

To the Graduate Council:

I am submitting herewith a thesis written by Monique Halloy de Grosse entitled "A Comparative Study of the Ontogeny of Prey Ingestion in Four Species of Thamnophis (Serpentes: Colubridae)." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Life Sciences.

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A COMPARATIVE STUDY OF THE ONTOGENY  
OF PREY INGESTION IN FOUR SPECIES  
OF THAMNOPHIS (SERPENTES: COLUBRIDAE)

A Thesis  
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## ABSTRACT

The feeding behavior of four species of garter snakes (Thamnophis butleri, T. melanogaster, T. radix, and T. sirtalis) was observed in an attempt to determine differences across species and between age groups with respect to capturing, handling and swallowing fish. The four species were chosen based on their similarities as well as their differences in habitat and prey preferences (T. butleri being known as an earthworm specialist, T. melanogaster as a fish specialist, and the other two species as generalists).

Wild-caught adult females, lab-reared yearlings, and newborn snakes were used for this study (total: 220 animals). In order to make comparisons possible, only fish prey, readily accepted in captivity by the four species, were used. Each snake was tested with two prey sizes: a fish that had a body width equal to the snake's head width (called a "small" fish) and another that was approximately 50% larger than the snake's head width (called a "large" fish). The region by which the fish was captured (head, middle or tail) and the region from where ingestion was initiated (head or tail) were recorded. Two durations were

also considered: handling latency (time it took a snake to handle a fish from capture to onset of ingestion) and swallowing latency (time it took a snake to ingest its prey).

Overall, feeding patterns were quite similar across species following a general sequence of capturing fish, maneuvering the jaws to either the head or tail of the fish (the head being "chosen" more often), and swallowing it. Head first ingestion was related to prey size: the larger the fish the greater the probability the snake would ingest it head first.

When this behavior was analysed more closely, species and age differences emerged. A major difference existed between adults and juveniles of the four species, although this difference was not as marked in the two specialist species as in the two generalists. Adults were more efficient at capturing and ingesting fish head first and took less time to handle and swallow their prey than did juveniles.

Across species, I. melanogaster stood out as different from the other three species, whereas I. butleri and I. radix proved to be the most similar.

Considering differences within species and age classes with respect to their handling behavior of either a large or a small fish, I. melanogaster handled both sizes of prey in a time period that was not significantly different, I. butleri took significantly more time to handle a large fish whereas I. radix and I. sirtalis took considerably more time to handle a large fish as newborns but not as adults. These results support field observations that I. melanogaster is a fish specialist, I. butleri, an earthworm specialist, and the other two species, generalists.

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## CHAPTER I

### INTRODUCTION

There are many studies on the feeding behavior of colubrid snakes ranging from field observations to laboratory testing to theoretical considerations. Examples include studies on foraging strategies (Drummond, 1980, 1983), prey utilization and habitat (Carpenter, 1952), geographic differences in foraging behavior (Drummond and Burghardt, 1983), intraspecific geographical variation in chemical food cue preferences (Arnold, 1981; Burghardt, 1970a), the mechanics of swallowing (Cundall and Gans, 1979), cues eliciting prey attack (reviews in Burghardt, 1970b, 1980; Drummond, 1979), and prey trailing (Kubie and Halpern, 1975, 1978). But in spite of the abundant and diverse literature on feeding behavior, little specific information is available as to how colubrid snakes handle their prey. Many of the accounts of natricine snakes preying on fish do not dwell on this aspect and are often anecdotal or fragmentary (e.g. Evans, 1942; Stoner, 1941; Trapido, 1943; Wendelken, 1978).

One area of interest relates to the almost universal observation that snakes swallow prey head first; for example, Ditmars (1936) mentions that adult Thamnophis

sirtalis (Colubridae) generally swallow their prey head first. Mertens (1960) describes snakes as examining constricted prey with their tongue until the head has been located; the prey is then swallowed head first. Carr (1971:55) explains how the "versatile jaw" of snakes enables them "to swallow their food headfirst and whole, even when the victim is larger in diameter than the snake's body". Bellairs (1970) notes that snakes usually start at the prey's head so that the limbs fold backwards and thereby offer the least resistance.

It has been observed that snakes feeding on mice usually eat them head first and that the possible cues involved are position of fur and/or chemical olfactory stimuli. In a study on the Japanese rat snake, Elaphe climacophora (Colubridae), Diefenbach and Emslie (1971) point out that the direction of mouse ingestion appears to be influenced by the shape of the body and position of capture while hair position and olfactory cues would be of secondary importance. Kardong (1975) observed occasional tail first swallowing of mice by cottonmouths, Agkistrodon piscivorous (Viperidae).

Voris and Moffet (1981) studied stomach contents in Enhydrina schistosa (Hydrophiidae), a sea snake that preys on spiny catfish (Ariidae); all the fish were swallowed head first. Although fins and dorsal spines may

present major obstacles to tail first swallowing, many prey do not present such obstacles.

Greene (1976) proposed that scale overlap is a directional sign stimulus for prey ingestion by ophiophagous and lizard-eating snakes. Nevertheless, he observed several exceptions to head first ingestion.

De Queiroz and de Queiroz (1987:57) suggest that head first feeding in captive Gilbert's skinks, Eumeces gilberti (Scincidae), might not always be advantageous and might be maintained "through phylogenetic inertia or generalization of a response to prey that are more difficult to swallow". These authors point out that not only squamates have a tendency for head first swallowing but there is anecdotal evidence that other vertebrates also show this tendency (e.g. owls in Bolles, 1890, cited in de Queiroz and de Queiroz, 1987; and many mammals in Ewer, 1968). Leyhausen (1979) did a study to investigate how domestic cats locate a mouse's head. He concluded that the cat's orientation to the prey's head is not visual but tactile and depends on the direction of the mouse's hair. Ewer (1968) suggests that this response probably originally evolved in relation to scales.

In a study on rodent-eating snakes, Loop and Bailey (1972) proposed that swallowing prey head first is related to the relative size of the prey, noting that the proportion

of head first ingestion increases with the size of the prey. Loop (1974) observed the same type of prey size effect on head first ingestion in the bengal monitor, Varanus bengalensis (Varanidae). Cooper (1981) found that head first swallowing of mice by the lizard, Eumeces laticeps (Scincidae), was more likely to occur after anterior attacks than after more posterior attacks.

Czaplicki and Porter (1974) describe four fish-feeding techniques for Nerodia rhombifera and Nerodia sipedon (Colubridae): lunging, remaining motionless, fishing and fly-catching. The authors do not mention how the fish were seized except that wherever the fish was captured, the snakes quickly worked their jaws to the head and ingested the fish from there. They did observe several (8 out of 18) attempts of snakes trying to swallow fish from the rear, but all were unsuccessful.

Several studies refer to the possibility of some aspects of feeding behavior being innate. The term "innate" is used here as Burghardt (1969:108) has proposed "to cover those aspects of the snake's behavior and perceptual selectivity present at birth before the snake has ever engaged in feeding behavior". Different species seem to have different potentials for learning (review in Burghardt, 1977a). Echternacht (1977:71) notes that in both constrictors and venomous snakes the young "will often try

to swallow prey tail first or even sideways but experienced snakes rarely do." On the other hand, observations of newborn rat snakes, Elaphe obsoleta (Colubridae), have shown that they swallow their prey head first (Klein, 1975). In this species the behavior might be innate. Fuchs and Burghardt (1971) showed that the responses of newborn garter snakes, I. sirtalis, to food chemicals were influenced by their feeding experience on either redworms, Eisenia foetida, or on guppies, Poecilia reticulata. Burghardt (1969) showed that I. s. parietalis learned to inhibit their response to slugs, which originally attracted them. Arnold (1978) in a study on I. sirtalis determined that experience depends on the type of prey. He writes (p.461), "experience with a particular prey may facilitate subsequent responses, inhibit subsequent responses or fail to change an already maximal response depending on the type of prey".

Burghardt (1967 and 1978:157) has observed that naive newborn snakes belonging to the family Colubridae are able to "recognize the chemical cues associated with their species-characteristic prey without any prior experience with that prey" although ontogeny is a factor. Burghardt (1978) investigated the length of time taken by 13 newborn garter snakes, Thamnophis sirtalis parietalis, to swallow their first 8 meals of 6 cm redworms (Eisenia foetida) and found a linear decline in latency. He

suggested that experience could be involved, as well as the size of the growing and maturing snake relative to a constant-sized worm.

In sum, the impression given by much of the literature on feeding behavior in Colubrids (with respect to seizing, handling and swallowing prey) is that it follows a general pattern of a snake grabbing a prey by any section of its body and usually going to the head for ingestion. (However, see Halloy, 1985a and 1985b for descriptions of tail and hind-leg-first ingestion of tadpoles and frogs respectively in Liophis poecilogurus and L. sagittifer, Colubridae).

