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Feeding behavior of the dice snake (*Natrix tessellata*)

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Abstract. Using measurable behavioral components and corporal characteristics we recorded and analyzed the feeding behavior of the piscivorous dice snake (*Natrix tessellata*).The analyzed parameters were: searching time, searching speed, attack speed, prey handling time, ingestion time, body condition index (BCI) and fish body size parameters. The correlation between these parameters and their effect on successful prey capture and consumption was also examined. Searching time and searching speed was not affected by the other parameters of the snakes or fish, however in case of repeated attacks the searching speed strongly correlated with the BCI. Attack speed was also strongly influenced by the BCI. The successful outcome of an attack depends on the searching speed: a high searching speed reduces the possibility of successful prey capture. Prey handling time is higher when fish is caught by trunk and ingested either from head or from tail, in comparison with grasping on fish head or tail and starting ingestion from the grasped body part. In two cases the fish caught by tail was ingested from head and in one case caught by head and ingested from tail. In these exceptional cases the prey handling time also became high. The ingestion time is independent of BCI but it is strongly affected by the weight and size of fish and also by the direction of ingestion.

Key words: BCI, searching speed, searching time, attack speed, ingestion time, prey handling time, piscivorous,

Introduction

All snake species are predators and due to their specific body structure are able to occupy ecological niches that are inaccessible for other vertebrate predators. The diet of snakes varies depending on species, age, sex, season and geographical distribution (Kardong 1980).

The identification of possible prey items is based on various cues, such as movement pattern (Diefenbach & Emslie 1971, Smith & Watson 1972, Hertzog & Burghardt 1974), size and shape (Wiedemann 1931), odor (Wiedemann 1931, Burghardt 1967, 1968, 1973, 1977), color (Smith & Watson 1972), thermal characteristics in certain species (Noble & Schmidt 1937, Gamov & Harris 1973). Following prey capture and immobilization, the ingestion is easier head first. Snakes rely on visual, olfactive and tactile cues to detect the anterior part of prey's body, but mistakes are common. The number of erroneous trials is higher in case of those snake species that are specialized on consuming newborns of prey species. In these cases tactile and olfactive stimuli are deficiently interpreted (Anajeva & Orlov 1982).

Prey preference is influenced by innate factors but during ontogenesis it can change and it is also affected by experience and learning (Burghardt 1969).

Snakes use a wide spectrum of senses in detecting and identifying their prey, such as: vision, thermo-reception, chemo-reception, tactile reception and auditory localization of ground born vibration (Friedel et al. 2008).

Vision is the most important sense in detecting prey (Shivik 1998, de Cock Buning 1984). Some snake species dispose of color vision but it is considered to be a character of evolutionary more primitive snake species (Underwood 1970, Peterson 1992).

Regarding foraging strategy, snakes can either adopt a sit-and-wait strategy (ambush predators) or they can be active foragers (Schooner 1971). The former strategy is energy conserving, but it also provides low prey capturing rate. The active foraging strategy is more rewarding, while requiring more energy. Both strategies are composed of active and inactive phases, but differ in the duration of these phases. In case of typical active predators the stops are short and represent only 5% of their total activity, while in case of typical sit-and-wait predators the inactive phases form 95% of their foraging behavior (Zug 1993).

Foraging strategies correlate with thermo-regulation, intraspecific interactions, body shape, morphology of digestive system and habitat preference. Active foraging snake species usually have thin bodies and relatively long tails and they hunt for less active prey items. Species that apply the sit-and-wait strategy possess a stout body and relatively short tail. (Shine 1980, Pianka 1981).

An active foraging strategy is common among members of Elapidae and Colubridae families, including batrachofagous and piscivorous snakes such as *Nerodia*, *Natrix* and *Cyclarges* (Ananjeva & Orlov 1982).

In piscivorous snakes evolution favored those characters that allow a tight hold and quick ingestion of prey. The ligaments of jaws become more elastic; and lateral jaw movements during ingestion are exaggerated.

Teeth are long, curved and sharp (Cundall 1983). As a result of adaptation to aquatic environment they are able to close their nasal cavity by specific valve; their intestine is twisted (McDowell 1979). Jayne et al. (1988) considered three stages in prey consumption of aquatic snakes: 1. initial phase, when the snake holds its prey, 2. Position finding phase, when the snake by lateral jaw movements turns the fish with its head oriented in the mouth of snake, 3. ingestion phase.

