rendered cytotoxic by exposure in vitro to either BCG or PPD (purified protein derivative). It is interesting that these challenged cultures give rise to an immune IF (*21*). A simple explanation for the immunologically specific induction of nonspecifically cytotoxic macrophages could be that this IF modifies macrophage activity.

The abilities of IF and IF-inducers to enhance resistance to nonviral intracellular pathogens (*22*) and to cancer (*7, 10, 23*) go well beyond IF's previously known role in the inhibition of virus replication at the molecular level. The evidence presented here broadens the scope of IF as an agent with discrete pharmacologic activity on macrophage function.

RICHARD M. SCHULTZ
JOSEPH D. PAPAMATHEAKIS
MICHAEL A. CHIRIGOS
Laboratory of RNA Tumor Viruses,
National Cancer Institute,
Bethesda, Maryland 20014

References and Notes

1. J. B. Hibbs, L. H. Lambert, J. S. Remington, *Science* **177**, 998 (1972).
2. M. H. Levy and E. F. Wheelock, *Adv. Cancer Res.* **20**, 131 (1974).
3. W. Regelson and A. E. Munson, *Ann. N.Y. Acad. Sci.* **173**, 831 (1970).
4. C. F. Nathan, M. L. Karnovsky, J. R. David, *J. Exp. Med.* **133**, 1356 (1971).
5. R. P. Cleveland, M. S. Meltzer, B. Zbar, *J. Natl. Cancer Inst.* **52**, 1887 (1974); R. Keller, in *Immunobiology of the Macrophage*, D. S. Nelson, Ed. (Academic Press, New York, 1976), p. 487.
6. R. M. Schultz, J. D. Papamatheakis, W. A. Stylos, M. A. Chirigos, *Cell. Immunol.* **25**, 309 (1976).
7. R. M. Schultz, J. D. Papamatheakis, J. Luetzeler, P. Ruiz, M. A. Chirigos, *Cancer Res.* **37**, 358 (1977).
8. P. Alexander and R. Evans, *Nature (London) New Biol.* **232**, 76 (1971).
9. R. M. Schultz, J. D. Papamatheakis, M. A. Chirigos, *Cell. Immunol.* **29**, 55 (1977).
10. R. M. Schultz *et al.*, in *Control of Neoplasia by Modulation of the Immune System*, M. A. Chirigos, Ed. (Raven, New York, in press).
11. J. D. Acton, *J. Reticuloendothelial Soc.* **14**, 449 (1973); A. L. Ibrahim, Y. C. Zee, J. W. Osebold, *Proc. Soc. Exp. Biol. Med.* **152**, 483 (1976).
12. R. M. Donahoe and K. Huang, *Infect. Immun.* **13**, 1250 (1976).
13. K. Huang, R. M. Donahoe, F. B. Gordon, H. R. Dressler, *ibid.* **4**, 581 (1971).
14. J. S. Younger and S. B. Salvin, *J. Immunol.* **111**, 1914 (1973); T. D. Flanagan, T. Yoshida, S. Cohen, *Infect. Immun.* **8**, 145 (1973).
15. I. Gresser and C. Maury, D. Brouty-Boye, *Nature (London)* **239**, 167 (1972).
16. I. Gresser, C. Bourali, *J. Natl. Cancer Inst.* **45**, 365 (1970).
17. C. A. Ogburn, K. Berg, K. Paucker, *J. Immunol.* **111**, 1206 (1973); K. Berg, C. A. Ogburn, K. Paucker, K. E. Mogensen, K. Cantell, *ibid.* **114**, 640 (1975).
18. W. Regelson, *J. Med.* **5**, 50 (1974); I. Gresser, D. Brouty-Boye, M. D. Thomas, A. Macieira-Coelho, *Proc. Natl. Acad. Sci. U.S.A.* **66**, 1952 (1970).
19. R. Evans, *Transplantation* **14**, 468 (1972).
20. R. Evans and P. Alexander, *Nature (London)* **236**, 168 (1972).
21. L. B. Epstein, M. J. Cline, T. C. Merigan, *Cell. Immunol.* **2**, 602 (1971); L. A. Glasgow, *J. Bacteriol.* **91**, 2185 (1966).
22. K. Mizunoe, M. Hiraki, Y. Nagano, N. Maehara, *Jpn J. Microbiol.* **19**, 235 (1975); R. J. Jahiel, J. Vilcek, R. S. Nussenzweig, J. Vanderberg, *Science* **161**, 802 (1968).
23. M. A. Chirigos and J. W. Pearson, *J. Natl. Cancer Inst.* **51**, 1367 (1973); P. E. Came and D. H. Moore, *Proc. Soc. Exp. Biol. Med.* **137**, 304 (1971).