The goal of the present study is to determine if the above observations gathered from the literature apply to four species of garter snakes (Thamnophis butleri, T. melanogaster, T. radix, and T. sirtalis) and how a closer inspection of their feeding behavior might reveal not only similarities but differences across species and age groups.

Feeding behavior seems to be a potentially good "tool" to determine differences between closely related species, and between juveniles and adults. An important reason for choosing this behavior as a tool is that it is readily observable in a laboratory situation with an apparently minimum amount of disruption to the snakes.

A. LIFE HISTORY SYNOPSES: the genus Thamnophis

Garter snakes (Thamnophis) are typically characterized by the presence of stripes running the length of their bodies on a dark background. These stripes may be very vivid, somewhat obscure, or entirely absent, depending on the species, or subspecies (Breen, 1974).

Garter snakes are widely distributed from southern Canada to Central America (Pope, 1960) occupying a great variety of habitats from sea level to high in the mountains (Stebbins, 1966). These snakes as a group go from strictly terrestrial species to aquatic species. Several species of garter snakes are, in fact, as aquatic as the related genus of true water snakes, Nerodia (Ditmars, 1936; Schmidt and Inger, 1957). Like water snakes, garter snakes are live-bearers and usually have large litters.

In an overly generalized statement, Schmidt and Inger (1957:192) write that garter snakes prey on "any animal of suitable size that they encounter". This is probably meant to show how varied are the food preferences of garter snakes, but it could also be misleading since some species of garter snakes accept very few types of prey while others accept a greater variety, as will be shown in individual life history synopses below. Pope (1960) notes that they

prey on frogs, tadpoles, salamanders, fishes and earthworms as well as some crawfishes, insects and an occasional mammal or bird. The inclusion of insects as part of the diet of garter snakes is probably incorrect. Fitch (1965) and Drummond (1983) believe insects are secondary items ingested by small vertebrate predators such as frogs or toads. Captive garter snakes showed no interest in insects offered to them (Fitch, 1965; Burghardt, pers.comm.).

Garter snakes use the "grab-and-swallow" technique in feeding and use no special means for subduing their prey (Echternacht, 1977:70). The teeth of these snakes are aglyphous (solid and ungrooved). They are able to swallow relatively large objects without help of limbs chiefly because of the elasticity of the skin, the loosely connected bones of the jaws, and the arrangement and form of the teeth (Pope, 1960). The prey is swallowed whole since the teeth have no cutting action.

Snakes use a combination of senses to locate their prey: sight (perception of moving prey) (Burghardt and Denny 1983; Drummond, 1979, 1985; Naulleau, 1964, 1966) and a combination of the tongue and the Jacobson's (vomeronasal) organ, the latter being probably the most important, especially in terrestrial species (Burghardt, 1966, 1969; Burghardt and Hess, 1968; Burghardt and Pruitt, 1975; Fox, 1952; Wilde, 1938).

1. Butler's garter snake, Thamnophis butleri

Butler's garter snake (Fig. 1) is smaller than the other three species (see Table 1 for average weights and lengths). It is characterized by a small head which is the same width as the neck. The yellow stripes are strongly delineated.

This garter snake is found in the region from western New York, southwestern Ontario and western Pennsylvania through Ohio, Indiana, and southern Michigan to Wisconsin (Carpenter, 1952) (Fig. 2).

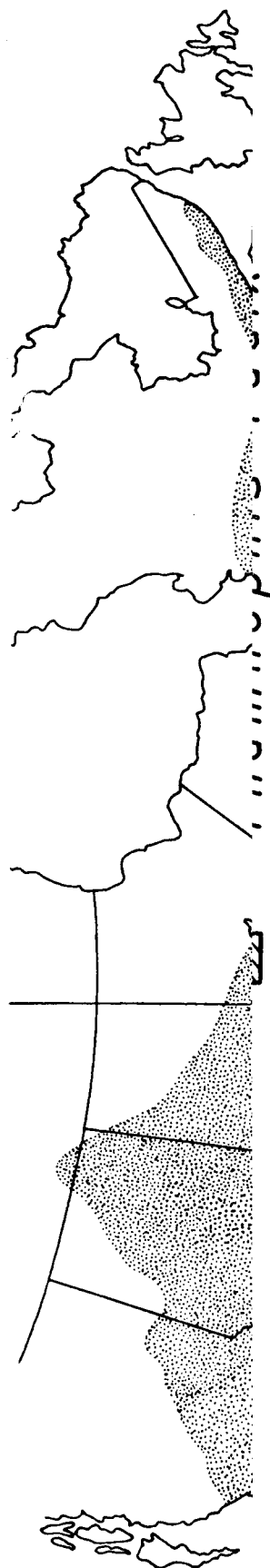
In a field study of T. butleri by Carpenter (1952), their main prey item was identified (by forced regurgitation) as earthworms (83%) with leeches (10%) being the only other food observed. Although in the field they seem to have specialized on earthworms, in captivity, Butler's garter snakes will eat fish and amphibians (Carpenter, 1952; Burghardt, 1967, 1969). Burghardt (1968:736) points out for two sympatric species of the related genus Nerodia that the responsivity of a snake to other prey-organisms "could be either a vestigial character or a mechanism guarding against the ecological hazards of specializing on one food source." Neonates of T. butleri used in the present study refused small fish when offered at their first meal, although they readily



FIGURE 1 - Adult Butler's garter snake, Thamnophis  
butleri (SVL 430 mm), with newborn  
(SVL 163 mm) of the same species.

TABLE 1 - Weight, snout-vent length (SVL), and total length (TL) measurements for the four species of ADULT female garter snakes (Thamnophis) used in this study.

| Species                | n  | Weight (g) |      | SVL (mm)  |      | TL (mm)   |      |
|------------------------|----|------------|------|-----------|------|-----------|------|
|                        |    | $\bar{X}$  | SD   | $\bar{X}$ | SD   | $\bar{X}$ | SD   |
| <u>T. butleri</u>      | 15 | 48.6       | 12.9 | 430       | 40.8 | 540       | 49.3 |
| <u>T. melanogaster</u> | 15 | 129.8      | 38.4 | 546       | 51.2 | 671       | 58.2 |
| <u>T. radix</u>        | 14 | 126.9      | 27.0 | 659       | 59.7 | 817       | 82.1 |
| <u>T. sirtalis</u>     | 12 | 95.1       | 35.4 | 610       | 61.4 | 751       | 64.2 |



*Thamnophis butleri*



*Thamnophis melanogaster*

FIGURE 2 - Geographical distribution of the four species of *Thamnophis* used in the study. Source for first 3 species, Conant (1975, maps 116, 118 and 113 respectively), and for fourth species Conant (1963:496).

accepted pieces of worms. Only later (when at least 2 months old and more often when about 4 months old) did they accept fish.

Even though these garter snakes generally live in the vicinity of water, they seem to avoid going into it, preferring to stay in the thick grasses and sedges bordering it. It is generally believed that Butler's garter snake evolved from the plains garter snake (T. radix), found in the prairie and plains of the mid-west (Carpenter, 1952; Burghardt, 1967).

## 2. Mexican garter snake, Thamnophis melanogaster

The Mexican garter snake (Fig. 3) is the heaviest bodied snake of the four species (Table 1) and is generally brownish colored. It is found in the plateau of Central Mexico at an altitude of approximately 1000 to 2500 m (Conant, 1963) (Fig. 2)

It is the most aquatic of the four species and is usually found near courses of water. This species is active during the day and sometimes at night during the warmer months (Drummond, 1983). These snakes prey on fish and tadpoles, sometimes on frogs. Drummond and Macias Garcia (in preparation) add leeches and crayfish. Drummond (1980) regards this species as a specialist with respect to its feeding habits.



FIGURE 3 - Adult Mexican garter snake, Thamnophis  
melanogaster (SVL 546 mm), with newborn  
(SVL 190 mm) of the same species.

### 3. Plains garter snake, Thamnophis radix

The plain's garter snake (Fig. 4) is the largest of the four species in this study (Table 1). It has 3 well-marked yellow stripes running the length of its body with prominent black bars on the upper labials. It can have broods of over 90 young (Stebbins, 1966), although half that number is more common.

Its range is from south Canada to northeast New Mexico and from central Montana to central Indiana (Stebbins, 1966) (Fig. 2). It inhabits wet prairies and farmlands and is found near ponds, sloughs, swamps, lakes, streams and rivers. Stebbins (1966) and Wright and Wright (1957) mention frogs, toads, tadpoles, fish, earthworms, insects and carrion as their food. Again, insects are probably secondary items (Drummond, 1983; Fitch, 1965). A controlled study (Burghardt, 1969) of chemical prey preferences in newborn T. radix showed that these snakes respond most strongly to worms, and less so to fish. They also showed some response to amphibian, larval salamander, and turtle leech extracts.

