, or whether they represent gene flow between geographic regions with different selective pressures. However, the proximate cause of polymorphism is known. Distinct feeding morphs emerge when perceptual variation straddles thresholds for prey attack. Perceptual variation in prey recognition is quantitative, continuously distributed within populations, and heritable in part.

I will briefly review the major findings by reconstructing the process of niche microevolution in *T. elegans*. This reconstruction is based on the assumption that the inland population is representative of the ancestral population that first invaded coastal California.

When *T. elegans* expanded its range westward into the humid environment of coastal California, it encountered several new prey taxa. Slugs were the most important of these novel prey. In the first coastal population of *T. elegans* there was a continuous distribution of abilities to recognize slugs by chemoreception and about 17 percent of the variance in this distribution was heritable. But only a small proportion of snakes, with well developed ability for chemical recognition of slugs, actually attacked slugs. These snakes enjoyed a slight increment in reproductive success, relative to other snakes in the population, since they alone preyed on slugs. This state of affairs constituted directional selection for chemical recognition of slugs, which continued for hundreds or thousands of generations (see Fig. 19-11). Eventually the distribution of abilities to recognize slugs by chemoreception was shifted nearly two standard devia-

tions, with the consequence that a majority of the population was then likely to attack slugs.

A tendency to attack leeches evolved as a simple correlate of adaptation for slug predation. In ancestral inland populations, leeches were probably hazardous prey because they remained alive in the gut after ingestion and inflicted damage. Ancestral inland populations tended to avoid leeches and showed a poor ability to recognize leeches by chemoreception. However, chemoreceptive responses to slugs and leeches were genetically correlated; genes that enhanced chemical recognition of leeches also enhanced chemical recognition of slugs. Thus enhanced ability for chemical recognition of leeches evolved as a correlated response to selection for slug predation in coastal California. But since coastal snakes adopted terrestrial foraging habits, they did not encounter leeches and so experienced no liability.

Fish were deleted from the diet of coastal populations as a consequence of abandoning aquatic foraging, but they were retained in the diets of ancestral inland populations. Despite this dietary difference, coastal populations never lost their ability to recognize fish by chemoreception. Thus coastal populations retained an ancestral ability to respond to fish odor; the potential for fish predation was simply no longer expressed.

An ancestral potential to respond to salamander and anuran odors preadapted the first coastal *T. elegans* population for predation on novel amphibians, like plethodontid salamanders. Apparently no new abilities to recognize these new prey taxa (e.g., *Aneides* and *Batrachoseps*) by chemoreception evolved in coastal populations.

Discussion

The Genetics of Behaviors Influencing Resource Utilization

The results of behavioral genetics indicate that even simple genetic change has the potential for profound influence on resource utilization. Several perceptual abilities in humans are known to have a simple genetic basis. For example, color blindness is controlled by sex-linked alleles at two closely linked loci (Ehrman and Parsons, 1976). Ability to taste phenylthiourea and other molecules with a N - C = S group is governed by an autosomal locus with almost complete dominance (Kalmus, 1971). The mode of gene action is not

known but may involve differences in receptor proteins. A number of anosmias for specific classes of molecules are known to be heritable in humans (Amoore, 1975) and mice (Wysocki et al., 1977). Likewise, there are genetic differences among strains of cockroaches (*Periplaneta americana*) in ability to perceive naphthoquinones that apparently reflect differences in receptor macromolecules (Rozenthal and Norris, 1975). An autosomal mutant for olfactory perception has been isolated in *Drosophila melanogaster* (Kikuchi, 1973). Capacity for conditioned feeding behavior (mediated by chemoreception) responds to selection in the blowfly, *Phormia regina* (Hirsch and McCauley, 1977; McGuire and Hirsch, 1977). Thus, genetic study of behaviors likely to influence resource utilization has implicated perceptual inheritance in a number of instances. In addition, genetic differences in motor patterns are also known. For example, feeding rate in *Drosophila melanogaster* larvae responds to selection in both directions without producing correlated differences in the activity of adult flies (Burnet and Connolly, 1974).