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Polymorphism and Geographic Variation in the Feeding Behavior of the Garter Snake *Thamnophis elegans*

Abstract. *Geographic variation in behaviors that influence resource utilization is a key component in current ecological theory, but the phenomenon has been poorly documented. Propensity to attack slugs varies geographically in a western garter snake,* Thamnophis elegans. *Many naive, newborn snakes from inland localities in California refuse to eat slugs. In contrast, virtually all naive young from coastal localities eat slugs. There is, however, no demonstrable polymorphism or geographic variation for propensity to eat anurans. Both coastal and inland snakes consistently eat anurans.*

We know relatively little about the extent of genetic variability for feeding behavior within and between animal populations. Consequently we can only guess at the behavioral alternatives that are vulnerable to natural selection and speculate about the response of populations to selection for resource utilization. Those rare demonstrations of polymorphism and geographic variation in behavior usually deal with behaviors that are unlikely to be modified by experience, for example, social signals (*1*). Because of inherent difficulties in controlling for effects of experience, geographic variation in behaviors that influence resource utilization is seldom studied. One promising approach to the problem is to assay behaviors in inexperienced animals. Studies of newborn snakes indicate that feeding behavior may show genotypic differences within and between populations (*2*).

I now present evidence for a bimodal distribution of behavioral phenotypes in a snake population. The bimodality appears in tests of naive, newborn snakes and cannot easily be attributed to differences in experience. In addition, distributions of behavioral phenotypes vary geographically.

The garter snake *Thamnophis elegans* has a wide range in western North America (*3, 4*). Within California, this species shows geographic variation in its natural diet. Coastal populations feed predominantly on slugs, mice, plethodontid salamanders, and anurans. Inland populations, inhabiting the Sierra Nevada and southern Cascade mountain ranges, prey mainly on fish, anurans and their larvae, and mice (*3, 5–7*). Differences in foraging behavior and morphology coincide with this dietary variation. Inland snakes are more aquatic than coastal snakes and differ in scalation, body proportions, and coloration (*3*). The functional significance of this morphological differentiation is not known.

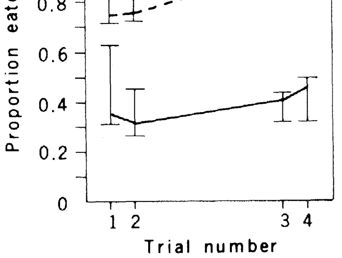

Fig. 1. The feeding responses of newborn coastal (dotted line) and inland (solid line) *T. elegans* to the slug *A. californicus*. Vertical bars indicate the ranges for three inland and two coastal localities (*10*). Sample sizes at the four trials were: coastal snakes, $N = 293$, 292, 173, 169; inland snakes, $N = 101$, 101, 92, 91.

The response of newborn snakes to slugs was studied in three laboratory experiments. The native slug *Ariolimax californicus* was used as a test prey. Slugs of the genus *Ariolimax* are commonly eaten by coastal populations of *T. elegans* in nature (*3, 8*). In California, *Ariolimax* is restricted to the coast and to the western foothills of the southern Cascade Range (*9*). Most inland populations of *T. elegans* are allopatric with this slug. Other slug genera are uncommon in the inland mountain ranges of California, probably because of dry summers, and are virtually absent from the natural diets of inland *T. elegans* (*5, 7*).

