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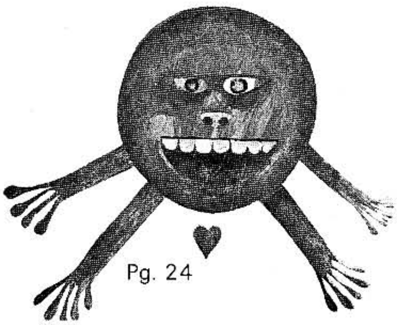
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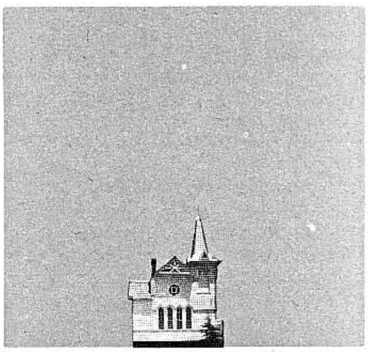
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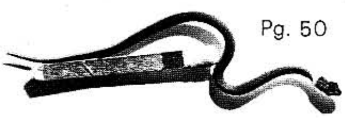
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Chemical Perception in Newborn Snakes

By Gordon M. Burghardt

A FACE IN A CROWD, a familiar voice in a busy conversation, a delicate perfume in a summer evening's breeze, a hint of spice in a culinary masterpiece—each of these sensations leaps forward forcefully into our consciousness. We see the face, not the crowd; we hear that special voice, not any of the others; we smell the perfume, to the momentary exclusion of Summer's other scents; we taste the spice, for a moment forgetting the impression of the dish as a whole. Out of what William James called the blooming, buzzing confusion of our raw sensory experience, we selectively admit into our consciousness only some of these myriad perceptions.

It is not simply a matter of our being especially sensitive to these salient perceptual events. Each face in the crowd, for example, is equally large and equally bright—perhaps even equally interesting on close examination. Rather, some events excite our interest and attention because they have particular meaning to us as individuals.

One source of this meaning is, of course, our past experience. The mother has come to recognize and respond to her baby's cry among all those in the nursery; the chef comes to detect the missing spice in the complex aroma rising from the stew; the wine taster comes to sense the particular essence that identifies the truly great vintage. All of us, highly trained or not, constantly select perceptual events from all the hundreds of stimuli imposed on us—and in so doing we project a perceptual structure onto the entire outside world.

The perceptual world of the normal human adult seems at first glance to be largely a matter of experience. Each of us finds a different face in the crowd to be particularly exciting and interesting. But perception also is tempered by natural, inherited limitations and saliences. It is true that a musician learns by experience to appreciate a great composition, but the range of tones which he can hear and the discriminations between tones which he can make are determined largely by the inherited structure of his ear. It also is true that each individual develops his own personal set of appreciated forms and colors. But commonly shared illusions and hallucinations suggest commonly inherited characteristics within both our visual and nervous systems.

In fact, perhaps the most amazing and instructive cases of imposed perceptual structure are those which are not learned by a lifetime of experience but rather are dictated by nature through generations of evolutionary experience. The young child, for example, without any specific training or experience, will select a balanced diet from a multitude of offered foods, even if left solely to his own devices. My research with snakes has shown that the infant snake is peculiarly fitted out by its inheritance to snap at and eat specific nutritious objects from among the countless hundreds of objects which it will encounter in its first few days of life. More important yet is the finding that the snake seems prepared by nature to eat only those objects which it normally will encounter in its natural habitat. The wisdom of generations of evolutionary development has imposed on these small animals a perceptual structure which facilitates their survival from the moment of birth.

Releasers and Perception

We owe most of our knowledge of this form of natural perceptual selectivity to the ethologists who have elaborated the concept of the "releaser." Basically, they have discovered that a given behavior often is critically dependent on just one aspect of the stimulus situation, while other equally perceivable qualities are without effect. For example, the red belly feathers of the male British robin trigger an attack by another male robin. A dummy, accurate in all respects except that the belly is not red, elicits no attack, but a bundle of red feathers alone is sufficient to release the behavior.

There are many other examples of these critical relations. From them, pioneers of ethology such as Jacob von Uexküll and Konrad Lorenz arrived at a seminal concept known as the releasing mechanism. This mechanism is "keyed" to respond to perceptual cues from the relevant stimulus object, and these cues are known as releasers or sign stimuli. Another aspect of interest was that in many cases these releaser-response relations did not have to be learned in any normal sense during the individual organism's life. Eckhard Hess, at the University of Chicago, has shown that newborn inexperienced chicks prefer to peck at some colors rather than at others. Why this should be is not known yet, but the point is that previous pecking experience was not necessary; releasing mechanisms are innate. It is almost as if there is an Innate Perceptual Schema somewhere inside the organism, to which the environment must correlate in order for a response to occur. Thus nature imposes structure on the organism's perceptual world.

Whereas most work on releasers is and was concerned with vision, my research has been with chemical releasers, odors, which elicit behavior patterns.

The Sense of Smell

The chemical sense of smell is perhaps the most interesting and intriguing sense that we possess. We are certainly selective in our response to odors, many of which elicit profound emotional experiences. Why is there such a mystery surrounding perfumes, and why do only a small proportion of those developed win lasting favor? Why do some smells repel us, while others brighten our outlook throughout the entire day? Yet the mechanisms of smell, even the stimuli themselves, are little understood. There are even authorities who believe that, through generations of disuse and societal taboos, Western man has become insensitive to his sense of smell.