A relationship between genetic differences and resource utilization has been shown in tephritid flies. Host selection by ovipositing females of two closely related species is governed by a major gene whose expression is modulated by larval experience (Huettel and Bush, 1972).

Behavioral Variation Within Natural Populations

The study of behavioral variation within natural populations has just begun. Quantitative studies of behavioral variation are rare (Barlow, 1968; Dane et al., 1959; Jenssen, 1971; Stamps and Barlow, 1973) and data on the frequency distributions of behaviors are almost nonexistent. The issue of heritable variation has also been neglected. Aside from the present results on garter snakes, I know of no demonstrations or estimates of heritability of feeding behavior in natural populations.

Only a few studies have demonstrated polymorphism for feeding behavior under controlled conditions. Brockhusen and Curio (1975) and Brockhusen (1977) studied prey selection in large samples of newly hatched lizards, *Anolis lineatopus*. The lizards were repeatedly offered five different species of insect prey. Individual lizards accepted different combinations of prey, and initially, several feeding morphs could be recognized. With repeated trials this array of morphs collapsed to three morphs: one that

accepted all five prey, one that accepted a combination of four, and one that accepted another combination of four. This pattern of discrete variation in acceptance of prey has also been reported in several studies of natricine snakes (Arnold, 1977, 1978; Burghardt, 1970, 1975; Dix, 1968; Gove and Burghardt, 1975) and is well known to curators of zoological gardens (R. Pawley and Chas. Shaw, personal communication). As in *Anolis*, snake populations show feeding morphs that consistently reject only particular classes of prey. Acceptance of some prey can be modified by experience (see Arnold, 1978 for a review), but some feeding morphs are ontogenetically stable.

Although polymorphism in prey acceptance by garter snakes can be attributed to heritable, continuous variation in chemoreceptive recognition, the mode of gene action is not known. Nor do we know whether inheritance is polygenic, as in the geotaxis of *Drosophila* (Dobzhansky, 1972; Hirsch, 1967; Hirsch and Erlenmeyer-Kimling, 1962). Heritable variation in chemoreception may reflect small changes in receptor macromolecules. The genetic studies cited above make this an attractive suggestion. Alternatively, the variation may not be due to variation in sensory apparatus; it may be central rather than peripheral. Recent neuro-anatomical studies of arthropods demonstrate heritable variation in networks of neurons in the central nervous system (Goodman, 1977).

Geographic Variation in Feeding Behavior

Our understanding of behavioral microevolution is crippled by a lack of attention to geographic variation. Although several studies have demonstrated geographic variation in various aspects of reproductive behavior (Ferguson, 1971; King et al., 1964; Littlejohn, 1965; Plomin and Manosevitz, 1974; Sawada, 1963), there are relatively few studies of feeding behavior and resource utilization. Ability to survive on wheat cultivars varies geographically in a ceidomyiid fly, *Magetiola destructor*. Survival ability is strongly affected by at least two loci, but the genic systems of the insect and host are complementary such that each resistant gene in wheat has a complementary gene for survival in the insect (Hatchett and Gallun, 1970). This microevolutionary pattern of gene-by-gene coevolution of parasite and host is known as the "gene-for-gene hypothesis," and a number of supporting examples are known for phytophagous fungi and insects (Day, 1974). Bush (1969, 1975) recently reviewed microevolution of feeding and speciation in

phytophagous, parasitic insects and documented shifts in host plant that have occurred in historical times. Singer (1971) demonstrated geographic variation in plant selection by ovipositing females of the butterfly, *Euphydryas editha*. A mosquito (*Aedes atropalvus*) shows geographic variation in blood-feeding tendency (O'Meara and Craig, 1970).