### 4. Common garter snake, Thamnophis sirtalis

The common garter snake's coloration is highly variable, but usually the dorsal and lateral stripes are

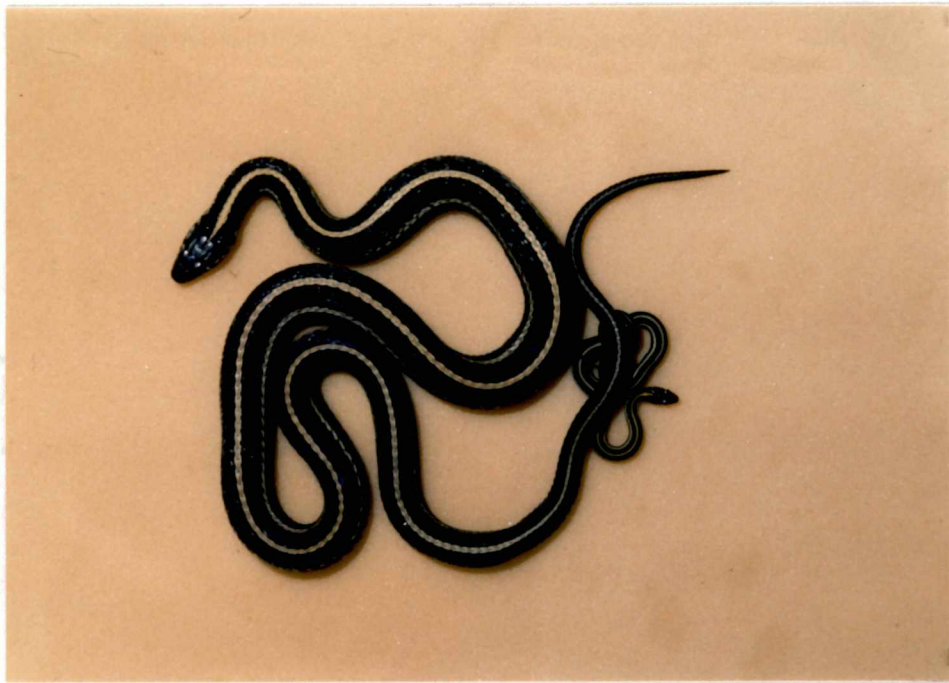


FIGURE 4 - Adult plains garter snake, Thamnophis  
radix (SUL 659 mm), with newborn (SUL  
192 mm) of the same species.

well defined and frequently spots can be seen between them (Fig. 5). It may have broods of 3 to 85 young with an average of one to two dozens depending on the locality (Stebbins, 1966).

Stebbins (1966:165) describes this snake as "the most widely distributed North American reptile, capable of living in many environments from the Everglades of Florida to the cold prairies of West Canada" (Fig. 2). Ditmars (1936: 151) points out that "this hardy reptile, ranging so far northward into Canada, is the last of the snakes to hibernate in the fall and the first to appear in the spring". These snakes tend to stay near water and can be found in ponds, marshes, prairies, roadside ditches, streams, sloughs, woods, and farm city lots. This species is largely diurnal (Drummond, 1983).

Thamnophis sirtalis usually forages aquatically in still and slow-moving water. Drummond (1983) notes that it may be unable to secure prey in open water and will prefer pools overcrowded with fish and tadpoles. They feed on a wide variety of animals: fish, toads, frogs, tadpoles, salamanders, birds, small mammals, earthworms, slugs and leeches (Stebbins, 1966). They are capable of discriminating between the different chemical cues of related prey organisms very early on (Fuchs and Burghardt, 1971).

Fitch (1965:518) points out that the common garter

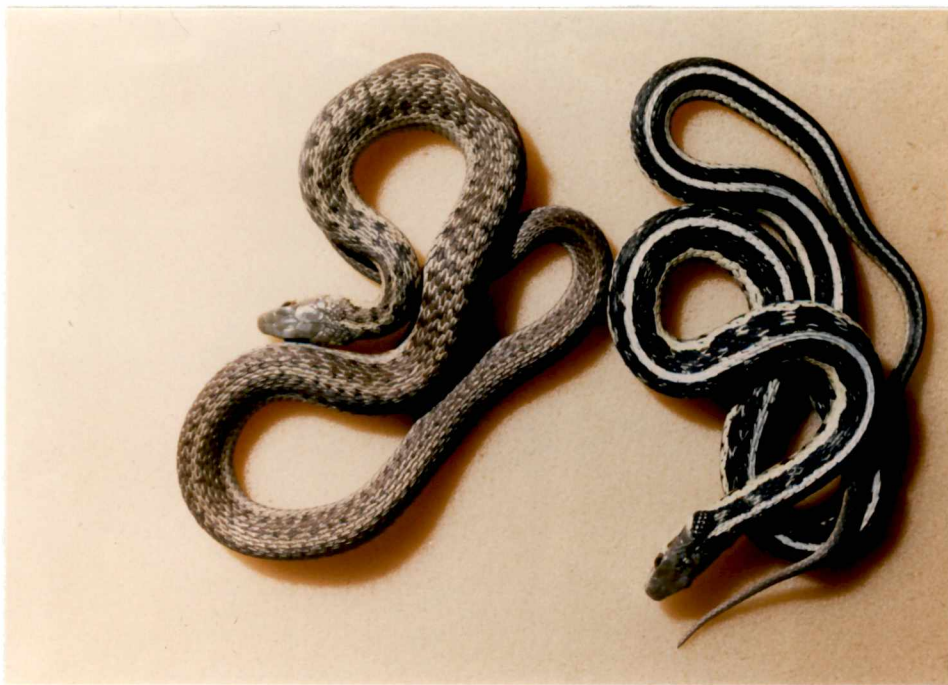


FIGURE 5 - Two yearling common garter snakes, Thamnophis  
sirtalis (SUL 373 mm), on the left from  
Michigan and on the right from Wisconsin.

snake is "more generalized in habits, habitat and food requirements than are any of these other species" of the same genus, an observation also made by Drummond (1980, 1983).

## B. WORKING HYPOTHESES

The habitat and food preferences of these species are important to consider as they will probably be related to whatever differences can be determined in the way each species handles and swallows prey. Overall, Thamnophis butleri seems to be a specialist living in grassy areas and preying mostly on earthworms. Thamnophis melanogaster seems to be also a specialist but of another kind, living close to water and preying mostly on fish or amphibians. Thamnophis radix and T. sirtalis both seem to be generalists, although the latter more so, living in a wider variety of habitats and preying on many different organisms.

Drummond (1983:1) defines a specialist as having a diet confined to "one family, genus, species, or size-class prey". The author further notes that "specialists possess superior feeding abilities in relation to the foods on which they specialized than do generalists, in relation to the same foods". In the particular case of handling

species-specific prey, a specialist would be more efficient and would take less time than a generalist. It is suggested here that the behavioral patterns involved in handling prey in a specialist might have a greater genetic basis and be less dependent upon experience than those for a generalist and that a generalist is capable of becoming as efficient as a specialist on prey it has had experience with. If this were so, both adult specialists and adult generalists would be efficient on prey on which the first specializes and on which the latter has "learned" to specialize through experience and/or through maturation defined as "those ontogenetic processes that reliably produce species-typical forms and functions" (Oyama, 1982:127) which doesn't mean that it is independent of experience. In other words, if an adult generalist can "learn" to handle fish through experience/maturation as well as an adult specialist, newborn generalists would not handle fish as well or as quickly as the adults of the same species nor as well or as quickly as the newborns and adults of the specialist species. On the other hand, newborn snakes of a fish specialist species would be able to handle fish as well or almost as well as the adults of their own species.

The hypotheses proposed here are the following:

1. The overall feeding behavior in the four species is similar and corresponds to what has generally been

stated in the literature (see Introduction). However, differences will possibly emerge when studying this behavior more closely.

2. Even though newborn garter snakes do not require any parental care and are on their own from the day they are born, their behavior is not necessarily a copy of that of the adults. Some differences are expected between the feeding behavior of newborn snakes and that of the adults, the latter probably being more efficient in prey handling than the former.
3. Differences are expected across species based on what is known of their life histories. Thamnophis melanogaster, a fish specialist, will probably be most efficient when handling fish whereas T. butleri, an earthworm specialist, could be the least efficient. Thamnophis radix and T. sirtalis, both generalists, might show more variation between newborns and adults than the former species (see discussion below) and would fit between them with respect to prey handling.

