56 percent of the nests lost to predators were in the nestling stage.

The causes of the increased predation are unknown. Possibly there may be a decrease in fruit for omnivorous predators. There could also be an increase in the predator's reproductive activities that may necessitate a higher protein diet.

Birds breeding in the dry season have about a 42 percent chance of fledgling young whereas those breeding in the early rainly season have a 15 percent chance. This difference in predation pressure has apparently been enough to cause this species to breed during a period when nestling food is relatively scarce. But young fledged during the dry season, although low in weight, probably reach independence from parental care near or during the period of increased food abundance after the rains begin.

Predation may be an important factor in the selective value of a low clutch size in tropical birds. It has been hypothesized that, given a high rate of nest predation, smaller clutches may be favored by selection if this reduces the chance of a nest being found (*8*). We must now add to this the hypothesis that predation may cause breeding to occur when food for nestlings is scarce. A small clutch would be favored by selection as an adaptation to low food availability.

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Chemical-Cue Preferences of Newborn Snakes: Influence of Prenatal Maternal Experience

Abstract. *Newborn garter snakes* (Thamnophis sirtalis) *responded similarly to worm and fish surface extracts regardless of whether the mothers were fed exclusively on fish or worms during the gestation period. Worm extract was the more effective. This result is in contrast with the easy modifiability of chemical-cue preferences in young snakes after birth. The initial stimulus control of the attack response in newborn snakes thus seems relatively unmodifiable.*

Ethological work on early experience and imprinting has revitalized concern with the modifiability of many species-characteristic behaviors. However, along with reemphasizing the importance of early experience, ethologists also emphasized the fact that many animals will respond with a stereotyped response to only a small portion of the total stimulus situation presented by a naturally occurring object, even without prior experience with that object. The cues eliciting such specific responses, termed sign stimuli, can be shown to be influenced by genetic factors if specific prior experiences are controlled (*1*).

For a number of years I have been working on the prey-attack response of newborn snakes which seems to involve such an innate sign stimulus. For example, young garter snakes (*Thamnophis sirtalis*) will give increased tongue flicking and actual overt attacks to cotton swabs dipped in chemicals extracted from the surface substances of normally eaten prey such as fish and earthworms (*2*). This response is mediated primarily by the tongue—Jacobson's organ system (*3, 4*). Clear species differences exist in the type of prey extracts responded to by inexperienced young, and these differences are closely related to differences in the prey normally eaten by the various species (*5*). An evolutionarily based explanation for the presence of such selective discrimination is certainly reasonable—that is, a mechanism which is ultimately dependent upon some type of genetically encoded information. However, the question remains as to which experiences, if any, can alter the prey-attack behavior of newborn snakes to chemical stimuli.

Results up to now indicate that if naive snakes are force-fed an unnatural food such as strained liver for up to 6 months, the resulting chemical-cue and feeding behavior deprivation seems to have no effect either on the overt behavior itself, on the elicitation of attacks by chemical stimuli, or on the relative hierarchy of releasing values of various effective extracts (*4*). Consequently, we can conclude that the "innate schema" of newborn snakes does not change without some experience other than that of deprivation itself.

Such results support the view that rigid, built-in preferences are present in newborn snakes. However, unmodifiable preferences would certainly have unfavorable consequences under many conceivable environmental conditions. In fact, actual overt or "voluntary" feeding by the animal *is* capable of modifying the chemical preferences of the newborn snake (*6*). A further experiment separated the effects of food reinforcement from the chemical extract experience itself and found that under certain circumstances preexposure of newborn snakes to chemical prey extracts was sufficient to alter later responsivity to prey extracts (*7*). Therefore, postnatal experience can alter the chemical preferences shown by newborn snakes.

Although such evidence seems to point to the presence of an ethological innate releasing mechanism modified by postnatal experience (*8*), it might be argued that the differential responding to chemicals by newborn snakes is not a genetic, evolutionary, innate, or similarly labeled behavior at all. Prenatal experience may be an important, if not the sole, influence. In considering how such a mechanism might work, maternal feeding experience is one of the few nongenetic paths which might provide some specific information dealing with the type of precise knowledge of adaptive food habits possessed by the newborn snake. This possibility has been mentioned earlier (*5*), although it is difficult to see how it could provide the range of information possessed by the neonate. The newborn young of some species can recognize many classes of chemical stimuli such as those from frogs, leeches, salamanders, fish, and earthworms.