Among vertebrates, geographic variation in feeding behaviors has been demonstrated only for deer mice of the genus *Peromyscus* (Gray, this volume, Chapter 20), for garter snakes (Arnold, 1977, this volume, Chapter 19; Burghardt, 1970; Dix, 1968) and for the fish of the genus *Astyanax* (Schemmel, 1967, 1974). Only in the last case have crosses been made between behaviorally divergent populations.

Since we know so little about the scale of geographic variation in feeding behavior, we should first look for behavioral adaptation to large scale environmental differences rather than to very local conditions. The basis for this pragmatic suggestion is the theoretical observation that populations will fail to genetically track certain spatial and temporal differences in selection. For example, small scale spatial differences in the occurrence of particularly profitable prey may produce a corresponding spatial pattern in the fitnesses of feeding morphs. But this does not guarantee response to selection, and there may be no local adaptation in behavior. Evolution in response to local conditions will depend on the magnitudes of gene flow and spatial differences in selection, and there is a lower bound below which response to selection will not occur (Hanson, 1966; Nagylaki, 1975; Slatkin, 1973). Similar arguments apply to temporal fluctuations in the environment. For example, the extent of polymorphism or niche width will track the environment only if there is a critical level of predictability in temporal fluctuations (Levins, 1965; Slatkin and Lande, 1976). Populations are likely to track only major environmental differences that vary on a grand, geographic scale. In the case of feeding behaviors, a geographic survey of diet can be an instructive adjunct to a study of local ecology and may indicate the appropriate scale for assays of geographic variation.

Summary

The important contribution of this chapter is the demonstration that it is feasible to estimate behavioral heritabilities in natural populations and that it is possible to detect geographic variation

in behavior. Both of these important evolutionary issues have been neglected by behaviorists. For example, this chapter provides the first estimates of behavioral heritabilities for any natural population of vertebrates. (Greenwood et al., 1979 have recently estimated the heritability of dispersal distance in a population of passerine birds.)

Field and laboratory studies of garter snakes (*Thamnophis*) provide a case study of feeding behavior microevolution. A geographic survey of diet in the polytypic species *T. elegans* set the stage for laboratory assays of geographic variation in feeding behavior. In particular, field studies in western North America indicated that slugs were the main prey of coastal populations, but that inland populations were largely allopatric with these prey. Propensity to attack slugs was studied in the laboratory using wild-caught snakes as well as large samples of naive, newborn snakes. These tests revealed a consistent geographic pattern. Coastal snakes were congenitally prone to attack slugs, but inland snakes tended to refuse them. Geographic variation in tendency to attack slugs was ontogenetically stable as well as congenital. In addition both coastal and inland populations were polymorphic for slug-feeding, and geographic differences took the form of dramatic shifts in the frequency of feeding morphs. The nature of behavioral variation within populations was further clarified by tests of chemoreceptive recognition of prey.

Studies of chemoreceptive response to prey odors by naive, newborn snakes indicated that differences in chemoreceptive response to slug odor underlie the slug-feeding polymorphism. Feeding response to slugs was correlated with chemoreceptive response, but there was a threshold relationship between these two variables. Thus, feeding polymorphisms emerged within populations when chemoreceptive variation straddled an attack threshold. In addition, variation in chemoreceptive recognition of slugs and several other prey was heritable. The latter observation was particularly important since it indicated that behavioral variation within populations was vulnerable to natural selection.

Feeding polymorphisms and chemoreceptive recognition of prey can evolve in response to geographic differences in prey availability. The observation of attack thresholds suggested a simple model of directional selection that favored prey feeding morphs in areas of sympatry with particular prey. Computer simulations suggested a time scale of hundreds to tens of thousands of years for the divergence between coastal and inland populations

in slug-feeding tendency. Coastal and inland populations also showed marked divergence in chemoreceptive recognition of leeches. Responses to slugs and leeches showed high genetic correlations in both populations, and thus these two traits could not evolve independently. Parallel divergence in perceptual recognition of these two prey was apparently a consequence of selection for slug predation in coastal populations and selection for avoidance of hazardous leeches in inland populations.