When we try to study smell in man, methodological problems appear immediately. These include the inaccessibility of the sensory receptor itself, the difficulty of presenting an odor in a standardized manner, problems of adaptation and conditioning, and our inability to specify what in the physical stimulus correlates with the subjective impression. There have been some ingenious attempts to overcome these problems. For instance, John Amoore, with the U.S. Department of Agriculture, has had considerable success in correlating the smell of a substance with its molecular shape. But the fact remains that at present man is not a very good organism to use in the study of the chemical senses. Man's reliance on other sensory modalities confounds the precise assessment of the role and mechanism of smell.

Enter the Serpent

What would be a good experimental animal other than man? Many mammals below the primates rely on the chemical senses, but with them a behavior is rarely completely dependent upon olfaction. Most closely related to the mammals are the reptiles, the behavior of which is without question the least studied of all the vertebrate classes. Nevertheless, no one questions the great importance of the chemical senses to snakes. Snakes evolved from lizards and have reached a degree of specialization of the chemical sense unrivaled by any other group of terrestrial vertebrates.

Snakes possess numerous advantages as experimental animals and many species do very well in captivity. Since some species such as garter snakes are viviparous and often give live birth to 60 or more babies at a time, they are especially useful in the study of early development. Nevertheless, snakes have been neglected as experimental subjects, probably because of society's antipathy toward them. The Biblical story of the Garden of Eden probably didn't help. But perhaps a different attitude is needed. As Robert G. Ingersoll put it back in the year 1872:

> If the account given in *Genesis* is really true, ought we not, after all, to thank this serpent? He was the first schoolmaster, the first advocate of learning, the first enemy of ignorance, the first to whisper in human ears the sacred word "Liberty," the creator of ambition, the author of modesty . . of inquiry . . of doubt . . of investigation . . of progress . . and of civilization.

Snakes, besides having a well developed sense of smell, have another modality derived from their olfactory nervous apparatus. The receptor for this modality is known as Jacobson's organ or the vomeronasal organ. It is present in some amphibians, reptiles, and mammals, but it reaches its highest degree of specialization in snakes. The organ consists of a pair of sacs which open into the anterior roof of the mouth. The epithelial lining of the sacs contains typical olfactory cells and their cytoplasmic extensions form a branch of the olfactory cells which terminates on a specialized portion of the olfactory bulb.

The chemical senses in snakes and their behavioral importance were studied by a number of workers 25-45 years ago. While the discussion of the individual contributions of such scientists as Baumann, Kahmann, Noble, Weidemann, Wilde, and Bogert is not possible here, we can list what seem to be the major results of often conflicting research. First, taste seems to be of rather minor importance and plays a role only when food objects are actually in the animal's mouth. Secondly, Jacobson's organ functions in conjunction with the tongue. The snake's frequent tongue-flicking is a mechanical means of picking up and transferring chemical substances to the vicinity of Jacobson's organ within the mouth. (Of interest is the fact that snakes have an indentation in the upper lip which allows them to flick the tongue without opening the mouth at all.) The third point is that many behaviors in snakes—including prey trailing and courtship—seem to involve both Jacobson's organ and normal olfaction. However, Wilde in 1938 demonstrated that the attack on prey by the adult common garter snake is dependent almost totally upon Jacobson's organ. By severing various nerves, Wilde was able to show that only when Jacobson's organ was functioning did an attack take place. Olfaction alone was neither necessary nor sufficient. To prove that only a chemical stimulus was involved, he used a clear and colorless solution of earthworm mucus, which was presented to the snakes on cotton attached to glass rods. The snakes, which normally ate earthworms, attacked this cotton as they would a normal prey object. Wilde's research inspired ours. The behavior pattern and its elicitation were clearly commensurate with the ethological concept of the releasing mechanism. Perhaps feeding behavior in newborn snakes could tell us a great deal, not only about serpent behavior but also about the potentialities and functioning of chemical sensory mechanisms in general.

Analysis of Prey Attack Behavior in Newborn Snakes

We started by asking questions: Would newborn garter snakes respond to chemical stimuli from worms with prey-attack behavior before they ever had experience with any type of food object or its odor? Would they respond to extracts from other normally-eaten classes of prey? And if the above answers were affirmative, was this stimulus-response connection reasonably permanent? If the answer to these three questions were yes, then we would be dealing with a highly precise biological relationship which would offer limitless opportunities for studying, among other things, learned versus unlearned factors in chemical perception, the relations of selective chemical releasers to evolution and ecology, and the development of a behavioral bioassay technique for chemical stimuli.

Using a litter of three-day-old previously unfed garter snakes *(Thamnophis s. sirtalis)*, we found that the answer to all three questions was yes. The chemical stimuli were prepared by placing a standard weight of either redworms, minnows, mealworms (larvae of a beetle), or horsemeat into warm distilled water for one minute. The prey then were removed, and the resulting water solution filtered and refrigerated until use. Of the four items, the first two (redworms and minnows) readily are eaten in nature by this species of snake; the other two are rarely, if ever, eaten.