If maternal feeding does play a role in the selectivity shown by newborn

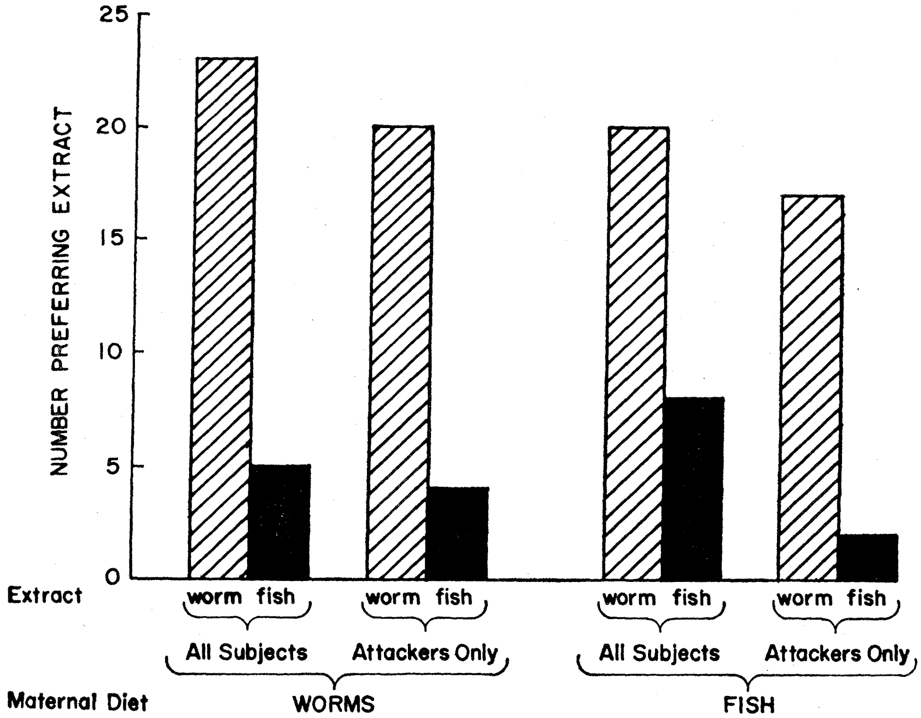

Fig. 1. The preference of newborn snakes for worm and fish extracts as a function of maternal diet. No significant differences in offspring behavior were found. The "preference" measure is defined in the text.

snakes, it would seem most likely that such influence would occur during gestation in these viviparous snakes, especially the latter part of the gestation period when the embryo would have a better-developed sensory system to allow the encoding of any such chemical messages. A type of prenatal "imprinting" may thereby occur. The possibility of such prenatal chemical modification in garter snakes was evaluated by selectively feeding gravid snakes either fish or worms and testing their young on both fish and worm extracts.

Two gravid Chicagoland garter snakes (*T. sirtalis semifasciata*) were captured in the same area of Illinois about the middle of June 1968 and began the feeding regime on 27 June. Subject No. 1 was fed exclusively night crawlers (*Lumbricus terrestris*) while subject No. 2 was fed exclusively upon goldfish (*Carassius auratus*). The snakes were kept in isolation from each other and were offered as many prey as they would eat about every 5 days. The food was presented by forceps to both. Subject No. 1 gave birth to 29 live young on 12 August after eating ten average-sized night crawlers (about 2 to 4 g each). Subject No. 2 gave birth to 28 live young about 2 weeks later (21 August). The second female ate considerably more goldfish than the first female ate worms; she ate 89 average-sized goldfish (about 1 g each). If anything, the greater experience (quantitatively and temporally) of the fish-fed female should bias the results in favor of fish. One of the young in litter No. 1 was a "runt," considerably smaller than its littermates, weak, and relatively inactive. He was discarded from subsequent testing, leaving 28 subjects in each litter.

The young of both litters were tested in an identical fashion on the sixth and seventh days after birth. They were housed and tested individually under conditions previously described (*5*). On both test days the snakes were tested once with each prey extract, except that the order varied, with equal numbers of snakes in each litter (14) receiving each extract first. Each snake was tested a total of four times.

The fish and worm extracts were prepared by placing the goldfish or night crawlers in distilled water at 60°C in the ratio of 6 g of prey per 20 ml of water. The prey was stirred gently and removed after 2 minutes, and the resulting liquid was centrifuged at 3000 rev/min for 10 minutes. The supernatant was transferred to small vials and frozen until use.

The testing procedure involved dipping a cotton swab into the thawed extract and slowly bringing it closer to the snake's mouth (about 1 to 2 cm). The test interval was a maximum of 60 seconds. If a snake did not attack the swab in that time, only the number of emitted tongue flicks was recorded and the swab was removed. If a snake did attack, the latency was recorded to the nearest 0.1 second with a stopwatch. The essential criterion for an attack was opening the jaws, although a forward lunge was also usually present.

The results can be summarized simply. No significant differences were found in the responses to the fish and worm extracts by snakes whose mothers had been fed exclusively either fish or worms for many weeks prior to giving birth. In Fig. 1 the number of snakes in each litter preferring the fish or worm extract is shown. Preference is based on both tests with each extract given each snake. If attacks occurred (right columns), the preferred extract was that which elicited the greater number of attacks. If an equal number of attacks occurred, then the extract having the shortest combined latency was scored as preferred. If no attack occurred, then the extract releasing the greatest number of tongue flicks was considered preferred. Whether one uses all subjects or only those that attacked an extract does not alter the finding that no differences in the preference data exist between litters (for all subjects, $\chi^2 = 0.40$; d.f. = 1; $.5 < P < .7$; for attackers only, $\chi^2 = 0.02$; d.f. = 1; $.8 < P$

