FEEDING BEHAVIOUR OF SNAKES, PART I.

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INTRODUCTION

Animal behaviour has now become a subject of intense research. Of great interest in this respect are reptiles, among which snakes appear to be the least investigated. For this there are a number of reasons (Carpenter, 1977; Carpenter & Ferguson, 1977), primarily, the difficulty of observing these secretive animals in their natural habitat, as well as of maintaining them in captivity. Most works on behavioural psychophysiology (learning ability, elaboration of conditioned reflexes, functioning of sensory organs) have been made on tortoises (Burghardt, 1977). The last two decades have seen intense research on the behaviour of lizards owing to the advances made by the so-called "objectivist" school of ethology (Chauven, 1972). The number of observations on the behaviour of snakes has increased as well. Many zoologists have long realized that knowledge of reptilian behaviour would be incomplete and many concepts untenable until work on reptiles included snakes.
Wagner (1928), who pioneered research into animal behaviour in Russia, separated most behaviours into three large complexes, namely 1) feeding 2) reproduction and 3) self-preservation.
The present paper deals with the first of the three problems and summarizes material on snake feeding habits collected from twelve years of observations in terraria and supported by studies

in the wild of the snake fauna of the USSR. It omits description of the maintenance conditions of the examined species (20 *Boidae*, 3 *Elapidae*, 100 *Colubridae*, 20 *Viperidae*, 15 *Crotalidae*). An account of these can be found elsewhere.

Most snakes show unique morphology including: elongate body shape; absence of limbs to dismember the prey; tooth system adapted for the capture; retention, or killing in the case of venomous snakes and swallowing of the prey and a highly moveable skull allowing the swallowing whole of relatively large prey. This accounts for the specificity of many forms of ophidian behaviour, in this context, their feeding behaviour.

Common defensive, threating postures and movements as well as those of aggressiveness and reproduction have long been noted. Defence and attack responses, as interrelated components of the "triotroph system" (Manteifel, 1980) are extremely important for the understanding of different forms of feeding behaviour and "predator-prey" relationships. Snakes show a set of stereotyped movements and complex defence and attack responses. These responses are most characteristic of interspecific aggression and most apparent in reproductive behaviour (mating, male fighting, courtship) in which they appear ritualized. Ritualization (i.e., development of informative, signal function, Lorenz, 1969; Dewsbury, 1981) along with a total or partial reduction of the primary locomotor function is seen in a number of head and tongue movements, as well as in those of the body and tail. They can be either smooth or abrupt, dorsoventral or lateral. There are over 100 stereotyped movement patterns (Carpenter & Ferguson, 1977), most of which appear to be trophic responses. Reference here is to the primary function of the movements, which are observed as ritualized pattern in other situations.

Identical responses may occur in different behavioural situations. This paper deals with the entire complex of feeding behaviour, beginning with the search for prey to its killing and swallowing. The latter aspects seem particularly essential for the identification of trophic behaviour, which must not be confused with other behaviour, such as exploratory patterns.

STRATEGIES FOR FEEDING

Most snakes hunt prey from ambush, which may be facilitated by colouration or body shape. The snake may also move towards the prey or actively pursue it over a short distance. More often, snakes use combined strategies, as do *Dendrelaphis*, *Ahaetulla* and *Oxybelis*, which hide in trees and attack from above (Biswas et al., 1977). Species of the genera *Coluber*, *Psammophis*, and *Spalerosophis* pursue the prey over some distance. Batrachophages frequently engage in active pursuit of the prey. These snakes (*Nerodia*, *Natrix*, *Cyclagras*) move at about 16 m per 10 seconds. They also make abrupt thrusts of the head following the leaps of the frog with open mouth, until the teeth catch the prey.
Ambush tactics are used by many *Boidae*, *Viperidae* (Shine, 1980; Pianka, 1981) and *Crotalidae*. After an unsuccessful ambush these snakes may pursue or slowly scan the trail of the prey using olfactory cues.
Luring is often employed in feeding. The well disguised body of the snake may give the impression of a branch on which a bird, a lizard or a mammal may "perch". Still more striking is the imitative behaviour of the twig snake, *Thelotornis kirtlandi* (Goodman & Goodman, 1976), which creates in African sunbirds an illusion of a fledgling, by inflating the anterior part of the body and

elevating its head to display the pointed tip. It has been reported, that birds fly close to the snake, facilitating its hunting. It remains uncertain, whether the birds approach the snake because its head simulates a fledgling. This seems doubtful, first, because brooding birds become restless and alarmed in the presence of a potential enemy and will "swoop down" on it attempting to distract it. Also, comparison of the snake head with the fledgling may be antropomorphic considering high resolution of avian vision.