The relationship between snake size and relative prey size is becoming subject of many studies.

The relative prey size is larger in case of large snakes than in case of small snakes (Seigel et al. 2001). Adaptation to large prey may have its disadvantages despite its higher energetic benefits. Larger snakes have a reduced mobility; larger prey can cause more several injuries (Shine 1991).

The main factors that influence snakes' seasonal diet are climatic conditions, availability of prey among certain climatic circumstances and energetic needs of snakes that represent seasonal variation (Carpenter 1952, Arnold & Wassersug 1978, Slip & Shine 1988). In reproducing season the energetic need of female snakes increases (Luiselli et al. 1996). Low temperature inhibits digestive enzymes this is the reason why snakes cannot feed at low temperatures (Hailey & Davis 1987). The dice snake (*Natrix tessellata*), a diurnal aquatic species, is widespread in central and southern Europe. It prefers lowlands up to 800 m height, and can be found in both riverine and lacustrine environments. The snakes emerge from hibernacula in April and retreats in October. Males stay at the hibernation site waiting for females to emerge. Mating occurs in spring and lasts until half of May; after copulation females start to feed, meanwhile males try more copulation. Eggs are laid in June or July; with clutch sizes of 5-25 eggs depending on the female size. Incubation lasts usually 10 weeks (Fuhn & Vancea 1961).

The aim of this study was to determine the prey capture behavior of the dice snake, by measuring and calculating behavioral parameters such as: searching time, searching speed, attack speed, prey handling time, and ingestion time.

Materials and methods

Study subjects. 6 adult *Natrix tessellata* (3 males and 3 females) were used for this experiment. They were collected in Constanța County, in May 2003, after emerging from hibernation. The experiment lasted 6 months, during this period the weight of individuals significantly increased and by the end of the experiment it reached the optimal weight for this species.

Prey species. It was used live fish for feeding, species that form the natural diet of dice snake: *Carassius auratus*, *Gobio gobio*, *Rhodeus sericeus*, *Alburnus alburnus*, *and Pseudorazbora parva*. The size of the fish specimens was relatively small (Table 1).

Experiment design. Snakes were housed in separate terraria (70x 95x 95 cm) furnished with soil and gravel that imitated natural environment. Each terrarium was equipped with a plastic water container (50x 25x10 cm). Water was changed every second day and the soil was also wetted to maintain optimal humidity. Heating and light was provided by an electric bulb of 100 W and two XX W fluorescent lights. A clay pot in each terrarium served as hiding place for the snakes. The electric bulbs were placed in one corner of the terraria, so that the snakes could choose the optimal temperature by selecting different distances from the heating source. Light was provided 8 hours per day. The experiment started only after an accommodation period (two months), after which the snakes got used to human presence and started feeding.

During the experiment a live fish was introduced into the water container and the prey catching behavior of dice snakes was recorded by video camera. Snakes were offered fish of different sizes in order to determine the effect of prey size on snake behavior. If the snake did not start searching for prey after 10 minutes of fish introduction, the experiment was stopped.

In case of successful attack the snake was offered another fish until it became satiated. To record the feeding behaviour we used a Hitachi VM-H620E 8mm video camera recorder. The film was analyzed with Video Wave software.

Data analysis. Parameters used to define the behavior of snakes were the following:

1. **Searching time**: the interval between fish introduction and snake attack
2. **Searching speed**: proportion of performed distance and time of searching
3. **Attack speed**: proportion of attack distance and time
4. **Prey handling time**: time period between attack and ingestion when the snake arranges fish into an optimal position to swallow.
5. **Ingestion time**: time between the last arranging lateral movements of jaws and the finish of ingestion, marked by the first tongue flicks.