Referring to this last point it is hoped that based on results of how newborn and adult snakes of the same species handle prey, it would be possible to predict whether a particular species (other than the ones considered here) is more of a generalist or more of a specialist with respect to

other species. The reverse is possible: based on what is known about a particular species with respect to habitat and prey preferences (whether a generalist or a specialist), it could be predicted how efficient this species (newborns and adults) would be with respect to handling prey.

In particular, the following predictions are to be evaluated:

- a. Thamnophis melanogaster, being a fish specialist, is expected to handle fish quickly and efficiently in newborn and adult snakes. It is possible that this particular behavior is mostly stereotyped and that the newborn's behavior resembles that of the adult.
- b. Thamnophis butleri, an earthworm specialist, is expected to show a lack of efficiency in handling fish both in newborn and adult snakes.
- c. Thamnophis radix and T. sirtalis, both generalists, are expected to show a significant difference between newborns and adults with respect to handling fish. Newborn snakes are expected to be less efficient in handling fish than their adult counterparts. It is suggested that in these species the handling behavior is less stereotyped in favor of a more "open"-type system which would allow greater flexibility and adaptability to changing environments

with the corresponding change in prey availability (Mayr, 1974, but see Burghardt, 1977b). Behavioral flexibility is defined by Fagen (1982:365) as "the capacity of an animal to alter its behavior or its ecology through behavioral means when faced by novel challenges so as to increase its chance of leaving surviving offspring or kin". This implies a capacity to learn from experience and to adapt to new habitats and new prey. As they grow older, young snakes would specialize on certain prey based on their availability (Arnold, 1981, for I. elegans; Gove, 1971, for Nerodia sipedon). "Open"-type behavioral programs would tend to close with practice, as they become more habitual and automatic (Gass, 1985). Speed and efficiency acquired by adults with a corresponding increasingly more automatic and stereotyped behavior program are gained at the expense of flexibility. Fuchs and Burghardt (1971:278) propose that snakes "may develop chemically based 'search images' dependent upon prior encounter with prey" (also see Krebs, 1973). Once a search image is established, snakes might specialize on particular prey. Previous to those experiences, snakes could have a search image for food that had broad characteristics. These would narrow down with experience and hence the snake would become more

efficient on those preys that are available in its habitat. Burghardt (1975) has shown intraspecific variability in different populations of T. sirtalis in their response to chemical prey cues. Gove and Burghardt (1975) note that there do seem to be genetic predispositions for prey species normally eaten although these preferences can be enhanced or inhibited during ontogeny.

## CHAPTER II

### MATERIALS AND METHODS

#### A. SUBJECTS

Four species of snakes were used in this study: Thamnophis butleri, I. melanogaster, I. radix, I. sirtalis. With one exception, all adults were wild-caught females. Most were originally gravid and provided neonates for this and other studies. Their measurements are given in Table 1. The 59 adult females came from the following areas:

- 15 I. butleri from Wayne County, Michigan,
- 15 I. melanogaster from Lake Chapala, Jalisco, Mexico,
- 14 I. radix from South Dakota,
- 15 I. sirtalis of which 1 was lab-reared (her mother came from Raleigh County, North Carolina), 1 from Wayne County, Michigan, 2 from Knox County, Tennessee, 2 from Wolf River Drainage, Wisconsin, and 9 from Oshkosh, Wisconsin.

The "yearlings" comprise a group of 39 snakes born in captivity in the summer of 1985 and were first tested for their feeding behavior when approximately one year old.

Measurements are given in Table 2. The animals used were:

17 I. melanogaster: 7 males and 10 females,

22 I. sirtalis: 11 males and 11 females.

The "newborns" correspond to 122 snakes born in captivity during the summer of 1986 and which were first tested for their feeding behavior between their first and second months of life. Measurements can be found in Table 3. The animals used were:

20 I. butleri: 12 males and 8 females,

34 I. melanogaster: 13 males and 21 females,

30 I. radix: 12 males and 18 females,

38 I. sirtalis: 20 males and 19 females.

The yearling and the newborn snakes were chosen from as many different litters as possible (usually not more than two individuals from the same litter and whenever possible a female and a male) in order to avoid litter effects (Herzog and Burghardt, in press).

For these three groups (total: 220 animals), the numbers given correspond to the maximum number used for this study. Not all animals could be used in each testing session. Some animals did not respond to the prey on the testing days (possibly because they had entered an ecdysis period or experienced temporary illness), and a few died during the course of this study (see section on Procedure and Table 4 for further information).

TABLE 2 - Weight, snout-vent length (SVL), and total length (TL) measurements at birth and at various ages (in months) for the two species of YEARLING garter snakes (Thamnophis) used in this study.

| Species                | Age | n  | Weight(g) |      | SVL (mm)  |      | TL (mm)   |      |
|------------------------|-----|----|-----------|------|-----------|------|-----------|------|
|                        |     |    | $\bar{X}$ | SD   | $\bar{X}$ | SD   | $\bar{X}$ | SD   |
| <u>I. melanogaster</u> | 0   | 16 | 2.79      | .37  | 168       | 8.0  | 212       | 12.5 |
|                        | 4   | 11 | 3.79      | .37  | 169       | 6.3  | 213       | 9.3  |
|                        | 14  | 9  | 23.00     | 6.14 | 313       | 27.3 | 383       | 60.2 |
|                        | 17  | 15 | 28.13     | 6.03 | 340       | 22.7 | 425       | 40.7 |
| <u>I. sirtalis</u>     | 0   | 22 | 1.76      | .32  | 154       | 8.2  | 198       | 10.6 |
|                        | 4   | 21 | 2.21      | .43  | 162       | 11.0 | 205       | 11.8 |
|                        | 14  | 9  | 16.80     | 1.95 | 317       | 25.6 | 401       | 36.5 |
|                        | 17  | 22 | 20.10     | 4.51 | 373       | 47.4 | 474       | 41.1 |

TABLE 3 - Weight, snout-vent length (SVL), and total length (TL) measurements at birth and at 4 or 5 months of age for the four species of NEWBORN garter snakes (Thamnophis) used in this study.

| Species                | Age | n  | Weight(g) |     | SVL (mm)  |      | TL (mm)   |      |
|------------------------|-----|----|-----------|-----|-----------|------|-----------|------|
|                        |     |    | $\bar{X}$ | SD  | $\bar{X}$ | SD   | $\bar{X}$ | SD   |
| <u>I. butleri</u>      | 0   | 27 | 1.50      | .27 | 122       | 7.8  | 154       | 9.9  |
|                        | 5   | 25 | 2.90      | .65 | 163       | 16.4 | 202       | 21.9 |
| <u>I. melanogaster</u> | 0   | 34 | 2.53      | .54 | 152       | 13.2 | 191       | 17.0 |
|                        | 4   | 30 | 5.95      | .96 | 190       | 12.7 | 235       | 15.2 |
| <u>I. radix</u>        | 0   | 30 | 1.64      | .26 | 154       | 8.1  | 197       | 11.3 |
|                        | 5   | 30 | 3.74      | .66 | 192       | 11.4 | 244       | 18.5 |
| <u>I. sirtalis</u>     | 0   | 33 | 1.37      | .18 | 141       | 8.6  | 183       | 11.3 |
|                        | 4   | 28 | 3.93      | .78 | 201       | 16.1 | 260       | 23.8 |

TABLE 4 - Number (n) of animals used by age class and by species of Thamnophis with respect to the number of times the snakes were tested on "small" fish (some snakes having been tested more than once), on "large" fish, the total amount of testing per group of animals, and the number of true pairs formed (same snake tested on a "small" fish and later on a "large" fish") that were used in the analysis of the data. For I. melanogaster, 5 extra pairs were used when statistical analysis did not require true pairs (total number given in parenthesis). (See text for further details.)

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ADULTS

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|                        | n  | Small<br>fish | Large<br>fish | Total<br>test | # of pairs<br>used |
|------------------------|----|---------------|---------------|---------------|--------------------|
| <u>I. butleri</u>      | 15 | 19            | 12            | 31            | 12                 |
| <u>I. melanogaster</u> | 15 | 17            | 10            | 27            | 5(10)              |
| <u>I. radix</u>        | 14 | 25            | 15            | 40            | 13                 |
| <u>I. sirtalis</u>     | 15 | 16            | 14            | 30            | 12                 |

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YEARLINGS

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|                        |    |    |    |    |    |
|------------------------|----|----|----|----|----|
| <u>I. melanogaster</u> | 17 | 19 | 13 | 32 | 10 |
| <u>I. sirtalis</u>     | 22 | 22 | 18 | 40 | 18 |

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NEWBORNS

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|                        |    |    |    |     |    |
|------------------------|----|----|----|-----|----|
| <u>I. butleri</u>      | 20 | 19 | 15 | 34  | 12 |
| <u>I. melanogaster</u> | 34 | 33 | 32 | 65  | 24 |
| <u>I. radix</u>        | 30 | 31 | 37 | 68  | 21 |
| <u>I. sirtalis</u>     | 38 | 69 | 36 | 105 | 26 |

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|        |     |     |     |     |          |
|--------|-----|-----|-----|-----|----------|
| TOTALS | 220 | 270 | 200 | 472 | 153(158) |
|--------|-----|-----|-----|-----|----------|

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## B. MATERIALS

The adults were housed individually. The adult I. butleri were kept in glass terrariums (36 x 21 x 27 cm high). The rest of the adults were housed in plastic boxes measuring 40 x 25 x 17 cm high. Each cage was provided with an artificial carpet, a cover object and a water bowl (13cm diameter x 5.5 cm height, filled 2/3 with water).