Naive newborn snakes dramatically attacked a cotton swab that had been dipped in either worm or fish extract. They did not attack swabs dipped in the insect extract, meat extract, or pure water. The attack response, given an effective stimulus, comprised the following: The snake increased its rate of tongue flicking and then lunged forward at the swab with its jaws wide open at about a 45° angle. [*See illustration, page 55.*] This response was identical with that seen toward live redworms and small fish. Moreover, although these young snakes normally refused to eat pieces of horsemeat, they readily attacked and ate horsemeat dipped in the worm extract. The inexperienced snake somehow can recognize, on the basis of chemical stimuli alone, what it "should" attack as a potential prey object.

The stability of the response to chemical stimuli first was tested in completely naive snakes from the same litter by presenting the worm extract at five-minute intervals for 20 trials. An attack was given every time and no progressive weakening of the response was apparent. In a later test for stability, 40 trials were given to a snake with still no weakening of the response. [*See illustration, page 54.*] Naturally, the response cannot be elicited indefinitely at such short intervals. However, the stability shown is more than sufficient for the testing of the same individual repeatedly with the same or with a different extract.

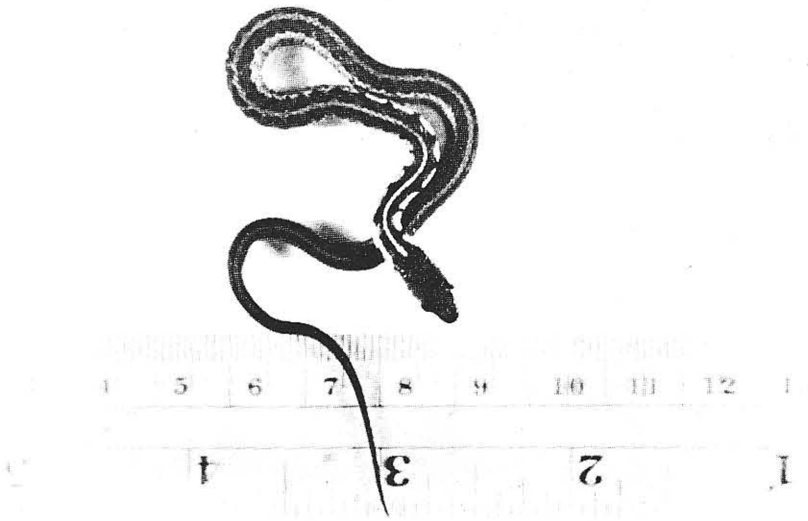
After we obtained the above results, we were convinced that this phenomenon was worthy of intensive study. A series of experiments was designed to investigate various aspects of chemically released attacks by newborn snakes.

One of the first experiments concerned the role of vision in eliciting this behavior. With the same litter, we investigated the responses to visual aspects of prey animals from which the snakes could obtain no chemical information. A variety of small sealed glass vials was introduced into the home cage of each individual snake. Vials were either empty or contained a type of small organism, which was either dead or alive. The results were as follows: If there were moving organisms in the vials, the snakes would orient themselves, flick their tongues, and explore; however, they never opened their mouths or tried to attack the animals through the glass. Further, the amount of interest in the vial shown by the snakes was clearly proportional to the amount of movement going on in the vial at the time. For instance, quickly-swimming guppies elicited the greatest response, while dead guppies of exactly the same size and coloration elicited no response. This response to movement in the vials disappeared rapidly when the vials were reintroduced a short while later, indicating that the novelty of the moving animals was involved. Indeed, at this point we can conclude that the role of vision is limited to the orientation toward and exploration of a potential food object, particularly if moving, but that the attack of prey can be elicited in naive subjects only by chemical stimuli.

Further experiments with inexperienced garter snakes whose eyes or nostrils (or both) had been artificially closed showed that neither olfaction nor vision is at all necessary for the prey-attack response to occur. Jacobson's organ is apparently responsible. Naturally, the attacks of blind snakes were not well-directed, but attacks they were.