Gravid snakes were captured at three inland localities outside the range of *Ariolimax* and at two coastal localities within the range of this slug (*10*). The subjects of this report were the captive-born progeny of 42 such wild-caught, gravid females (*11*). Relatively large samples were obtained from one inland locality, Eagle Lake (64 progeny from 9 females) and from one coastal locality, Scott Creek (221 progeny from 16 females).

In experiment 1, each newborn snake was offered a small piece of *A. californicus* at each of four trials (*12*). For trial 1, all snakes were 14 days old, and the *Ariolimax* presentation represented their first exposure to prey; for trial 2, all snakes were 20 days old. All snakes were tested on the same date for trial 3 in order to simplify logistics. Due to dif-

Table 1. Test for homogeneity in the proportion of slug-eating snakes among litters from an inland locality. The expected frequencies were calculated from the total proportions of all litters combined. Progeny from the first six litters were pooled in order to avoid small expected frequencies in the calculation of χ^2.

Litter	Slug-refusing snakes (No.)		Slug-eating snakes (No.)		Total (No.)		Proportion of slug-eating snakes	χ^2
1	1	14	0	10	1	24	0.42	0.06
2	0		1		1			
3	1		1		2			
4	1		4		5			
5	5		1		6			
6	6		3		9			
7	5		5		10		0.50	0.14
8	2		9		11		0.82	6.35*
9	12		2		14		0.14	5.04*
Total	33		26		59		0.44	11.59†

*$P < .05$; d.f. = 1. †$P < .01$; d.f. = 3.

ferences in birth dates, the snakes were between 9 and 12 weeks old during trial 3 (*13*). Trial 4 took place 5 days later. On each trial a piece of *Ariolimax* was placed in each snake's cage and left there for 24 hours. The result (ingestion or refusal) was then recorded, and uneaten pieces of slug were removed.

The results of these four trials are shown in Fig. 1. Naive coastal snakes were more prone to eat *Ariolimax* than were inland snakes (trial 1, $\chi^2 = 50.6$, d.f. = 1, $P < .001$). This geographic difference in feeding propensity appears to be stable. The two groups remained significantly different on the final three trials (trial 4, $\chi^2 = 80.4$, d.f. = 1, $P < .001$).

The difference between coastal and inland snakes in the tendency to eat slugs could not be attributed to a simple difference in hunger. The snakes were offered dead control foods on the day after each slug trial. The control-food species, recently transformed toads (*Bufo boreas*) and tree frog tadpoles (*Hyla regilla*), are sympatric with both inland and coastal snakes (*14*). Both prey species were consistently eaten by both groups of snakes; there was no evidence for geographic variation. For example, 96 percent of 220 coastal snakes and every one of 83 inland snakes ate *B. boreas* on the day after the first slug trial, and this was their first exposure to anuran prey.

The possibility of a difference in hunger threshold was investigated in experiment 2. The purpose of the experiment was to determine whether the slug-refusing tendency of the inland populations would persist despite increasing hunger. Two groups of snakes were used in the experiment: a group of 148 snakes (representing 11 litters) from Scott Creek (coastal), and a group of 59 snakes (representing 9 litters) from Eagle Lake (inland). Each snake was offered a small piece of *A. californicus* on each of ten successive days. No other food was offered during this test period, and the snakes received no food for 3 days prior to the test period (*15*).