Tongue luring has been shown to be employed in feeding behaviour in *Oxybelis* (Mole, 1924; Rabb, 1972). Here, the tongue is both the analyzer and the lure for small animals, which mistake it for larval insects. However, an alternative hypothesis (Keiser, 1975) holds, that prolonged extrusion of the tongue causes the prey to freeze rather than luring it. Prolonged olfactory contact is also supposed to have a role in this display.

Caudal luring is a common behaviour that has now been observed in juvenile *Chondropython viridis* (Murphy et al., 1978), juvenile *Boa constrictor* (Radcliffe et al., 1980), juvenile *Vipera russelli* (Henderson, 1970), adult *Cerastes vipera* (Heatwole & Davison, 1976), adult *Bothrops bilineatus* (Greene & Campbell, 1972), juvenile and adult *Sistrurus miliarius* (Jackson & Martin, 1980) and adult *Acanthophis antarcticus* (Carpenter et al., 1978).

Tail luring is most commonly employed by juveniles and is reinforced by a bright contrasting colouration of the tail tip. Neill (1960) used this morphological feature to predict tail luring in several species; this prediction was subsequently confirmed (cf. *Acanthophis antarcticus*, Carpenter et al., 1978; *Trimeresurus gramineus*, our data). A young *Chondropython viridis* (Orlov, 1981), will

coil on a branch and elevate its brightly coloured caudal tip, undulating it while the rest of the body remains immobile. *Hyla arborea* and *Rana temporaria* have been observed to attack the tip, apparently mistaking it for a prey object. Both frogs were instantly seized and swallowed. However, the python showed different tactics when hunting *Lacerta vivipara*. It hooked its body over a branch, with the head and the tail hanging down. Neither head nor body moved, but the tail moved worm-like, horizontally, rather than vertically, as in the former situation. The lizard attempted to catch the tail and was captured and consumed. Not only has caudal luring now been documented so has the fact that snakes can discriminate between prey types and employ different luring patterns. The successfull caudal luring in *Trimeresurus gramineus* seems to disagree with Greene & Campbell (1972) who feel that this movement is merely defensive and warning behaviour. On the other hand, we have observed lure-like caudal movement in terrestrial species (*Agkistrodon contortrix, Agkistrodon blomhoffi, Vipera kaznakovi, Vipera ammodytes transcaucasiana, Vipera lebetina turanica, Bothrops schlegeli, Bothrops neuwiedi, Boa constrictor*), when hunting rodents of different ages. Some rodents do not respond to the caudal lure and the snakes therefore employ a different hunting strategy. Indeed, we are not convinced by the reported rodent responses to lure (Henderson, 1970; Carpenter et al., 1978). We are more in favour of the current view (Greene & Campbell, 1972; Heatwole & Davison, 1976; Jackson & Martin, 1980) that the wide-spread occurrence of tail luring in juveniles is basically due to their diet of frogs and lizards. This behaviour in adults is normally confined to species which show no ontogenetic differences in their feeding, but are batrachophages or saurophages as adults. Lizards and frogs are apparently highly sensitive to caudal

luring, particularly insectivorous ones. This kind of lure seems inappropriate for most birds and mammals, the vision of which is capable of high resolution. Incidentally, a mouse may engage in aggressive or defensive movements in new surroundings, which can easily be erroneously understood as feeding responses to luring.

Various hypotheses exist on the origin of the caudal lure. The most interesting, as well as plausible is that expressed by Radcliffe and co-authors (Radcliffe et al., 1980) to the effect that tail movements in predator snakes result from displacement activity in a conflict situation due to the incongruous purposes: to remain unnoticed and to pursue the prey. A comparable movement is caudal undulations in hunting cat. It would seem reasonable to assume that selection would favour movements attracting prey yet allowing the predator to keep out of danger.

This type of trophic behaviour is obviously advantageous to more vulnerable juvenile animals. We have seen tail luring in juvenile *Chondropython viridis* in the absence of prey, caudal luring is also more frequently and more persistently employed by a hungry snake. In a review of defensive tail display of snakes and amphisbaenians Greene (1973) concludes that ritualization of primary movements either repels prey or attracts it.

We have repeatedly observed such caudal movements in mating behaviour (involving fighting) of *Vipera lebetina turanica, Vipera lebetina obtusa, Echis multisquamatus, Coluber rhodorhachis, Elaphe climacophora, Elaphe quadrivirgata.* Important signals, widely employed in diverse behavioural situations, including feeding, defensive and mating behaviour, apparently have common origin. They appear to be involved in different behavioural systems, due to the action of endo- and exogenic factors. This independence on the original motivation context is known for displays arising as a result of displacement activity (Dewsbury, 1981).