Calculated ratios that can influence prey catching behavior:

R1: SVL (snot vent length) / snake head width

R2: snake head length x head width / SVL

R3: R1 / fish height

R4: R2 / fish height

R5: fish head length x fish head width / fish height

We also determined the body condition index (BCI), as implemented by Bonnet & Naulleau (1994). This index is highly correlated with the weight of nutriment reserve and liver weight of the snake. The BCI was calculated according to the formula: BCI = M / MT, where M is the measured weight of snake while MT is the theoretical weight of snake. MT = $(L / l)^3$ x m; where L is the measured length of the snake, l is the average length of newborn snakes of this species and m is the average weight of newborn snakes.

Because there was no literature data on average length and weight of the dice snake we used the average of our measurements (l= 19.94 cm and m= 4.78 gr.) on 20 newborn snakes captured in 30/07/2003.

Obtained data was stored in the program File Maker Pro 5.0 and statistical analyses were performed using STATISTICA 6.0.

Table 1. Body size parameters of the fish specimens used in the experiment.

Fish species	Height (cm)	Length (cm)	Weight (gr)
Alburnus alburnus	1.0-1.5	4.0-6.0	3.0-6.0
Carassius carassius	1.0-3.5	3.0-10.0	2.0-20.0
Gobio gobio	1.0-1.5	6.0-9.0	6.0-12.0
Pseudorazbora parva	1.0-2.0	3.0-7.0	1.0-7.0
Rhodeus sericeus	1.0-2.0	4.0-5.0	2.0-4.0

Results and discussion

Body condition index (BCI). The body condition index helps to determine the feeding motivation of snakes, because it predicts the physiological status of individuals. In spring, when snakes emerge from their hibernacula the value of BCI is low, however the index is higher in case of females than males. In our study the initial values of BCI were measured in July.

These values proved to be lower (x= 0.261 in males and x= 0.326 in females) than average BCI after hibernation (x=0.298± 0.049 in males and x= 0.364± 0.057 in females), but the reason for this is that the snakes did not accept food in captivity for two months after collecting them. After the specimens started feeding, their BCI increased constantly, until it reached a presumably optimal value. There was no data in literature regarding the optimal BCI of the species *Natrix tessellata*. In other species such as *Vipera aspis,* the optimal value of body condition index is 0.57± 0.18 while in *Coulber viridiflavus* this value is 0.48± 0.16 (Bonnet & Naulleau 1994). In general, the body condition index of colubrid species is lower than that of viperid species, because colubrids are active foragers, while viperids are ambush predators. The reason why females have slightly higher BCI values is that they accumulate reserves for oviposition.

Searching, localization and identification of prey. When snakes reached the water they were guided by vision to detect and attack fish, however they also showed high frequency of tongue flicks. Snakes in general rely on visual, chemical and tactile stimuli to detect and capture prey. In water the dice snake is attracted by moving prey, then prey presence is confirmed by chemical information (Shivik 1998, de Cock Buning 1984). The reason why the dice snake needs more senses to capture its prey is that fish move relatively fast in the water (Chiszar et al. 1988). Most of the snake species use chemical perception to locate their prey but the importance of vision in dice snake is higher, because fish odor in the water is not persistent so it offers little information on the momentary position of prey. Regarding the foraging strategy of the *Natrix tessellata*, is obvious that it is an active forager.

After a longer period of searching it can rest, taking its head out of water. However in some cases the dice snake can adopt a sit-and-wait strategy, staying at the edge of the water container and waiting for the fish to reach an optimal position to attack. This behavior is characteristic for less motivated snakes that consumed other fish specimens before. In applying the sit-and-wait strategy the snake may use its tongue as a decoy, as we observed. In this species the tip of the tongue is colored yellow or orange, while the snake body imitates the color of its environment. During this luring behavior the snake keeps its tongue out of the mouth with slow flicks. Our observations prove that the fish seems to be attracted by this slow tongue flicks. This luring behavior of the dice snake was not described in other snake species until now, but it is already known that *Acanthophis* species can use their tail as a decoy (Carpenter et al. 1978). Our results indicate that although the **searching time** of *Natrix tessellata* in average is 47.72±71.71, this time interval varies greatly. Searching time does not correlate with other considered parameters such as: snake weight, BCI, fish length, fish weight, fish height, fish mobility and fish species.

A specific situation was when after an unsuccessful attack the snake did not loose visual contact with prey, in this situations searching time was extremely low heaving an average of 0,32 seconds.Regarding **searching speed** its average is 0.15±0.08 m/s. Searching speed is not affected by BCI (Pearson correlation analysis: r(x,y)= 0.07; p=0.371; n=153).

