FEEDING BEHAVIOUR OF SNAKES, PART II.

By: N.B. Ananjeva and N.L. Orlov, Zoological Institute, Department of Herpetology, 199164 Leningrad, V-164, U.S.S.R.

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SOCIAL FACILITATION OF FEEDING BEHAVIOUR

Social facilitation may play an important role in feeding behaviour (Dewsbury, 1981). This phenomenon investigated largely in mammals, consists of increased frequency of certain type of behaviour in the presence of other individuals. Such facts are known to physiologists as examples of meditated learning or of imitation conditioned reflexes (Manteifel, 1980). In reptiles the socalled "social feeding" involving social facilitation and imitation was first observed in the iguana lizards *Anolis carolinensis*, *Sceloporus cyanogenys* and *Dipsosaurus dorsalis* (Greenberg, 1976). The phenomenon is generally easier to observe in experimental conditions when the animals are kept in a "group", within sight of another. We have observed it in snakes. We have elicited feeding activity in eight *Vipera kaznakovi*, which otherwise exhibited no feeding response when offered *Mus musculus*. The effect was achieved by installing a new snake already adapted to the experimental conditions and already feeding. The snake instantly responded to the presence of prey and showed feeding behaviour, i.e. head elevation, rapid tongue flicks. The conspecifics gradually began sensing the surroundings as indicated by increased tongue flicks and also showed other signs of feeding arousal. The vipers become still more strongly

stimulated when the newly arrived snake starts trailing the stricken prey. All the snakes become restless and begin moving about, some attempting to intercept the prey at the sight of engulfment by the hunting snake. They then start actual hunting and feeding. Such stimulation of feeding activity due coaction effects is particularly characteristic for mobile *Colubridae* and for all *Viperidae*, and *Crotalidae* (*Agkistrodon, Trimeresurus, Bitis, Coluber, Coronella, Elaphe, Lampropeltis, Natrix, Spalerosophis*). It is most common in batrachophages; the abrupt lunges at the prey serve as a strong stimulus for their conspecifics (*Cyclagras, Ptyas, Nerodia, Xenodon*). We have observed this facilitation of feeding behaviour in *Boidae* (*Boa, Chondropython, Corallus, Liasis, Python*), in small entomophages (juvenile *Coluber, Eirenis, Vipera*) and saurophages with characteristic abrupt movements (*Coluber, Psammophis, Telescopus*). Pursuit movements in these situations have a marked signal function. According to our data, social facilitation and imitation effect is maximum in the group of frog-eaters. The hunting snakes begin grabbing rapidly moving objects and even one another. Occasionally accidents occur and the snakes, with their mouths wide open, ingest pieces of the substrate that smell of the food item (*Cyclagras gigas, Elaphe rufodorsata, Elaphe quadrivirgata, Natrix tessellata, Ptyas mucosus, Rhabdophis tigrina*).

Imitation and facilitation of feeding are sometimes elicited by certain snake species in interspecifics. However, the effect depends on specialization in feeding: the closer the specialization, the more marked the effect. Concrete movements i.e. "locomotor" hunting, appear to be indices of the above specialization. For example, *Elaphe rufodorsata* fails to respond when the green python *Chondropython viridis* lunges at frogs and subsequently slowly constricts the

latter. *Elaphe rufodorsata* does show the response if a conspecific or some species of the genus *Natrix* are hunting. This may reflect the fact that the first stages of hunting and prey retention in *Chondropython viridis* and *Elaphe rufodorsata* are markedly different, whereas in *Elaphe rufodorsata* and *Natrix*-species they are basically the same. The difference is in the later stages: *Elaphe rufodorsata* strangles the prey before ingestion, while *Natrix* ingests it alive.
Experiments support the idea that feeding arousal in snakes is elicited as a reponse to specific movements by other snakes and not merely as a response to the smell of the prey. When two glass containers are placed close to one another, each with a specimen of *Rhabdophis tigrina* but only one with a frog, the hunting snake will stimulate the other snake to show all the signs of feeding arousal (rapid tongue flicks, prey searching, specific body movements, active motion).
An inhibiting effect of snakes in the group on the trophic activity of the other can also be noted. This situation occurs when dominant specimens suppress the activity of weaker individuals. Bigger *Cyclagras gigas* of one age group suppress feeding activity of smaller animals. Neck flattening and violent lunges at the prey performed by big snakes would frighten frog-hunting individuals of smaller size, the latter would take refuge and not resume feeding for a long time.

THE PATTERNS OF PREY DETECTION AND PURSUIT

All snakes are predators. The common feature of their trophic behaviour is that they hunt for living animals and in the case of successful hunting swallow the prey whole. However, cases of consumption of dead animals have been recorded (Shilov, 1956; Patten & Banta, 1980). We have fre-

quently observed in the terraria consumption by snakes (*Boidae, Colubridae, Viperidae, Elapidae*) of dead rodents, birds, fishes and frogs. Moreover, there is practice in the Zoo to feed snakes a mixture.