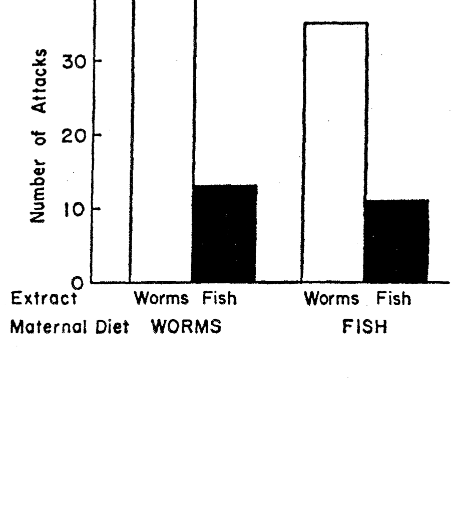

Fig. 2. Number and latency of attacks to worm and fish extracts as a function of maternal diet. As in Fig. 1, no significant differences are evident.

$< .9$). Figure 2 gives information concerning the number of attacks and the mean latencies for attacks by snakes that attacked both extracts at least once. If the attack frequency data alone are considered more closely, no differences are noted, except that overall the fish-fed group was slightly less responsive (for total number of attacks, $\chi^2 = 0.03$; d.f. $= 1$; $.8 < P < .9$). More effective extracts generally lead to more attacks and shorter latencies (as well as higher tongue-flick frequencies) (*9*), and this finding is repeated here. Earthworms were more effective than fish throughout (maternal diet worms: all subjects, $P < .002$, binomial test, two-tailed; attackers only, $P < .002$; maternal diet fish: all subjects, $P < .02$; attackers only, $P < .001$).

This experiment shows that maternal chemical-feeding experience has no significant effect on the chemical preferences of young snakes if this experience is given as long as 9 weeks before parturition. Feeding of the mother was controlled from about the gastrulation stage of embryonic development (*10*), which would seem to encompass any conceivable prenatal critical period. While the lifelong feeding experience of the mother may be involved, it would seem more profitable to focus study on the genetic-developmental processes involved. In addition, an explanation based on maternal feeding must deal with possible differences between adult and neonatal diets.

The combined results of this and the postnatal experiments show that the process of being born seems to radically change the ability of the animal to make use of chemical experience, although the very nature of the differences between the pre- and postnatal environments make experimental equivalence impossible. Indeed, whether the newborn snake can even perceive chemicals from its mother's diet is unknown, yet remains so far the only possible normal path for a nongenetic shaping of the differences seen at birth in chemical-cue preference. In oviparous species which evidence similar selective perception upon hatching, it would appear that even this channel of information would have severe limitations (*11*). Prenatal processes are certainly important, but clearly they cannot be considered the source of all the specific perceptual information possessed by neonates.

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Classical Conditioning of a Complex Skeletal Response

Abstract. *The pigeon's so-called "arbitrary" response of pecking an illuminated disk can be established and maintained by procedures resembling those of classical conditioning. This phenomenon was shown to be independent of the specific signaling relationships between illumination of the pecking disk and presentation of food; it will appear as long as the key is differentially associated with food. When a nondifferential condition is introduced, pecking "extinguishes" even if it has previously been established and even when the new condition involves as much reinforcement as the old one. Reinstating differential conditions reestablishes pecking. The initial conditions determine the speed and apparently the asymptote of pecking rates in the differential condition; initial exposure to a nondifferential procedure retards subsequent acquisition, possibly quite permanently. These findings are discussed in the context of mechanisms of adaptive learning, not involving reward and punishment, which lead to selection of effective behaviors on a nonarbitrary basis.*

Brown and Jenkins (*1*) recently reported that hungry pigeons would spontaneously begin pecking a disk mounted on the wall of an experimental chamber if illumination of the disk signaled the forthcoming presentation of grain. The procedure closely resembled Pavlovian delay conditioning, and its effectiveness with pecking—a complex skeletal act directed outward at the environment—potentially represents a significant extension of the domain of classical conditioning. The delay conditioning procedure exerts such powerful control that birds frequently peck the disk even when conditions are changed so that pecking the disk prevents the opportunity to eat (*2*). Under these artificial laboratory conditions, such behavior appears maladaptive and is difficult to encompass in a biological approach to learning based on the reward value of external events.

In the experiments reported here, we explored the limits of applicability of the classical conditioning paradigm by using a procedure that avoids the specific "pairing" relationship between response key and food, which was characteristic of the earlier procedures. Pairing the response key with food according to the Pavlovian delay paradigm involves the precise signaling of the time of presentation of the unconditioned stimulus (for example, food). By circumventing this intimate signaling relationship, we hoped to determine whether the remarkable stimulus control over the act of pecking was attributable to a peculiarity of the Pavlovian procedures used earlier or whether it represents a more general manifestation of associative learning through classical conditioning.

The new procedure that we used was a variant of one introduced by Rescorla (*3*). Throughout the course of these experiments, a pecking disk was illuminated for 8.6-second periods, which were distributed randomly throughout each experimental session with a mean interstimulus interval of 30 seconds. In the presence of the illuminated disk, 4-second periods of access to a grain hopper were provided on a random basis; the probability of initiating such