Other authors' study on amphibian eating snakes (*Nerodia*, *Natrix*, *Cyclarges*) show a 10 times higher searching speed (1.6 m/s) (Ananjeva & Orlov 1982).

The explanation can be that the species they studied were terrestrial, feeding on frogs. In case of repeated attacks the BCI seems to affect searching speed (R=0.79; t(n-2)=2.908; p=0.033* - Spearmann Correlation) (Figure 1).

Searching time is characteristic for each individual. The better is the physiological status and BCI of a specimen, the higher speed it can afford.

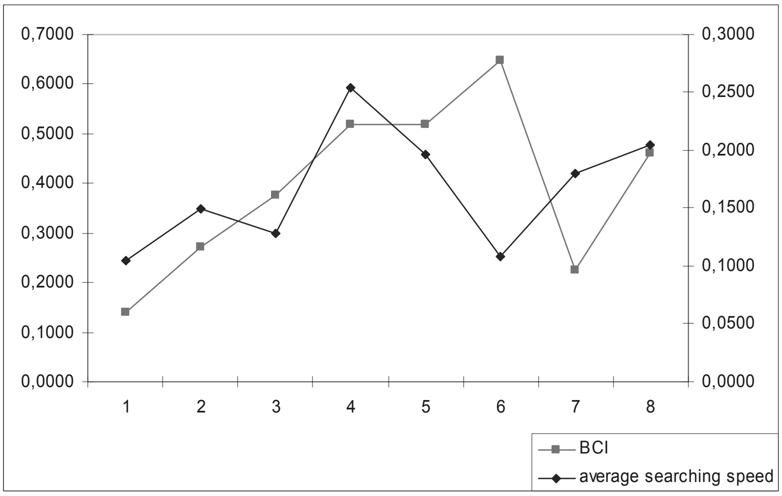

Figure 1. Variation of the average searching speed (repeated attacks) in correlation with body condition index (BCI).

Attack . The attack is elicited by the motion of prey, if the fish stays immobile, the snake can pass near it without attacking. The attack is launched when the snake is completely dived; this fact demonstrates that it is highly adapted to aquatic environment. The **attack distance** varies between 0.1 and 8 cm and it is usually horizontal. The **speed of attack** varies between 0.02 and 1.00 m/s.

In snakes that capture prey on land, the average attack speed is 1.6- 3.5 m/s in *Crotalus* species (Van Riper 1953), 1.22- 2.85 m/s in *Pituophis* species (Greenwald 1974), 0.6- 2.1 m/s in *Elaphe* species (Alfaro 2002). The attack speed of *Natrix tessellata* approaches the speed of terrestrial snakes, which is unusual, because the water has a higher density than air.

The hydrodynamic form of its head helps this species to overcome water resistance. The head of *Natrix natrix*, that hunts on land as well is less pointed. The attack speed is highly correlated with BCI, suggesting that a snake with better physiological condition is capable of faster movements. There is no relationship between fish mobility and attack speed.

The attack of the dice snake has a preparing phase and it can be included into the category of fast attacks, according to the definition of Cundall & Greene (2000). After an unsuccessful attack the snake may repeat it up to 15 trials. We observed that in case of 2 or 3 unsuccessful attacks the snake may chase its prey with opened jaws at a high speed.

Capturing prey. The dice snake does not use any special method to capture prey. It is not a venomous snake and does not apply constriction, it simply grabs prey with its jaws.

In our findings 54.54% of attacks resulted in successful captures. We considered more parameters that can influence pray capture efficiency (Table 2).

Table 2. Correlation (Pearson) between pray capture efficiency and BCI, snake-prey distance, attack speed, and searching speed.

	df	F	p
BCI	148	4.16966	0.042930*
Snake-Pray distance	148	10.22086	0.001698*
Attack speed	148	12.16464	0.000642**
Searching speed	148	19.13356	0.000023***

The most important factor that influences prey capture is searching speed. The higher the searching speed is, the less accurate the attack becomes, this way the number of efficient prey captures is reduced. On the contrary, attack speed exerts a positive effect on capture success. Regarding the distance between snake and prey, it was showed that in shorter distances attack speed and accuracy increase. The BCI also affects attack, speed determining a higher number of successful prey captures. It is obvious that the capture outcome depends on the prey behavior as well ($Z=2.60$; $p=0.0092$*; $N1=142$; $N2=8$; Mann Whitney U Test). If fish mobility and vigor is increased the number of successful attacks is reduced.