The yearling and newborn snakes were isolated from birth and kept in individual cages. The yearlings were housed in plastic boxes measuring 29 x 19 x 9 cm high (water bowls measured 9 x 4.5 cm) while the newborns were kept in smaller styrene boxes measuring 18 x 13 x 5 cm high (water bowls measured 6 x 2.5 cm). Aside the water bowl, each cage was provided with a carpet and a cover object.

All snakes were kept on a 12/12 light/dark cycle and room temperatures varied between 22-25°C.

## C. DIET

All adults were fed once a week with minnows, Pimephales promelas. The amount of fish offered depended on the size of the snake and how readily it would approach the fish and eat. In addition to the fish, every two or

three weeks the I. butleri received nightcrawlers, Lumbricus terrestris.

The yearlings were fed once a week like the adults and were provided with smaller minnows, Pimephales promelas. The newborn snakes were fed twice a week beginning on their third week of life. Newborn I. butleri rarely accepted fish during their first months of life. Their main diet was composed of pieces of L. terrestris. Newborn snakes of the other three species were divided into groups (formed by separating members of the same litter) and provided with different diets. Half of the snakes from the groups of I. melanogaster and I. radix received a small fish, Gambusia affinis, while the other half received a larger fish P. promelas. The I. sirtalis were divided into three groups: one was given pieces of nightcrawlers, the second was given G. affinis and the third received P. promelas. The larger fish, P. promelas, were not given until the snakes were about 3 months old. These different diets were incorporated in order to evaluate the effect of different feeding experiences on fish handling and ingestion within and across species.

#### D. PROCEDURE

Each snake was tested in its home cage and was offered a fish in its water bowl. The test day typically corresponded to the snake's usual feeding day.

##### 1. Prey sizes and predator head ratio

In order to make comparisons possible between age groups and across species, the following ratio was used: lateral width of the fish to the head width of the snake (see Table 5 for averages of snakes' head widths by species and by age group). This meant that different sizes of fish had to be used and eventually different species (Fig. 6), since, unfortunately, no one of them had a wide enough range of sizes. The average weights and lengths for five fish of each species using the body widths shown in Figure 6 are:

|                                | Width(mm) | length(mm) | weight(g) |
|--------------------------------|-----------|------------|-----------|
| <u>Gambusia affinis</u>        | 6         | 28         | .25       |
| <u>Pimephales promelas</u>     | 10        | 52         | 2.0       |
| <u>Carassius auratus</u>       | 15        | 54         | 3.5       |
| <u>Notemigonus crysoleucas</u> | 23        | 88         | 8.2       |

The fish species were chosen on the basis of their similarities. Morphological obstacles, such as dorsal spines, were avoided.

Two major prey sizes were employed: one where the fish

TABLE 5 - Means and standard deviations of the head widths (in mm) for 4 species and 3 age classes (age, when given, is in months) of Thamnophis used in this study.

|           |     | <u>T. butleri</u>      |      |      | <u>T. radix</u>    |      |      |
|-----------|-----|------------------------|------|------|--------------------|------|------|
|           | age | $\bar{X}$              | (n)  | SD   | $\bar{X}$          | (n)  | SD   |
| Adults    | -   | 9.6                    | (13) | .67  | 15.3               | (14) | 1.53 |
| Newborns  | 0   | 5.5                    | (9)  | .46  | 5.5                | (24) | .32  |
|           | 5   | 5.8                    | (25) | .29  | 6.2                | (30) | .22  |
|           |     | <u>T. melanogaster</u> |      |      | <u>T. sirtalis</u> |      |      |
|           | age | $\bar{X}$              | (n)  | SD   | $\bar{X}$          | (n)  | SD   |
| Adults    | -   | 14.5                   | (13) | 1.52 | 14.6               | (13) | 1.82 |
| Yearlings | 14  | 9.0                    | (9)  | .89  | 8.7                | (9)  | .73  |
|           | 17  | 9.3                    | (14) | .84  | 9.3                | (21) | .88  |
| Newborns  | 0   | 6.3                    | (25) | .42  | 5.6                | (24) | .36  |
|           | 4   | 7.1                    | (30) | .38  | 6.7                | (28) | .38  |

FISH WIDTH

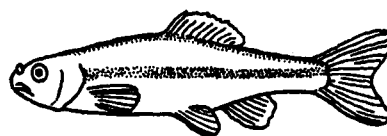
LATERAL VIEW

6<sub>mm</sub> ↑↓



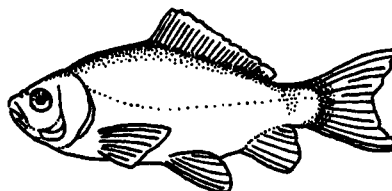
*Gambusia affinis*

10<sub>mm</sub> ↑↓



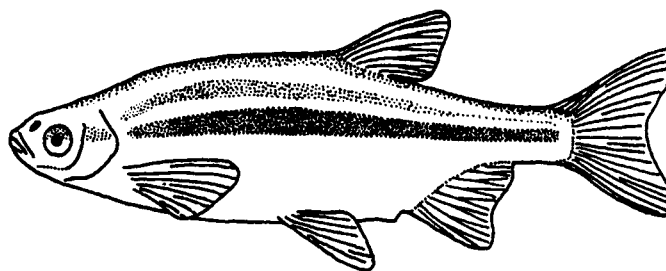
*Pimephales promelas*

15<sub>mm</sub> ↑↓



*Carassius auratus*

23<sub>mm</sub> ↑↓



*Notemigonus crysoleucas*

FIGURE 6 - Four species of fish employed in feeding tests of four species of *Thamnophis*, with corresponding body widths most often used (see text for fish weights and lengths).

was about as wide as the snake's head, generally presenting no major difficulty to the snake, and one where the fish was approximately 50% wider than the snake's head (usually between 45 and 50%, although adult I. radix received fish about 55% wider than their head widths due to problems of fish size availability). These are termed "small" fish and "large" fish respectively.

Two test sessions were planned for each snake. The first session employed a "small" fish and typically preceded by a few weeks the second session with a "large" fish. These were:

- a. On the first test session, the snakes were offered a fish that had a body width approximately equal to the snake's head width ("small" fish situation). Newborns were offered a Gambusia affinis, the yearlings received a small Pimephales promelas, the adult I. butleri a large P. promelas, and the adults of the other three species received either a goldfish, Carassius auratus, or, in some cases, a large minnow, P. promelas, depending on the width of the snakes' head.
- b. On the second test, the snakes were offered a fish that had a body width about 50% wider than the snake's head (the "large" fish situation). This presented a major difficulty to the snake and in a

few cases, the snakes were unable to swallow it. Newborns received small P. promelas that were 50% wider than their heads. Yearlings were offered large P. promelas while the adult I. butleri received C. auratus and the other three adult species received larger sizes of C. auratus (baltimores) or Notemigonus crunoleucas (golden shiners) depending on the width of their heads.

## 2. Recording of observations

Once a fish was placed in the water bowl, recording of the feeding behavior started. There was a check-list (Fig. 7) with the identification number of the snake, date and hour of testing, type and size of fish used, and a small table where various responses could be recorded.

Two major aspects were considered: where the fish was grabbed and by which end it was swallowed. With respect to the first point, the following were observed (Fig. 8):

- a. strike location: where a snake seized a fish (either by the head, the middle or the tail),
- b. strike direction: from what direction the snake struck the fish (from the front, back, top, bottom, lateral right or lateral left). Combining these two factors (strike location and strike direction), 14 state categories can be determined. Four combinations (front

Date:                      Time:  
 Snake #:                      Sex:                      Age:  
 Snake's head width:  
 Fish (species):  
 Fish's lateral width:  
 Remarks:

| SD / SL        | Head | Middle | Tail     |
|----------------|------|--------|----------|
| Front          |      |        |          |
| Back           |      |        | Time 1 - |
| Right          |      |        |          |
| Left           |      |        | Time 2 - |
| Top            |      |        |          |
| Bottom         |      |        |          |
| <hr/> SW <hr/> |      |        |          |

FIGURE 7 - Sample observation sheet for recording strike location (SL) and strike direction (SD), swallowing (SW), handling latency (Time 1) and swallowing latency (Time 2) during feeding trials of Thamnophis.