The results of experiment 2 are shown in Fig. 2. It is informative to compare the results with a binomial distribution. If the probability of eating a slug were constant throughout the ten trials and the same for all snakes, feeding scores should be binomially distributed. The inland group, however, shows a bimodal distribution of feeding scores. This distribution is certainly not a binomial distribution ($\chi^2 = 214.8$, d.f. = 5, $P < .001$). There are two classes of snakes at the inland locality, those that consistently ate and those that consistently refused slugs. In contrast, the feeding scores of the coastal group show a skewed, but unimodal, distribution. Ninety percent of the coastal snakes ate slugs at all ten presentations. Heterogeneity among coastal snakes is less marked than in the inland group, but it is statistically significant. The distribution of scores for coastal snakes is also significantly different from a binomial distribution ($\chi^2 = 46.7$, d.f. = 2, $P < .001$).

The difference between the two localities in the distribution of feeding scores suggests geographic variation in genotypes that affect slug-eating behavior. In addition, the bimodal distribution of behavioral phenotypes at the inland locality may reflect genotypic polymorphism for slug-eating behavior.

A comparison of the nine litters from the inland locality provides additional evidence for genotypic polymorphism in slug-eating behavior. Since the distribution of feeding scores is bimodal (Fig. 2), we can classify snakes into two groups: those that ate slugs on fewer than five occasions (slug-refusers) and those that ate slugs on five or more occasions (slug-eaters). The proportion of slug-eating snakes varies considerably among the litters, and this heterogeneity is statistically significant (Table 1). The differences among litters may be a consequence of differences in parental genotypes.

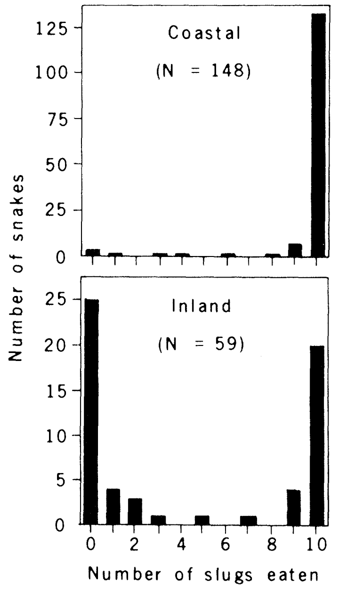

Fig. 2. Distributions of feeding scores for ten successive presentations of the slug *A. californicus*. Distributions are shown for newborn *T. elegans* from a coastal and an inland population.

The specificity of slug responses was investigated in experiment 3. Snakes were simultaneously offered slugs of two genera, *A. californicus* and *Deroceras reticulatus* (*16*). This experiment used the same two groups of snakes used in experiment 2 (*17*). For each group the experiment tested the hypothesis that the probability of eating a slug is the same for the two slug genera (*18*). The results indicated that neither group distinguished between the two types of slugs. Ninety percent of the snakes either ate both slugs or refused both slugs. Thus slug responses studied in experiments 1 and 2 may represent a general response to slugs rather than a specific predilection or aversion for *Ariolimax*.

The simplest interpretation of these results is that the behavioral polymorphism of the inland population and the geographic variation in behavior reflect genotypic differences within and between snake populations. Several results support such an interpretation. (i) Completely naive snakes show geographic variation in the behavioral responses to slugs; (ii) geographic differences persist after feeding experience with other prey; (iii) one inland population shows a polymorphism for slug-eating behavior, while a coastal population is nearly monomorphic; and (iv) an inland population shows heterogeneity among litters in the proportions of the two behavioral morphs. These results suggest a genetic basis for differences in slug-eating behavior, but some alternative hypotheses cannot be ruled out. A maternal effect might explain some of the results, but the prey preferences of newborn snakes apparently are unaffected by the mother's diet during gestation (*19*). Other explanations are possible, however. For example, one can construct a purely phenotypic model consistent with the results on the assumption that some snakes develop an aversion to slugs at their first exposure to this prey.

If slug-eating proves to be a heritable trait, then sympatry with slugs may be the selective force responsible for the geographic variation found. Snakes sympatric with slugs are congenitally disposed to eat them, while allopatric snakes often avoid slugs. Although the advantages of a slug-eating disposition are obvious if slugs are abundant, the disadvantage of a slug-eating trait where slugs are rare or absent is not apparent. It is possible that a slug-eating propensity causes unprofitable attacks on shelled molluscs, but I have no evidence that this occurs or represents a liability for inland *T. elegans*.