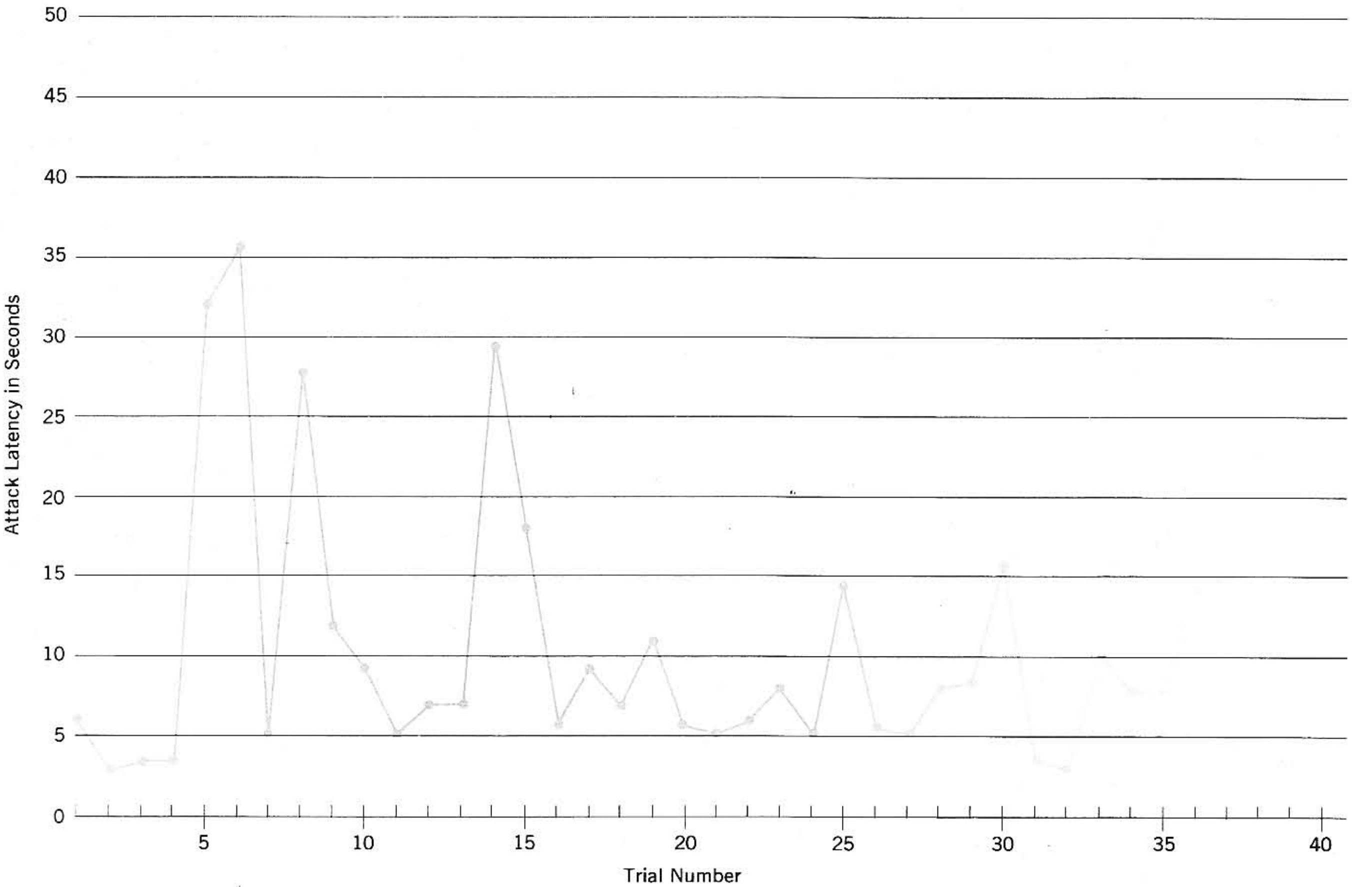
Comparative Studies

One of our main interests has involved the study of species of snakes which have feeding habits in nature and captivity that are quite different from those of the garter snakes with which our work began. Would newborn young of these species respond to chemical stimuli from animals which the species normally ate? We began by looking at other species of snakes in the garter snake group, the genus *Thamnophis*. In this large and widespread group of snakes are found forms with very different food habits. We tested seven species and subspecies