Behavioral microevolution is a promising field with a limited data base. The study of behavioral microevolution, as revealed by geographic variation among conspecific populations, allows us to scrutinize the process of evolution as well as its results. To better focus our vision we need: (1) quantitative studies of behavioral variation in natural populations, (2) estimates of behavioral heritability in natural populations, (3) studies of geographic variation in behavior, (4) genetic studies of behaviors that vary geographically, and (5) attention to behaviors with clear ecological and phylogenetic implications.

Acknowledgments

I am grateful to Hilary Arnold, Laura Arnold, Donald Kephart, Hugh Drummond, Cynthia Houck and Lynne Houck for help with field work. Stuart Altmann, Gerald Borgia, Gordon Burghardt, Hugh Drummond, Harry Greene, A. R. Kiestler, Russell Lande, Michael Wade, and an anonymous reviewer made helpful comments on the manuscript. Donald Kephart programmed the computer simulations. I am grateful to Lavy Abromovitch and David Wallace for statistical consultation. Jean Gladstone assisted with laboratory work.

References

- Amoore, J. E. 1975. Four primary odor modalities in man: Experimental evidence and possible significance. In *Olfaction and taste*, V., eds., D. Denton and J. P. Coghlan. New York: Academic Press.
- Arnold, S. J. 1972. Species densities of predators and their prey. *American Naturalist* **106**:220-236.
- Arnold, S. J. 1977. Polymorphism and geographic variation in the feeding behavior of the garter snake, *Thamnophis elegans*. *Science* **197**:676-678.
- Arnold, S. J. 1978a. The evolution of a special class of modifiable behaviors in relation to environmental pattern. *American Naturalist* **112**:415-427.
- Arnold, S. J. 1978b. Some effects of early experience on feeding responses in the common garter snake, *Thamnophis sirtalis*. *Animal Behaviour* **26**:455-462.
- Arnold, S. J. and R. J. Wassersug. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): Social behavior as a possible defense. *Ecology* **59**:1014-1022.
- Barlow, G. W. 1968. Ethological units of behavior. In *The central nervous system and fish behavior*, ed., D. Ingle. Chicago: University of Chicago Press.
- Blanchard, F. C. 1943. A test for fecundity of the garter snake *Thamnophis sirtalis sirtalis* (Linnaeus) in the year following the year of insemination. *Papers of the Michigan Academy of Science* **28**:313-316.
- Brockhusen, F. von. 1977. Untersuchungen zur individuellen Variabilität der Beuteannahme von *Anolis lineatopus* (Rept., Iguanidae). *Zeitschrift für Tierpsychologie* **44**:13-24.
- Brockhusen, F. von, and E. Curio. 1975. Die innerartliche Variabilität der Beutewahl beuteerfahrungsloser *Anolis*. *Experientia* **31**:45-46.