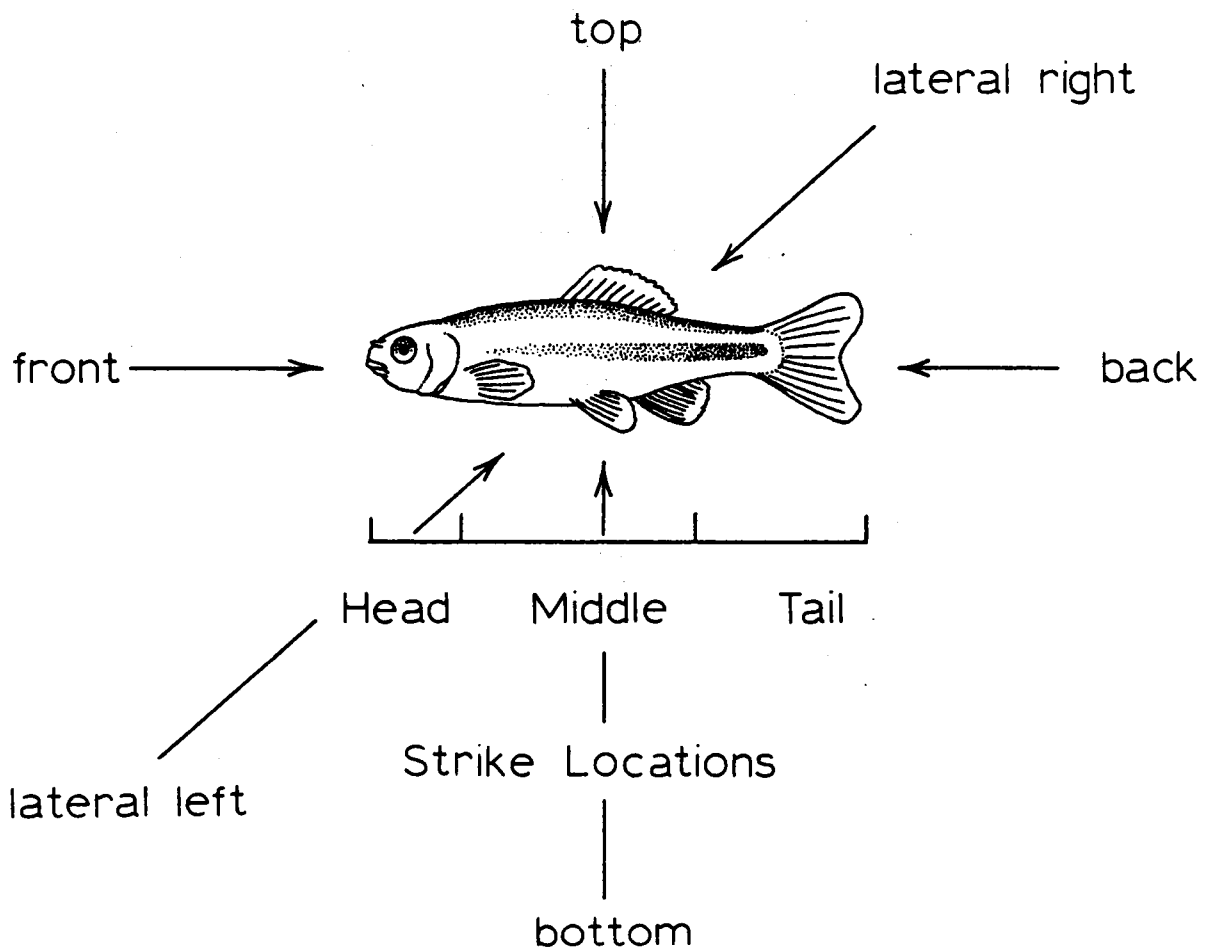


FIGURE 8 - Diagram of a fish illustrating the different strike locations and strike directions by which a snake (belonging to one of four species of Thamnophis) could capture its prey.

middle, front tail, back head and back middle) cannot occur (see Figs. 7 and 8).

The second point refers to direction of swallowing: whether the snake swallowed the fish beginning with the head or at the tail or, on some rare occasions, at the middle, the fish being awkwardly folded in two.

As soon as the fish had been grasped, two separate times (Fig.7) were recorded with a stop watch:

- a. Time in seconds from the moment the snake grasped the fish, holding on to it and moving to one end of the prey, to when it began swallowing it (defined as when the snake started left and right movements of the jaws, sometimes called the "walking movement" of the jaws (e.g. Pope, 1960:140). An exception was made for adult I. butleri. When feeding on large fish, these snakes typically did not hold on to it once they had seized it but dropped it repeatedly. After several attempts, they located the head and swallowed the fish from there. Handling time was therefore considered to be, in this particular case, an average of the time from the moment the fish was first grasped to when the head was located and seized, independently of the fact that the fish had been dropped several times.
- b. Time in seconds from the moment ingestion started until the snake finished swallowing (defined as when the

snake did its first tongue-flick just after finishing ingestion and closing its mouth).

The number of times each group of snakes was tested can be seen in Table 4. Since some snakes were tested more than once for either situation (small fish or large fish), some data had to be eliminated in order to create equally-paired testing situations that could then be analyzed statistically. The data kept for the statistical analysis corresponded to the results obtained the first time the snake was tested on a small fish and the first time it was tested on a large fish.

Several feeding sessions of snakes belonging to different species and to different age groups were videotaped with a Panasonic video camera (WV-3230/BAF) and a portable Panasonic video cassette recorder. All adult I. melanogaster were videotaped since these snakes would not eat in the presence of an observer. Some of the videotaped sessions were checked twice as a control for my accuracy in checking time: the results were very similar with a 2 to 3 seconds difference for small fish observations ( $n = 10$ ; median range for fish handling: 0 to 35 seconds, and for fish ingestion: 18.5 to 62.5 seconds), and a 4 to 5 seconds difference for large fish observations ( $n = 5$ ; median range for fish handling: 2.5 to 240 seconds and for fish ingestion: 82 to 1000 seconds).

## CHAPTER III

### RESULTS AND DISCUSSION

#### A. GENERAL DESCRIPTION OF THE FEEDING BEHAVIOR

##### 1. Approach to prey

When a live fish was placed in a water bowl, a hungry snake typically started tongue-flicking slowly approaching it. Upon reaching the bowl, the snake seemed to observe the fish's movements in the water, all the while tongue-flicking. This approach to the prey was basically the same in the four species. Once the fish was localized, I. melanogaster usually "plunged" into the water, aiming and striking directly at the fish. It sometimes missed but by the second or third trial the fish was caught. On the other hand, I. radix and I. sirtalis entered the water slowly and started swimming with the anterior third of their body. They almost immediately opened their mouths, accelerated their swimming, and ended up catching the fish apparently by chance. They sometimes jerked their heads sideways trying to strike at the fish passing by, often missing, but in general by the third trial they managed to catch their prey. These observations are in accordance with field observations by Drummond (1983) and would correspond

to two main strategies: the first to a specialist species specialized on fish, the other to a generalist species. The open-mouth search in I. sirtalis is also in agreement with its preference for overcrowded pools of fish or tadpoles.

Adult I. butleri, a specialist on worms, didn't seem to have any definite strategy. Both tactics just described were employed. However, another tactic observed was to "sit and wait" for the fish to jump out of the water bowl, which occasionally happened. The snake would then approach it, tongue-flick it, and grab it. Newborns of this species were extremely cautious compared to the other species or to conspecific adults. They showed interest in the fish by lifting their heads, increased tongue-flicking, and sometimes approaching the water bowl, but their movements were slower and the repertoire often stopped there. They then usually started "exploring" their cages in a way similar to that described for I. radix by Chiszar and Carter (1975) and Chiszar et al. (1976), even though their cages had not been cleaned for several weeks. The first newborns to grab and swallow a fish were 2 months old and most were 4 months old when finally they captured a fish.

## 2. Capture of prey

Generally, a snake seized a fish by whichever part it encountered first and from there worked its way to the head or to the tail in order to swallow it. A fish was rarely caught directly from the front or directly from the back (Fig. 8). It often was caught anywhere along the middle of the body (Fig. 9). Once the fish was well secured, the snake seemed to be at a point where it needed to make a "decision": go to the head or to the tail. Tactile orientation from scale overlap and fin position might be important for the snake in order to determine which end to go to (Greene, 1976). However, with the fish used in this study, this did not seem to be the determining factor. The factor that did seem important was prey size, as Loop and Bailey (1972) had proposed for rodent-eating snakes. The bigger the fish, the greater the probability that a snake ingested it head first (see Fig. 10 for an example), (statistical evidence will be given and discussed in the next section). The smaller the fish the greater the probability that a snake "chose" either end, depending on where the fish was first caught. If the fish was caught anywhere towards the head, the snake went to the head and swallowed its prey from there. If the fish was caught towards the tail, it was ingested from there. (See Cooper, 1981, for similar observations on a scincid lizard,



FIGURE 9 - Yearling garter snake, Thamnophis  
sirtalis (SVL 373 mm), holding a large  
minnow (10 x 52 mm) by the midbody.