The patterns of prey detection and pursuit, the sequence and measure in the use of analyzing organs, the food items themselves allow to divide snakes into behavioral sets (Ditmars, 1912; Wiedemann, 1931).

The general outline of hunting in most snakes species appear to be as follows:

1. The animal either actively searches for prey or lies in ambush.
2. The animal, while in an adequate state of motivation receives initial information of the proximity of prey (soil tremor-an impulse to the initiation of the Jacobson organ, visual signal-an impulse to the initiation of the Jacobson organ, thermoreceptor perception of the item-an impulse to the initiaton of the Jacobson organ).
3. Rapid tongue flicking following in prey search and pursuit.
   Many authors report progressive frequency of tongue flicks upon introduction of food items into the medium (Carr & Gregory, 1976; Williams & Brisbin, 1978; Dunbar, 1979; Gove, 1979). However, the above responses of the tongue as analyzing organ are actually seen in many situations: fright, reconnoitering, enemy encounter, intraspecific interactions, hunting, search for water, etc. (Scudder et al, 1980). A search involving active use of Jacobson organ proceeds the instant of sighting the prey.
4. Vision is involved, the snake begins an active pursuit of the prey or seeks to strike.
   A venomous snake chooses an appropriate moment and strikes the prey by stabbing its fangs, while pythons or *Colubridae* seek to attack the

prey, i.e. "to fix" it; Jacobson organ is again involved if the prey is lost to vision. In certain situations after olfactory response, snakes (many *Boidae* and *Crotalidae*) pass on to thermoreceptor orientation rather than visual (particularly in the dark).

5. Then follows a lunge in non-venomous snakes (many batrachophages -*Natrix, Nerodia, Thamnophis*) and swallowing the prey alive or killing it first shortly after the strike. Venomous snakes start trailing the prey by olfactory reception exclusively, although in the case of small non-dangerous animal or bird prey (which when stricken can run or fly a long way), the latter is not released until dead. The snake then releases the prey on the substrate, unmistakingly identifies the head and swallows the prey head first. Non-venomous snakes which constrict their prey (*Python, Boa, Elaphe*) also lay it on the substrate after constriction and swallow it head first.

This "ideal" picture of the hunting sequence is actually never demonstrated by one animal. Normally, certain behavioural actions in a particular situation appear to be irrelevant and are therefore omitted. It should be noted that discrimination of the prey objects is extremely high. The food item is discriminated by 1. movement pattern (Diefenbach & Emslie, 1971; Smith & Watson, 1972; Herzog & Burghardt, 1974), 2. size and shape (Wiedemann, 1931), 3. smell (Wiedemann, 1931; Burghardt, 1967, 1968, 1973, 1977) 4. colour Smith & Watson, 1972), 4a. extent of the irradiated infra-red (when thermoreception is available, Noble & Schmidt, 1937; Gamov & Harris, 1973) 5. "age".

We have repeatedly observed in many snakes (*Naja oxiana, Vipera lebetina, Coluber jugularis, Python regius*) their ability to identify the age

of the food item (in the context of imminent danger). Small blind mouse neonates were eaten without caution, swallowed alive, without being constricted or bitten, while adult mice capable of biting are constricted (or bitten by venomous snakes). The older the prey, the more cautious is the hunting.

When *Vipera lebetina*, *Vipera kaznakovi*, *Liasis mackloti*, *Elaphe schrenki* are presented with mouse neonates and adult mice, all the snakes kill and swallow adult rodents first, the swallowing of neonates comes after. The same snakes show a differentiated approach when offered furred little mice, which can see and are capable of movements and defence (i.e. biting) as well as neonate blind rats (three times the size of mice). The snakes kill, then swallow smaller yet more adult mice, while they swallow live helpless, though bigger, rats or else passively constrict and engulf them half-alive.

When *Python regius*, *Python molurus* and *Eunectes notaeus* are presented with adult rats and neonate rabbits, which are 2-3 times bigger than rats, they attack and constrict the rats. However, they crawl calmly towards the rabbits and swallow them.

The amazing ability of snakes to identify the prey head after killing (even by neonate *Elaphe* and *Lampropeltis* - Klein & Loop, 1975) to facilitate the swallowing is due to olfactory and visual orientation (Diefenbach & Emslie, 1971; Herzog & Burghardt, 1974; Duvall et al., 1980). Direction of the fur as well as the presence of vibrisses also play a role. The snakes sometimes "blunder" in finding the right direction of engulfment and swallow the medial or posterior end first. A much higher percentage of error was observed by us in the snakes swallowing of newborn naked animals of a fairly large size. A strong odour producing a powerful olfactory effect makes the choice of direction of swallowing difficult as in the case

of skin incision in the posterior end of the prey body ("blood smell"), which is misguiding. Olfactory reorientation resulting in error seems more likely in this situation. In "age" determination the snakes may be guided by the milk smell of neonate rodents.

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