- Burghardt, G. M. 1967. Chemical-cue preferences of inexperienced snakes: Comparative aspects. *Science* **157**:718-721.
- Burghardt, G. M. 1968. Chemical preference studies on newborn snakes of three sympatric species of *Natrix*. *Copeia* **1968**:732-737.
- Burghardt, G. M. 1969. Comparative prey-attack studies in newborn snakes of the genus *Thamnophis*. *Behaviour* **33**:77-114.
- Burghardt, G. M. 1970. Intraspecific geographical variation in chemical food cue preferences of newborn garter snakes (*Thamnophis sirtalis*). *Behaviour* **36**:246-257.
- Burghardt, G. M. 1971. Chemical-cue preferences of newborn snakes: Influence of prenatal maternal experience. *Science* **171**:921-923.
- Burghardt, G. M. 1975. Chemical prey preference polymorphism in newborn garter snakes *Thamnophis sirtalis*. *Behaviour* **52**:202-225.
- Burghardt, G. M., and C. H. Pruitt. 1975. Role of the tongue and senses in feeding of naive and experienced garter snakes. *Physiology and Behavior* **14**:185-194.
- Burnet, B., and K. Connolly. 1974. Activity and sexual behavior in *Drosophila melanogaster*. In *The genetics of behaviour*, ed., J. H. F. van Abeelen. Amsterdam: North-Holland Publishing Corporation.
- Bush, G. L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* **23**:237-251.
- Bush, G. L. 1975. Sympatric speciation in phytophagous parasitic insects. In *Evolutionary strategies of parasitic insects and mites*, ed., P. W. Price. New York: Plenum Press.
- Campbell, R. W. 1969. Notes on some foods of the wandering garter snakes on Millenatch Island, British Columbia. *Syesis* **2**:183-187.
- Cavalli-Sforza, L. L. and M. W. Feldman. 1978. The evolution of continuous variation. III. Joint transmission of genotype, phenotype and environment. *Genetics* **90**:391-425.
- Cock, A. G. 1966. Genetical aspects of metrical growth and form in animals. *Quarterly Review of Biology* **41**:131-190.
- Crow, J. R., and M. Kimura. 1970. *An introduction to population genetics theory*. New York: Harper and Row.
- Czaplicki, J. A., and R. H. Porter. 1974. Visual cues mediating the selection of goldfish (*Carassius auratus*) by two species of *Natrix*. *Journal of Herpetology* **8**:129-134.
- Dane, B., C. Wolcott, and W. H. Drury. 1959. The form and duration of the display actions of the goldeneye (*Bucephala clangula*). *Behaviour* **14**:265-281.
- Day, R. R. 1974. *Genetics of host-parasite interaction*. San Francisco: W. H. Freeman and Company.
- Devine, M. C. 1975. Copulatory plugs in snakes: Enforced chastity. *Science* **187**:844-845.
- Dix, M. W. 1968. Snake food preferences: Innate intraspecific geographic variation. *Science* **159**:1478-1479.
- Dobzhansky, T. 1972. Comment. In *Genetics, environment, and behavior*, eds., L. Ehrman, G. S. Omenn, and E. Caspari. New York: Academic Press.