STEVAN J. ARNOLD
Department of Biology, University of Chicago, Chicago, Illinois 60637

References and Notes

1. S. Sawada, *J. Sci. Hiroshima Univ. Ser. B. Div. 1* **21**, 167 (1963); M. J. Littlejohn, *Evolution* **13**, 452 (19 → G. W. Ferguson, *Syst. Zool.* **20**, 79 (1971).
2. M. W. Dix, *Science* **159**, 1478 (19 → G. M. Burghardt, *Behaviour* **36**, 246 (19 → *ibid.* **52**, 202 (1975).
3. W. Fox, *Univ. Calif. Publ. Zool.* **50**, 485 (1951).
4. R. C. Stebbins, *A Field Guide to Western Reptiles and Amphibians* (Houghton Mifflin, Boston, 1966).
5. H. S. Fitch, *Univ. Calif. Publ. Zool.* **44**, 1 (1940).
6. W. Fox, *Herpetologica* **8**, 4 (1952).
7. M. White and J. A. Kolb, *Copeia* **1974**, 126 (1974).
8. S. J. Arnold, unpublished observations.

→ A. R. Mead, *Am. Midl. Nat.* **30**, 675 (1943).

10. Gravid females were captured in July in California at the following inland localities (the numbers of progeny from these females are indicated in parentheses): extended vicinity of Eagle Lake (Eagle Lake, Colman Lake, Papoose Creek), Lassen County, 12 (75); Gardner Meadows, Tuolumne County, 4 (15); 5.3 km south-southeast of Woodfords, Alpine County, 2 (11); and at the following coastal localities: 8 km south-southwest of Orick, Humbolt County, 7 (60); Scott Creek, 16 (221), and Waddell Creek, 1 (12), in San Mateo and Santa Cruz counties.
11. Gravid females and newborn snakes were maintained at 27°C. All snakes were individually housed in plastic cages (15 by 30 by 9 cm) with a paper towel substrate and a water dish. Newborn snakes were separated from their mothers within 18 hours of birth and moved to individual cages.
12. Newborn *T. elegans* cannot eat adult *Ariolimax* because of the large size of these slugs. Consequently, *Ariolimax* were frozen, and the body wall was cut into pieces of uniform size (5 by 10 mm). One freshly thawed piece was then placed on the paper substrate of each cage.
13. The snakes were fed dead tree frog tadpoles (*Hyla regilla*) twice each week during the interval between the second and third slug trials. Frozen tadpoles were thawed for 20 minutes before presentation.
14. Frozen supplies of both control food species were thawed just before presentation. Two control species were used because *B. boreas* was initiated as a control, and the supply of this species was insufficient for the entire experiment. Consequently both *B. boreas* and *H. regilla* were used as controls for both groups at trials 1 and 2, but only *H. regilla* was used for trials 3 and 4. Each snake received only one of the two control foods after each slug trial.
15. The ten slug presentations began 8 days after trial 4 of experiment 1, so the age of the snakes ranged from 11 to 14 weeks.
16. *Ariolimax* preparation has been described (*12*). *Deroceras* were killed by freezing and presented whole after a thawing period of 20 minutes. Pieces of *Ariolimax* (0.28 ± 0.06 g) and whole *Deroceras* (0.29 ± 0.08 g) were approximately the same size (means and standard deviations are for samples of 10). Both types of slugs were placed in each cage simultaneously and 5 cm apart.
17. The test was conducted 19 days after the final slug presentation in experiment 2. The snakes were fed dead tree frog tadpoles (*H. regilla*) on five occasions during the interim period. The last maintenance feeding occurred 5 days before the test.
18. The data were tested using the McNemar test for significance of change [R. R. Sokal and F. J. Rolf, *Biometry* (Freeman, San Francisco, 1969), pp. 614–615]. Of 59 Eagle Lake snakes, 22 ate both *Deroceras* and *Ariolimax*, 3 refused *Deroceras* but ate *Ariolimax*, 6 ate *Deroceras* but refused *Ariolimax*, and 28 refused both types of slugs ($\chi^2 = 0.44$, d.f. = 1, $P > .05$). For 148 Scott Creek snakes, the comparable data are 134, 7, 4, and 3 ($\chi^2 = 0.36$, d.f. = 1, $P > .05$). Thus, at neither locality can we reject the hypothesis that the proportion of snakes eating slugs is identical for both slug genera.
19. G. M. Burghardt, *Science* **171**, 921 (1971).
20. I thank H. Arnold, L. Arnold, L. Houck, and S. Sweet for their help with field work and J. Gladstone for technical assistance. S. Altmann, L. Houck, and D. Wake made helpful comments on the manuscript, and M. Bulmer, M. Slatkin, and J. Maynard Smith sharpened my focus on particular issues. Supported by the Spencer Foundation, the Louis H. Block Fund of the University of Chicago, and NSF grant BNS 00619.