FIGURE 10 - Sequence showing an adult plains garter snake, Thamnophis radix (SVL 659 mm), grasping a large baltimore (25 x 87 mm), going to the head, and swallowing.

Eumeces laticeps, and next section for statistical analysis). However, if the small fish was caught by the middle, the response seemed random, either head or tail.

Young and adult I. melanogaster, and adult I. sirtalis and I. radix did not seem to have any difficulty determining and/or "deciding" to which end of the fish to go, be it small or large. However, when newborn I. sirtalis and I. radix captured a large fish by the middle (Fig. 9), they showed much "hesitation". Newborn I. sirtalis went back and forth over the middle part of the fish's body, apparently not knowing which end to go to. Newborn I. radix often dropped a large fish, then went back to it, grabbed it, dropped it again in a way similar to I. butleri (described below). As an aside, this would give support to the idea of I. butleri originating from I. radix (Burghardt, 1967; Carpenter, 1952).

Adult I. butleri had no difficulty handling small fish but had a hard time when handling large fish which adults of the other species and newborn I. melanogaster did not appear to have. The problem was not so much in determining where the head was, but more in handling and subduing a struggling large fish. Adults seemed to have difficulty holding on to their prey and, as a result, often dropped it. They would grab a fish by the middle, start the typical "walking" movements of the jaws towards head or

tail, but soon let go as the fish struggled. A few seconds later, they would try again, and let go. This could occur from three to fifteen times after which the snake either lost interest and left the fish or, the fish finally lying motionless, the snake would tongue-flick it, go to the head, grab it and swallow it.

Newborn I. butleri showed "indecision" towards fish small or large: they showed interest, approached the fish, tongue-flicked, then often started "exploring" their cage as described earlier. When they did attack and grab a fish, they often dropped it just as the adults had done for large fish. After dropping and grabbing their prey ten to twenty times they either abandoned it or seized it a last time. Instead of locating the head as the adults had done they often grabbed the fish by the middle and worked their way to one end.

## B. STATISTICAL ANALYSIS OF CAPTURE LOCATIONS AND SWALLOW SITES

### 1. Introduction

For the statistical treatment of the data two main aspects were considered: one, where capture and ingestion sites of fish were analyzed (categorical level, this section), the other, where latencies for handling and

ingesting prey were considered (ordinal and interval levels, sections C and D respectively). Moreover, in section D, interactions between species, age classes, fish sizes, capture locations and swallow sites, were analyzed.

Therefore, the statistical analysis of the data was divided into three main sections:

- a. Analysis at the nominal level of the capture locations (the 14 categories initially considered in the section on Methods were pooled into three categories (head, middle or tail) in order to increase the data set of each) and the swallow sites (head or tail).

The G-test for Goodness of Fit was used.

- b. Analysis at the ordinal level of the handling and swallowing latencies. These variables were treated ordinally since their values were not normally distributed and the variances were not homogeneous. The Wilcoxon matched-pairs signed-ranks test, the Mann-Whitney U-Test, and the Kruskal-Wallis one way analysis of variance were used (Machlis et al., 1985; Siegel, 1956; Sokal and Rohlf, 1981).

- c. Analysis at the interval level of the natural logarithms of the handling and swallowing latencies.

With the natural logarithms a normal distribution for the swallowing latencies and a more homogeneous variance for both variables were obtained. An analysis

of variance and Tukey's studentized range test for variability were used.

## 2. Within species and within age classes

### a. capture location (head, middle, or tail)

The frequencies (and percents) for capture locations by age class and by species are given in Table 6 (for a graphic representation see Figure 11). A G-test for Goodness of Fit was done to determine whether there were any differences in the four species and three age classes with respect to striking significantly more often at the head (assigning it a predicted frequency of .33) or at the middle and tail (assigning them a predicted frequency of .67) of the fish. G-test results, adjusted for Williams' correction, are given in Table 6.

Results showed no significant differences in newborns within prey sizes. At this stage, the snakes did not seem to have any preferred tactic in striking at a particular area of a fish whether it was large or small. In yearlings, only I. melanogaster showed a highly significant difference ( $p = .007$ ) when the fish was large.

In adults, I. sirtalis showed a significant preference for head first capture whether the fish was small ( $p = .04$ ) or large ( $p = .0002$ ). Thamnophis radix showed a significant preference for head first capture when the

TABLE 6 - Frequencies (and percents) of head, middle, and tail first CAPTURE of prey by four species and three age classes of Thamnophis with respect to a small fish (S) and a large fish (L). G-test for Goodness of Fit values (adjusted with Williams' correction when  $df = 1$ ) are given (with p values) for differences in capture location (head or middle and tail,  $df = 1$ ) and for differences in head first capture when fish is small or large ( $df = 2$ ). T.b. = T. butleri, T.m. = T. melanogaster, T.r. = T. radix, T.s. = T. sirtalis.

|           | n  | S/L | Head     | Middle  | Tail     | Gadj (p)     | G (p)      |
|-----------|----|-----|----------|---------|----------|--------------|------------|
| NEWBORNS  |    |     |          |         |          |              |            |
| T.b.      | 12 | S   | 5(41.7)  | 4(33.3) | 3(25.0)  | .17(.68)     | .22(.89)   |
|           | 12 | L   | 4(33.3)  | 5(41.7) | 3(25.0)  | 0 (1)        |            |
| T.m.      | 24 | S   | 8(33.3)  | 5(20.8) | 11(45.8) | 0 (1)        | 1.46(.48)  |
|           | 24 | L   | 11(45.8) | 6(25.0) | 7(29.2)  | .73(.39)     |            |
| T.r.      | 21 | S   | 10(47.6) | 7(33.3) | 4(19.1)  | .86(.35)     | 1.22(.54)  |
|           | 21 | L   | 9(42.9)  | 5(23.8) | 7(33.3)  | .39(.53)     |            |
| T.s.      | 26 | S   | 9(34.6)  | 7(26.9) | 10(38.5) | .01(.92)     | 1.96(.37)  |
|           | 26 | L   | 14(53.9) | 5(19.2) | 7(26.9)  | 2.15(.14)    |            |
| YEARLINGS |    |     |          |         |          |              |            |
| T.m.      | 10 | S   | 2(20.0)  | 3(30.0) | 5(50.0)  | .44(.51)     | 12.8(.002) |
|           | 10 | L   | 9(90.0)  | 1(10.0) | 0 (0)    | 7.16(.007)   |            |
| T.s.      | 18 | S   | 7(38.9)  | 6(33.3) | 5(27.8)  | .12(.73)     | 1.80(.41)  |
|           | 18 | L   | 11(61.1) | 4(22.2) | 3(16.7)  | 2.74(.10)    |            |
| ADULTS    |    |     |          |         |          |              |            |
| T.b.      | 12 | S   | 4(33.3)  | 5(41.7) | 3(25.0)  | 0 (1)        | 2.89(.24)  |
|           | 12 | L   | 8(66.7)  | 2(16.7) | 2(16.7)  | 2.56(.11)    |            |
| T.m.      | 10 | S   | 9(90.0)  | 0 (0)   | 1(10.0)  | 6.30(.01)    | 3.02(.22)  |
|           | 10 | L   | 7(70.0)  | 2(20.0) | 1(10.0)  | 2.40(.12)    |            |
| T.r.      | 13 | S   | 5(38.5)  | 4(30.8) | 4(30.8)  | .07(.79)     | 8.53(.01)  |
|           | 13 | L   | 11(84.6) | 2(15.4) | 0 (0)    | 7.07(.008)   |            |
| T.s.      | 12 | S   | 9(75.0)  | 2(16.7) | 1 (8.3)  | 4.07(.04)    | 4.59(.10)  |
|           | 12 | L   | 12(100)  | 0 (0)   | 0 (0)    | 14.24(.0002) |            |

FIGURE 11 - Graphic representation of the percents of head  
first capture for four species and three age  
classes of Thamnophis. (N = newborns,  
Y = yearlings, and A = adults).