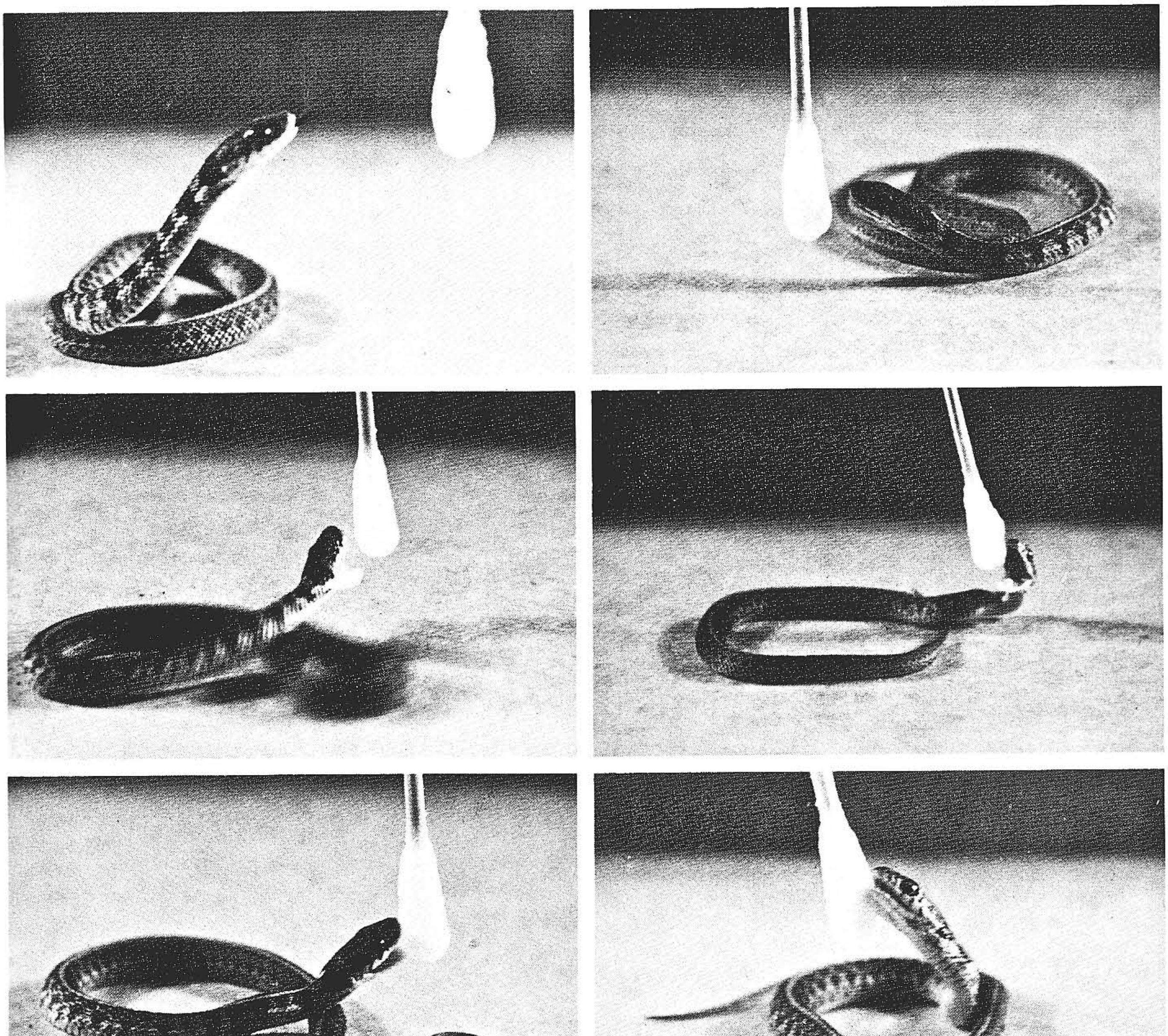


on a series of extracts from prey representing most classes of animals known to be eaten by at least some species in the genus. The congruence between the responses of the inexperienced newborn young and the known feeding habits of the species was very close. For instance, the Chicagoland garter snake *(Thamnophis sirtalis semifasciatus)* will eat fish, worms, amphibians, and leeches very readily and we obtained highly significant responses to those extracts, but not to extracts of slugs, mice, insects, and crayfish, which in fact this species rarely, if ever, eats. [*See illustration, page 56.*] As in many snakes tested, there was a big difference in the relative effectiveness of larval and adult salamanders. It appears that during metamorphosis changes occur in the chemicals from the skin which elicit prey-attack behavior.

Consider another species, the eastern plains garter snake, *Thamnophis r. radix,* which has similar habitat and feeding preferences. We tested a litter of 22 newborn young and obtained the profile of responses to various extracts. [*See illustration, page 57, top.*] Again, all extracts were significantly higher than the water control but for those of the baby mouse, slug, cricket, and metamorphosed salamander. Although no extensive ecological studies have been done on this species, it appears that earthworms, amphibians, fish, and leeches are eaten readily, with worms being probably most common in the natural diet. Extracts from three kinds of earthworms and three kinds of fish were tested.



Newborn garter snakes reliably and repeatedly attack a swab dipped in an extract made from worms normally eaten by adult garter snakes. Inexperienced snakes attacked on 40 successive trials at five-minute intervals. No habituation took place.



In a characteristic attack on a swab dipped in extract from a prey, the garter snake orients toward swab and increases its rate of tongue-flicking (upper photographs), lunges toward swab (middle photographs), and bites swab (bottom photographs).

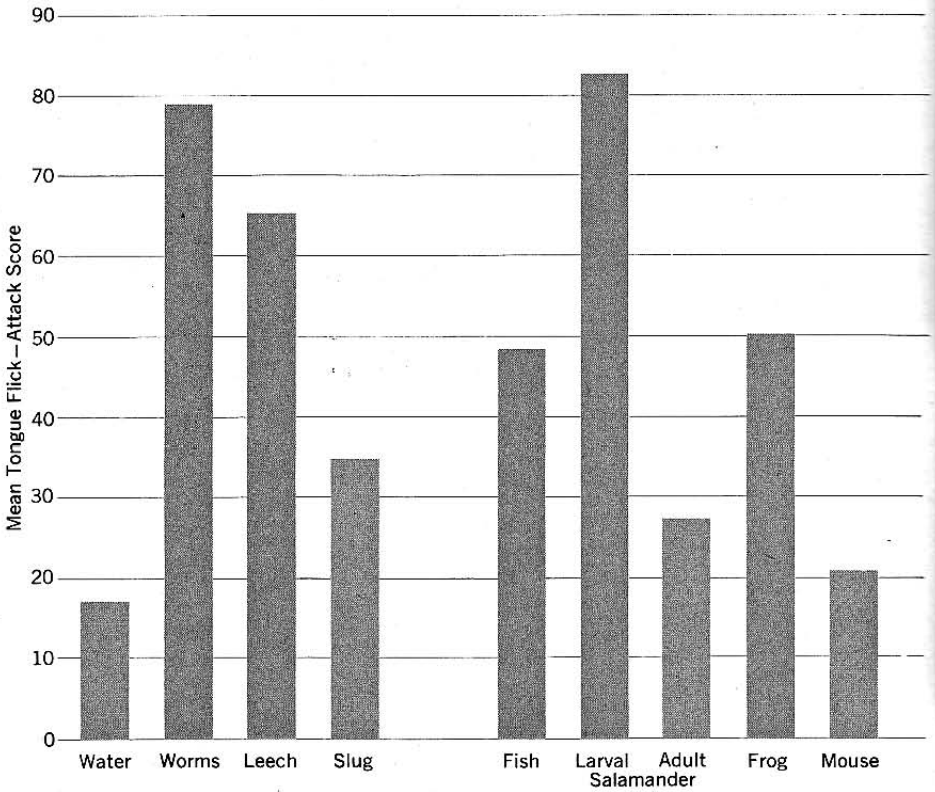
Again, it was found that the larval salamander had a higher releasing value than the adult form. This is a relationship which frequently has been found in species of newborn snakes that include amphibians in their normal diet. It may represent evolution's discovery that larva are tasty, while adults are tough—and perhaps dangerous.