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Resource Partitioning in Bumble Bees: The Role of Behavioral Factors

Abstract. *Small* Bombus ternarius *workers forage most frequently on the distal parts of goldenrod flower clusters when large* B. terricola *workers are present. This shift results from* B. ternarius *avoiding* B. terricola. *In this way* B. ternarius *can exploit, without conflict, resources whose availability changes constantly because of fluctuating numbers of larger consumers.*

Many ecologists believe that changes in feeding or habitat by animals often result directly from interactions among individuals (*1*, *2*). However, they have made few efforts to test this hypothesis experimentally with controls under natural conditions (*3*), given its potential importance in structuring communities (*1*, *2*). Further, none of the latter studies unequivocally show the mechanism responsible for the observed changes. Here I demonstrate shifts in the use of resources by bumble bees (*Bombus* spp., Apidae) in response to congeners and the mechanism by which it takes place.

I tested individually marked (*4*) *B. ternarius* Say workers in the presence and absence of *B. terricola* Kirby workers on Canada goldenrod (*Solidago canadensis* L.), the major food source of bumble bees along the Maine coast in mid-August. The shallow florets of this plant can be categorized as proximal, medial, or distal depending on their position in a continuum from the central stalk of the flower cluster to its exterior (Fig. 1).

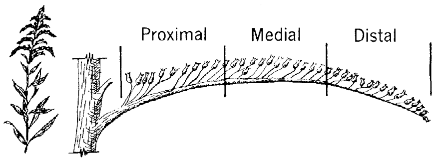

Fig. 1. (Left) A diagrammatic representation of a goldenrod plant with its flower cluster (inflorescence). (Right) Branch of a goldenrod flower cluster showing the parts recognized: proximal, medial, and distal. When the flower cluster is in full bloom the proximal and distal parts often lie at an angle to the horizontal, and the medial part is essentially horizontal in a position superior to the other parts. Each of the three divisions contains a similar number of florets.

Goldenrods were regularly visited for nectar by both species of bees. Workers of a wide size range feed from the same florets, but they seldom make bodily contact or near contact with each other. Given these conditions and the knowledge that individuals of large species usually are behaviorally dominant to those of small ones (*2*), I predicted that large *B. terricola* workers (the largest bees regularly visiting goldenrod) would replace *B. ternarius* workers, which were among the smallest bumble bees visiting the goldenrod.

Cages (1 m³) of coarse window screening were placed over a group of ten goldenrod plants, each with flower clusters of several hundred florets. Immediately, I introduced a marked *B. ternarius* worker that had just been captured in the field. After 30 seconds, I recorded the location of the next 50 florets that it visited. Ten *B. ternarius* were tested in this way.