- Drummond, H. M. 1979. In press. Stimulus control of amphibious predation in the northern water snake (*Nerodia s. sipedon*). *Zeitschrift für Tierpsychologie*.
- Ehrman, L., and P. A. Parsons. 1976. *The genetics of behavior*. Sunderland, Massachusetts: Sinauer Associates.
- Falconer, D. S. 1960. *Introduction to quantitative genetics*. New York: Ronald Press.
- Feldman, M. W., and R. C. Lewontin. 1975. The heritability hang-up. *Science* **190**:1163-1168.
- Ferguson, G. W. 1971. Variation and evolution of push-up displays of the side-blotched lizard *Uta* (Iguanidae). *Systematic Zoology* **20**:79-101.
- Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. *Transactions of the Royal Society of Edinburgh* **52**:399-433.
- Fitch, H. S. 1940. A biogeographical study of the *ordinoides* Artenkreis of garter snakes (genus *Thamnophis*). University of California, Berkeley. *Publications in Zoology* **44**:1-150.
- Fox, W. 1951. Relationships among garter snakes of the *Thamnophis elegans* Rassenkreis. University of California, Berkeley. *Publications in Zoology* **50**:485-529.
- Godley, J. S. 1979. Foraging ecology of the striped swamp snake, *Regina alleni*, in S. Florida. M.A. Thesis, University of S. Florida.
- Goodman, C. S. 1977. Neuron duplications and deletions in locust clones and clutches. *Science* **197**:1384-1386.
- Gove, D., and G. M. Burghardt. 1975. Responses of ecologically dissimilar populations of the water snake *Natrix s. sipedon* to chemical cues from prey. *Journal of Chemical Ecology* **1**:25-40.
- Greenwood, P. J., P. H. Harvey, and C. M. Perrins. 1979. The role of dispersal in the great tit (*Parus major*): The causes, consequences, and heritability of natal dispersal. *Journal of Animal Ecology* **48**:123-142.
- Gregory, P. T. 1978. Feeding habits and diet overlap of three species of garter snakes (*Thamnophis*) on Vancouver Island. *Canadian Journal of Zoology* **56**:1967-1974.
- Hanson, W. D. 1966. Effects of partial isolation (distance), migration, and fitness requirements, among environmental pockets upon steady state gene frequencies. *Biometrics* **22**:453-468.
- Hatchett, H. H., and R. L. Gallun. 1970. Genetics of ability of the hessian fly, *Mayetiola destructor*, to survive on wheats having different genes for resistance. *Annals of the Entomological Society of America* **63**:1400-1407.
- Hirsch, J. 1967. *Behavior-genetic analysis*. New York: McGraw-Hill.
- Hirsch, J., and L. Erlenmeyer-Kimling. 1962. Individual differences in behavior and their genetic basis. In *Roots of behavior*, eds., E. L. Bliss. New York: Harper & Row.
- Hirsch, J., and L. A. McCauley. 1977. Successful replication of, and selective breeding for classical conditioning in the blowfly *Phormia regina*. *Animal Behaviour* **25**:784-785.
- Huettel, M. D., and G. L. Bush. 1972. The genetics of host selection and its bearing on sympatric speciation in *Procedidochares* (Diptera: Tephritidae). *Entomologica Experimentalis et Applicata* **15**:465-480.
- Jenssen, T. A. 1971. Display analysis of *Anolis nebulosus* (Sauria, Iguanidae). *Copeia* **1971**:197-209.
- Kalmus, H. 1971. Genetics of taste. In *Handbook of sensory physiology*. Volume IV. *Chemical senses*. Part 2, ed., L. M. Beidler, Berlin, West Germany: Springer-Verlag.
- Kikuchi, T. 1973. Genetic alteration of olfactory functions in *Drosophila melanogaster*. *Japanese Journal of Genetics* **48**:105-118.
- King, J. A., D. Maas, and R. G. Weisman. 1964. Geographic variation in nest size among species of *Peromyscus*. *Evolution* **18**:230-234.
- Kubie, J. L., and M. Halpern. 1976. Laboratory observations of trailing behavior in garter snakes. *Journal of Comparative and Physiological Psychology* **89**:667-674.
- Lande, R. 1978. Evolutionary mechanisms of limb loss in tetrapods. *Evolution* **32**:73-92.
- Levins, R. 1965. Theory of fitness in a heterogeneous environment. V. Optimal genetic systems. *Genetics* **52**:891-904.
- Lewontin, R. C. 1967. Population genetics. *Annual Review of Genetics* **1**:37-70.
- Lewontin, R. C. 1970. The units of selection. *Annual Review of Ecology and Systematics* **1**:1-18.
- Littlejohn, M. J. 1965. Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). *Evolution* **19**:234-243.
- Lush, J. L. 1945. *Animal breeding plans*. Ames, Iowa: Iowa State College Press.
- Malnate, E. V. 1960. Systematic division and evolution of the colubrid snake genus *Natrix*, with comments on the subfamily Natricinae. *Proceedings of the Academy of Natural Sciences (Philadelphia)* **117**:19-43.
- Manning, A. 1975. Behaviour genetics and the study of behavioural evolution. In *Function and evolution in behaviour: Essays in honor of Niko Tinbergen*, F. R. S., eds., G. Baerends, C. Beer and A. Manning. Oxford, England: Clarendon Press.
- Mao, S., and H. C. Dessauer. 1971. Selectively neutral mutations, transferrins and the evolution of natricine snakes. *Comparative Biochemistry and Physiology* **40A**:669-680.
- Mayr, E. 1942. *Systematics and the origin of species*. New York: Columbia University Press.
- McGuire, T. R., and J. Hirsch. 1977. Behavior-genetic analysis of *Phormia regina*: Conditioning, reliable individual differences, and selection. *Proceedings of the National Academy of Science* **74**:5193-5197.