In sharp contrast to the above were results obtained from the western smooth green snake *(Opheodrys vernalis blanchardi)*. This species, unlike others we studied, is oviparous instead of bringing forth young alive. In one experiment, eggs were laid and hatched in captivity. The young were tested at the same ages as were the plains garter snakes, and with the same extracts. The same extracts were presented to the green snake as to the plains garter snake. [*See illustration, opposite, bottom.*] The cricket extract was the most potent; indeed, it was the only extract to which actual attacks were made and the only one significantly higher than the water control on the basis of the tongue flick-attack score. The result becomes more meaningful when it is realized that, out of all the extracts presented, the cricket extract is the only one which represents an organism eaten by the green snake. In fact, it appears that this species will eat nothing but insects, spiders, and soft-bodied arthropods.

The differences between the smooth green snake and the plains garter snake are striking. In contrast to green snakes, plains garter snakes never eat insects, and the cricket extract received the lowest score of all the extracts. It is obvious, therefore, that clear and biologically useful differences exist between the chemical perceptions of food objects by these two species of snakes.

The green snake and the plains garter snakes are rather widely removed from each other both taxonomically and ecologically. The common garter snake, discussed first, and the plains garter snake are much more closely related, live in similar habitats, and appear to eat the same food. With these two species, the extract-response profiles show no clear differences. Is it possible to find differences between closely related forms? Just how precise is the technique? A final answer to the last question cannot be given yet, but it is possible to generate some dramatic differences between species of the same or related genera. Let us look at a couple of examples:

Two species of garter snakes and one of the brown snakes *(Storeria)* were exposed to extracts from three earthworms, three fish, and one slug. We tested eight inexperienced newborn midland brown snakes *(Storeria dekayi wrightorum)*, known to eat only worms and slugs. The second species of naive young tested was Butler's garter snake *(Thamnophis butleri)*. We tested a litter of 15 from a female caught in southern Michigan. In captivity, Butler's garter snake readily eats worms and fish but not slugs. The third species to be compared on these three classes of extracts was the western aquatic garter snake *(Thamnophis elegans aquaticus)*, known to eat only fish. We tested a litter of nine from a female found in southern California.

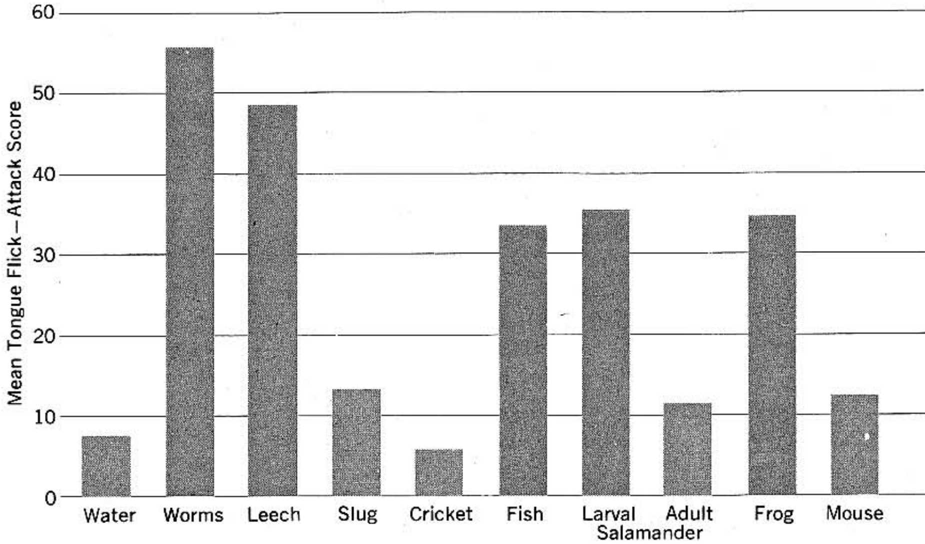


Newborn Chicagoland garter snakes were tested on extracts from common prey, scored high for prey normally eaten by adults (color), low for prey rarely eaten (grey).

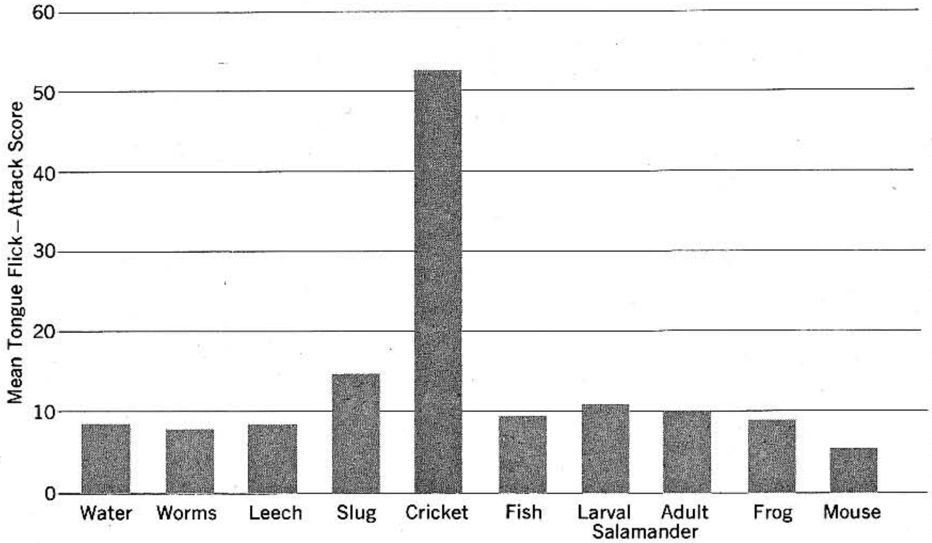
The results were clear. The responses of the different species of inexperienced snakes to skin extracts parallels the feeding habits manifested by specimens freshly caught in the field. [*See illustration, page 58.*] Scores for the brown snake were on a different scale from the garter snakes—about half as high, due to a lower frequency of tongue flicking. This reduction also was found in another species from the same genus.