The snake can grasp the fish from different parts: head, trunk and tail. In our study the dice snake did not show any preference to a certain body part of prey. Out of 83 captures in 29 cases (34.94) the fish was caught by head; in 34 cases (40.96%) captured by trunk and in 20 cases (24.10%) by tail. There was no significant difference in percentage of attacks to these three body parts of prey, but the ratio is the highest in the attacks to trunk. This can be explained by that fish trunk provides a larger contact surface. Attacks to head or tail may be the consequence of early or delayed attacks to fish trunk. However the grasped prey body part does not depend on distance between prey and predator, BCI and fish weight.

Prey handling. The prey handling time represents the time interval that the snake requires to find the right position of fish for ingestion. Prey handling is performed by lateral jaw movements. When fish struggles are powerful, the snake ceases lateral jaw movements and increases hold intensity. Prey handling time is affected by the grasped body part of prey and by direction of ingestion (Table 3). In most of the cases fish caught from head is also ingested from head and prey handling time becomes relatively short, 14.61±

15.47 seconds. We noticed only one case, when fish captured from head was ingested from tail. When fish is caught from trunk, in high ratio (85.29%) it is ingested from head, but comparing to the capture from head, obviously the prey handling time increases to 63.37 ± 71.62 seconds. When ingestion starts from the tail, the prey handling time is less (40.58 ±31.9) because it requires less jaw movements. When fish is caught from tail, the prey handling behavior is relatively short, 18.49 ± 11.37 seconds if the ingestion direction is also from tail, but it becomes high if the snakes starts ingestion from head. For piscivorous snakes it is very important to start ingestion from head, otherwise fish scales and fin radii result in higher risk of injury and involve higher ingestion time, which means that the snake itself is exposed for a longer period to possible predation (Cundall 1983).

Table 3. Average prey handling time in relation with grasped body part and direction of ingestion.

Grasped body part	Direction of ingestion	Number of cases	Percentage of cases	Average handling time ±St.Dev.
head	Head first	21	95.65	14.61±15.47
	Tail first	1	4.35	246.39
trunk	Head first	29	85.29	63.37±71.62
	Tail first	5	14.71	40.58±31.9
tail	Head first	2	14.28	201.19±220.88
	Tail first	14	85.72	18.49±11.37

Fish characteristics also have an influence on prey handing time.

There is significant relationship between relative prey size and prey handling time (r=0.2792; n=71; p=0.018* Pearson Correlation). Larger fish specimens require more handling time. When prey size is relatively large, the snakes preferred to drag it out of water (Anova: F=8.64; df=70; p=0.0044*; Mann Whitney U test: Z=3.55; p=0.00037**). This behavior facilitates ingestion because the resistance of fish is reduced and quick suffocation prevents struggle.

Ingestion. As fish is placed into a convenient position, the snake starts to ingest it. In most of the analyzed captures, the snakes were able to ingest the fish (86.75 %).

In other cases the fish managed to escape or it was too large for safe ingestion. The ingestion time is a very important parameter of feeding behavior. The interest of snake is to consume prey as quick as possible. In water the constraining factor is the need for respiration, while in land, the snake is exposed to predator attacks without opportunity to escape.

The ingestion time is independent on BCI, but it is strongly affected by the size and weight of fish species (Table 4). Ingestion time is also influenced by direction of ingestion; head first ingestion takes shorter time than tail first ingestion.After consuming its prey the dice snake may retreat to land to ensure its loss of heat or it may restart searching for a new prey.

Table 4. Correlation between ingestion time and fish body size parameters.

	Nr. of exp.	Spearman	T(n-2)	p
BCI	71	0.215249	1.83091	0.071432
R4	71	-0.553213	-5.51634	0.000001***
R5	71	-0.506197	-4.87558	0.000007***

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