- Mead, A. R. 1943. Revision of the giant West Coast land slugs of the genus *Ariolimax* Moerch (Pulmonata: Arionidae). *American Midland Naturalist* 30:675-717.
- Nagylaki, T. 1975. Conditions for the existence of clines. *Genetics* 80:595-615.
- O'Meara, G., and G. B. Craig, Jr. 1970. Geographical variation in *Aedes atropalus* (Diptera: Culicidae). *Annals of the Entomological Society of America* 63:1392-1400.
- Plomin, R. J. and M. Manosevitz. 1974. Behavioral polytypism in wild *Mus musculus*. *Behavior Genetics* 4:145-157.
- Rossman, D. A., and W. G. Eberle. 1977. Partition of the genus *Natrix*, with preliminary observations on evolutionary trends in natricine snakes. *Herpetologica* 33:34-43.
- Rozenal, J. M., and D. M. Norris. 1975. Genetically variable olfactory receptor sensitivity in *Periplaneta americana*. *Life Sciences* 17:105-110.
- Ruthven, A. G. 1908. Variations and genetic relationships of the garter-snakes. Washington, D.C.: Bulletin of the United States National Museum 61.
- Sawada, S. 1963. Studies on the local races of the Japanese newt, *Triturus pyrrhogaster* Boie, II. Sexual isolation mechanisms. *Journal of Science of Hiroshima University. Series B, Division 1 (Zoology)* 21:167-180.
- Schemmel, C. 1967. Vergleichende Untersuchungen an den Hautsinnesorganen ober- und unterirdisch lebender *Astyanax*-Formen. *Zeitschrift für Morphologie der Tiere* 61:255-316.
- Schemmel, C. 1974. Genetische Untersuchungen zur Evolution des Geschmacksapparates bei cavernicolen Fischen. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 12:196-215.
- Singer, M. C. 1971. Evolution of food-plant preference in the butterfly *Euphydryas editha*. *Evolution* 25:383-389.
- Slatkin, M. 1973. Gene flow and selection in a cline. *Genetics* 75:733-756.
- Slatkin, M., and R. Lande. 1976. Niche width in a fluctuating environment—density independent model. *American Naturalist* 110:31-55.
- Smith, M. 1969. *The British amphibians and reptiles*. 4th ed. London, England: Collins.
- Snedecor, C. W. 1956. *Statistical methods*. Ames, Iowa: Iowa State College Press.
- Sokal, R. R., and F. J. Rolf. 1969. *Biometry*. San Francisco, California: W. H. Freeman & Company.
- Stamps, J. A., and G. W. Barlow. 1973. Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). *Behaviour* 47:67-94.
- Stebbins, R. C. 1966. *A field guide to western reptiles and amphibians*. Boston, Massachusetts: Houghton Mifflin Company.
- Tanner, W. W. 1949. Food of the wandering garter snake, *Thamnophis elegans vagrans* (Baird and Girard), in Utah. *Herpetologica* 5:85-86.
- Webb, R. G. 1976. A review of the garter snake *Thamnophis elegans* in Mexico. *Natural History Museum of Los Angeles City Contributions in Science* 284:1-13.
- White, M., and J. A. Kolb. 1974. A preliminary study of *Thamnophis* near Sagehen Creek, California. *Copeia* 1974:126-136.
- Wright, S. 1968. *Evolution and the genetics of populations. Volume I. Genetic and biometric foundations*. Chicago, Illinois: University of Chicago Press.
- Wysocki, C. J., G. Whitney, and D. Tucker. 1977. Specific anosmia in the laboratory mouse. *Behavior Genetics* 17:171-188.
- Zweifel, R. G. 1954. Adaptation to feeding in the snake *Contia tenuis*. *Copeia* 1954:299-300.