Turning to the water snakes *(Natrix)*, we found some more remarkable differences. Most water snakes (such as *Natrix s. sipedon*, the common banded water snake) eat fish and amphibians, but Graham's water snake *(Natrix grahami)* and the queen snake *(Natrix septemvitatta)* eat practically nothing but crayfish, and newly molted ones at that. Here the newborn young attacked only crayfish extracts and even gave a greater response to extracts from newly molted crayfish. [*See illustration, page 59.*]

Taken together, these results dramatically indicate the species-specific nature of chemical perception in newborn snakes. That these are related to the natural feeding ecology of the different animals is equally clear. But what do these comparative results mean? First of all, they can best be understood in terms of evolutionary principles. By natural selection each kind of newborn snake comes to recognize, by chemical cues, the type of prey that it is best adapted to eat. Our present interpretation is that there is an Innate Perceptual Schema, or releasing mechanism, based upon genetic information which enables the newborn snake to recognize, by chemical cues, the type of prey that it should eat. Differences between species then easily can be seen as ecological adaptations that have evolved through natural selection. As such, they can be as useful in the study of the relationships and differences among species, such as skeletal structure, scale patterning, or other morphological characteristics. For instance, the two species of water snakes responding to crayfish extract are closely related by the usual taxonomic criteria. But too facile an evolutionary interpretation does not do justice to the data. This technique shows that a naive snake will respond to chem-



Strikingly different attack profiles were obtained with babies from two different species of snakes, the eastern plains garter snake (above), and the western smooth green snake (below). Nevertheless, the babies attacked extracts of prey normally eaten by the adult of the species (color) but did not attack the other extracts (grey).



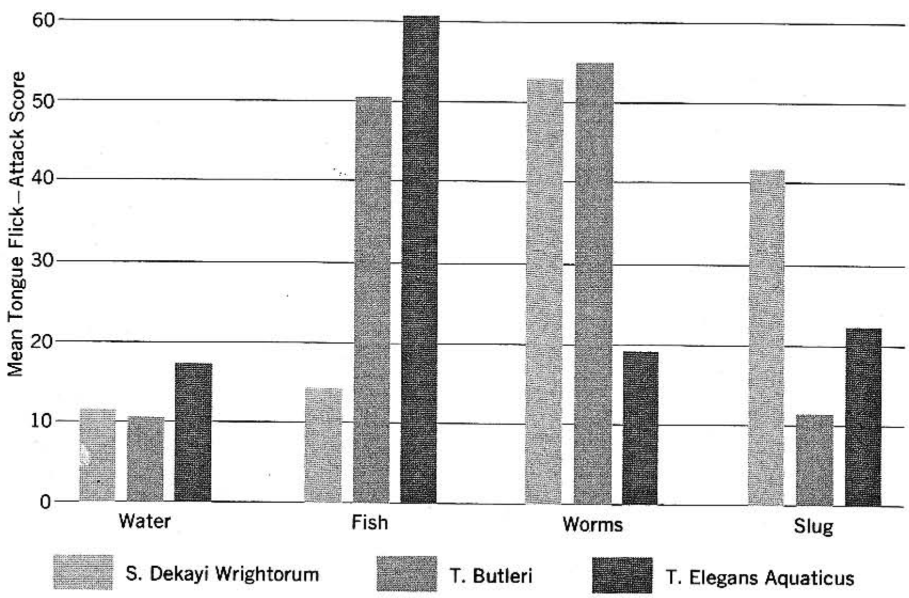
ical cues that cannot or do not figure in the normal feeding behavior of the species. For instance, where it is found, the aquatic garter snake would rarely, if ever, encounter the guppy, yet the newborn young responded to the guppy extract readily. However, since the aquatic garter snake normally eats fish, it is probable that the guppy possesses chemical cues similar or identical to those found in fish which the snake normally eats.

In Butler's garter snake the situation is quite different. An extensive field study by C. C. Carpenter, now at the University of Oklahoma, showed that in nature the diet of this species comprises only worms and leeches. Yet captive specimens readily eat fish and amphibians, and newborn young respond to extracts from all four groups. Indeed, the complete profile of responses to extracts by Butler's garter snake is very similar to those of the plains garter snake or the common garter snake, which does eat all four types of prey in nature. It is apparent, therefore, that the normal feeding habits and ecology of a species are not sufficient to "explain" the response to chemical cues in newborn young. But we should remember that evolution is a process of time and that the past may exist in the present. A feasible hypothesis in this instance is that Butler's garter snake has retained the perceptual side of a releasing mechanism which appears to be of no selective advantage in its present mode of life. Of course, retention of the potential of naive snakes to respond to chemical cues from fish would be advantageous if a change in the environment occurred so that fish became a necessary or more easily obtainable food source. The same could be true for amphibians in this species. It is interesting to note, in this connection, that on the usual taxonomic criteria several authorities feel that Butler's garter snake has evolved from the plains garter snake.

We are beginning the construction of species profiles based upon the responses of newborn young to a series of extracts. So far we have investigated over 15 forms from seven genera. It is by looking at very closely related forms, however, that the most valuable comparative conclusions may be gleaned, since here the traditional taxonomic canons of anatomical distinctions among species may be only of limited value.

Other Considerations

The problem of how these responses by naive snakes can be modified through subsequent experience is interesting, and work is underway in this area. However, the strength of these innate releaser-response ties is often more striking than is their lability. For instance, a large litter of garter snakes was divided into two groups. One group was tested on the standard series of extracts during the first week of life and then released. As with all our testing, it was possible to rank the stimuli in order of effectiveness. The rest of the litter was raised for either 64 or 191 days on an artificial, unnatural diet (strained liver). Since they would not eat this food, we periodically forced it down their throats. At the end of the predetermined number of days on the artificial food, the snakes were tested in an identical fashion on the same series of extracts as were the snakes in the litter tested at birth. Remember that for this period of time these snakes had never had the opportunity either to receive a chemical stimulus normally eliciting an attack response nor to perform the attack response itself. In



Attack profiles for newborn snakes of three species tested on three classes of extracts reflect diets of adult snakes. (Scores for S. Dekayi Wrightorum are doubled.)

nature a similar amount of deprivation would have resulted in the early death of the snakes. Yet the snakes in both deprived groups attacked the same extracts in the same way as did their littermates tested earlier. No degeneration of the releaser-response system had taken place during the long periods of inaction. The artificial diet, by the way, was refused at the end of the experiment as it had been at the beginning.

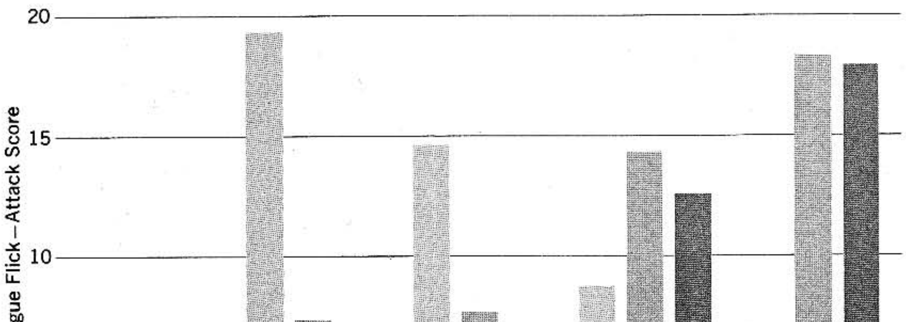
There is some evidence, however, that early feeding experience can influence subsequent behavior if the snake actually attacks and eats the prey object. Further experiments are in progress on this aspect of the problem.

Currently, studies also are being carried out, in collaboration with John Law of the biochemistry department at the University of Chicago, on the chemistry of the effective extracts. Once we know the nature of the chemical stimuli involved in this behavior, it should be possible to study stimulus structure and releasing value on a molecular level.

If the chemical perception of the newborn snake is so well adapted to the ecological and evolutionary aspects of its existence, it is reasonable to inquire into the possibility of similar situations elsewhere in the animal kingdom, including man. But many psychologists, while admitting the existence of complex inherited sources of stimulus information in birds, fish, and insects, feel that mammals, especially humans, are so perceptually and behaviorally plastic that evolutionary considerations of the type discussed here are unimportant or irrelevant, or perhaps even dangerous. Possibly a new approach is needed. Gene Sackett, at the University of Wisconsin, recently has shown that rhesus monkeys raised in visually restricted environments respond in species-specific fashion when confronted with pictures of monkeys having certain expressions such as threat. Robert Fantz has shown that the newborn infant brings into the world more complex visual abilities than previously thought and, on the physiological level, David Hubel and Torsten Wiesel have demonstrated the extensive visual abilities built into the newborn kitten. Daniel Freedman and Eibl-Ebesfeldt are directing our attention to the implications of evolutionary, ethological thought for our understanding of human behavior.

But as concerns the chemical senses we only can speculate. Probably no odor would elicit as specific an overt response in man as in the snake. But many of the responses of men to situations and stimuli are internalized. Feelings and affective states replace the motoric responses necessarily measured with animals. Perhaps many of the feelings aroused daily in the odoriferous world of man are influenced in part, at least, by evolutionary memories recorded in the genes many ages ago, fleeting emotional bonds with our ancestors. And this memory might be a little bit different for each of us, for we all have had a unique voyage from the past.

The highly precocial nature of young snakes and their dependence upon the chemical senses allow the phenomenon to be elucidated clearly. But the point is that we should not be concerned just with whether the newborn organism has or has not certain perceptual abilities of vision, olfaction, etc. We would like to know if he can use these abilities innately to recognize stimuli having biological and evolutionary significance. In many cases we may never find out. Nevertheless, the search is both exciting and meaningful.



Three species of snakes from the same genus, *Natrix* (water snakes), have different natural diets. The attack profiles of the newborn young show the same differences.