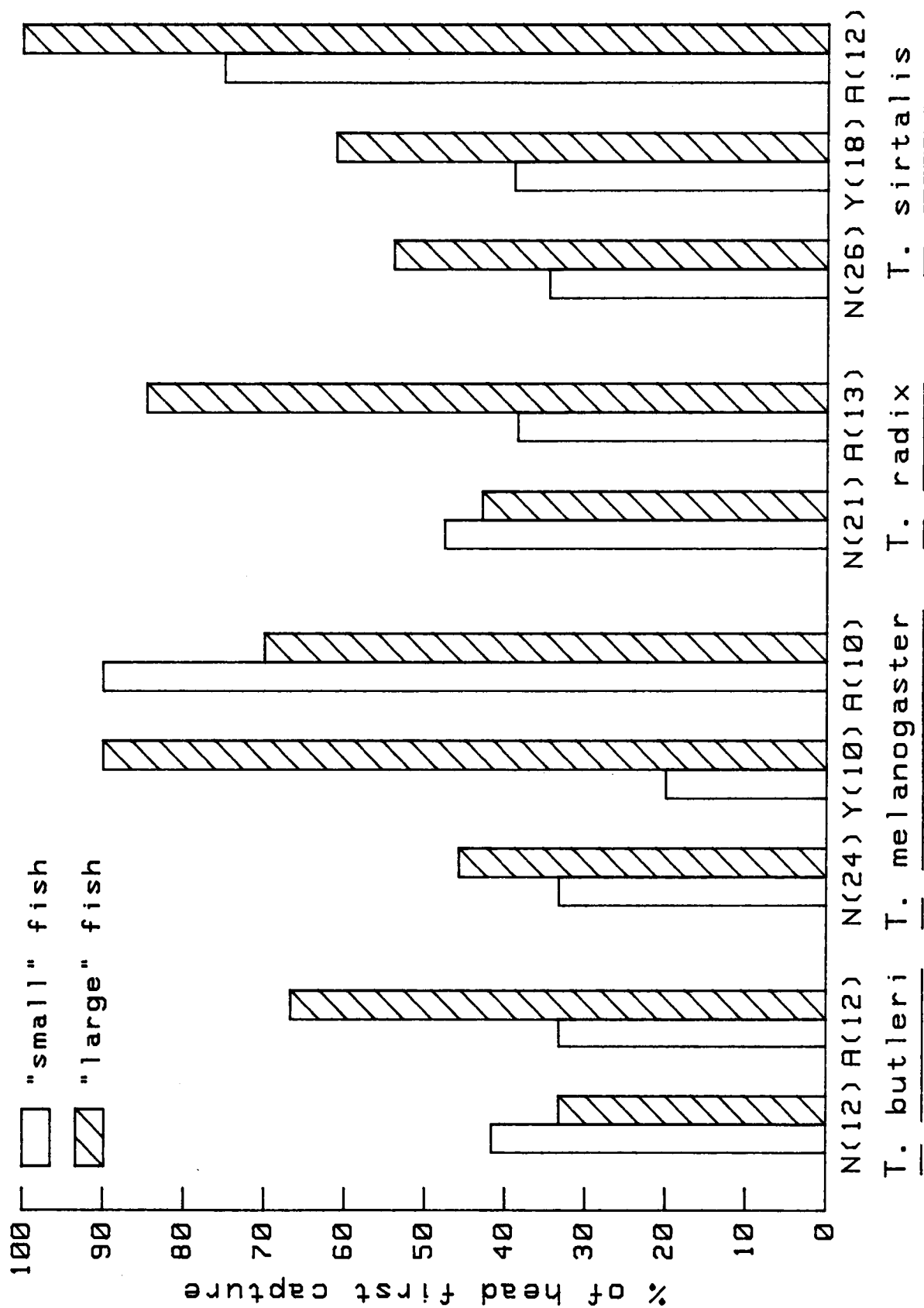


FIGURE 11

fish was large whereas I. melanogaster showed it when the fish was small. The other results were not significant. Nevertheless, in yearlings as well as in adults, for all species, large fish were captured head first at  $p < .12$ .

Another G-test was done to determine if there were significantly more head first captures when the fish was large compared to when it was small (Table 6). Again, there were no significant differences in any of the newborn species. However, in I. melanogaster yearlings, there was significantly more head first captures when the fish was large ( $p = .002$ ). There was no significant difference for I. sirtalis yearlings.

In the adults, only I. radix showed a change in tactics going significantly more often for the head when the fish was large ( $p = .01$ ). The other species showed no significant difference, although I. sirtalis had a  $p$  value of .10. This is important because these two species are known as generalists. They changed tactics when the prey was large, seizing its head first more often. On the other hand, the other two species, known as specialists, did not seem to basically change tactics when the fish was large. The reason seems to be that I. melanogaster already captured head first whether the fish was small or large whereas I. butleri, the earthworm specialist, only

improved slightly with larger prey (going more often for the head,  $p = .11$ ).

To summarize, newborns of the four species showed more random behavior in their prey capture than yearlings and adults which showed a preferred head first capture, especially when the fish was large.

#### b. Swallow site (head or tail)

The same procedure was followed with respect to preferred swallow site. Frequencies (and percents) are given in Table 7 (for a graphic representation see Figure 12). A G-test was employed to determine whether head versus tail first ingestion was significantly different from a random situation (each variable was assigned a predicted value of .5). Results, adjusted for Williams' correction, are shown in Table 7.

The newborns showed no significant difference with one exception, I. melanogaster. These snakes showed a significant preference for head first ingestion when the fish was large ( $p = .04$ ). In the yearlings, I. melanogaster showed a significant difference for head first ingestion in large fish ( $p = .004$ ).

In adults, I. sirtalis demonstrated significant differences for head first ingestion in both small and large fish whereas I. radix did so only for large fish.

TABLE 7 - Frequencies (and percents) of HEAD and TAIL FIRST SWALLOWING of prey by four species and three age classes of Thamnophis with respect to a small fish (S) and a large fish (L). G-test for Goodness of Fit values (adjusted with Williams' correction) are given (with p values) for differences in swallowing location (head or tail) and for differences in head first swallowing when the fish is small or large (both tests have df = 1).  
T.b. = T. butleri, T.m. = T. melanogaster,  
T.r. = T. radix, and T.s. = T. sirtalis.

|           | n  | S/L | Head     | Tail     | Gadj (p)    | Gadj (p)    |
|-----------|----|-----|----------|----------|-------------|-------------|
| NEWBORNS  |    |     |          |          |             |             |
| T.b.      | 12 | S   | 6(50.0)  | 6(50.0)  | 0 (1)       | .65(.42)    |
|           | 12 | L   | 8(66.7)  | 4(33.3)  | .65(.42)    |             |
| T.m.      | 24 | S   | 13(54.2) | 11(45.8) | .07(.79)    | 3.32(.07)   |
|           | 24 | L   | 19(79.2) | 5(20.8)  | 4.11(.04)   |             |
| T.r.      | 21 | S   | 14(66.7) | 7(33.3)  | 1.17(.28)   | .39(.53)    |
|           | 21 | L   | 12(57.1) | 9(42.9)  | .21(.65)    |             |
| T.s.      | 26 | S   | 14(53.9) | 12(46.1) | .08(.78)    | .70(.40)    |
|           | 26 | L   | 17(65.4) | 9(34.6)  | 1.22(.27)   |             |
| YEARLINGS |    |     |          |          |             |             |
| T.m.      | 10 | S   | 4(40.0)  | 6(60.0)  | .19(.66)    | 10.03(.002) |
|           | 10 | L   | 10(100)  | 0 (0)    | 8.34(.004)  |             |
| T.s.      | 18 | S   | 12(66.7) | 6(33.3)  | 1.00(.32)   | 0 (1)       |
|           | 18 | L   | 12(66.7) | 6(33.3)  | 1.00(.32)   |             |
| ADULTS    |    |     |          |          |             |             |
| T.b.      | 12 | S   | 6(50.0)  | 6(50.0)  | 0 (1)       | 2.89(.09)   |
|           | 12 | L   | 10(83.3) | 2(16.7)  | 2.89(.09)   |             |
| T.m.      | 10 | S   | 9(90.0)  | 1(10.0)  | 3.35(.07)   | 0 (1)       |
|           | 10 | L   | 9(90.0)  | 1(10.0)  | 3.48(.06)   |             |
| T.r.      | 13 | S   | 8(61.5)  | 5(38.5)  | .33(.57)    | 7.36(.007)  |
|           | 13 | L   | 13(100)  | 0 (0)    | 10.36(.001) |             |
| T.s.      | 12 | S   | 11(91.7) | 1 (8.3)  | 5.06(.02)   | .95(.33)    |
|           | 12 | L   | 12(100)  | 0 (0)    | 9.50(.002)  |             |

FIGURE 12 - Graphic representation of the percents of head first swallowing for four species and three age classes of Thamnophis. (N = newborns, Y = yearlings, and A = adults).

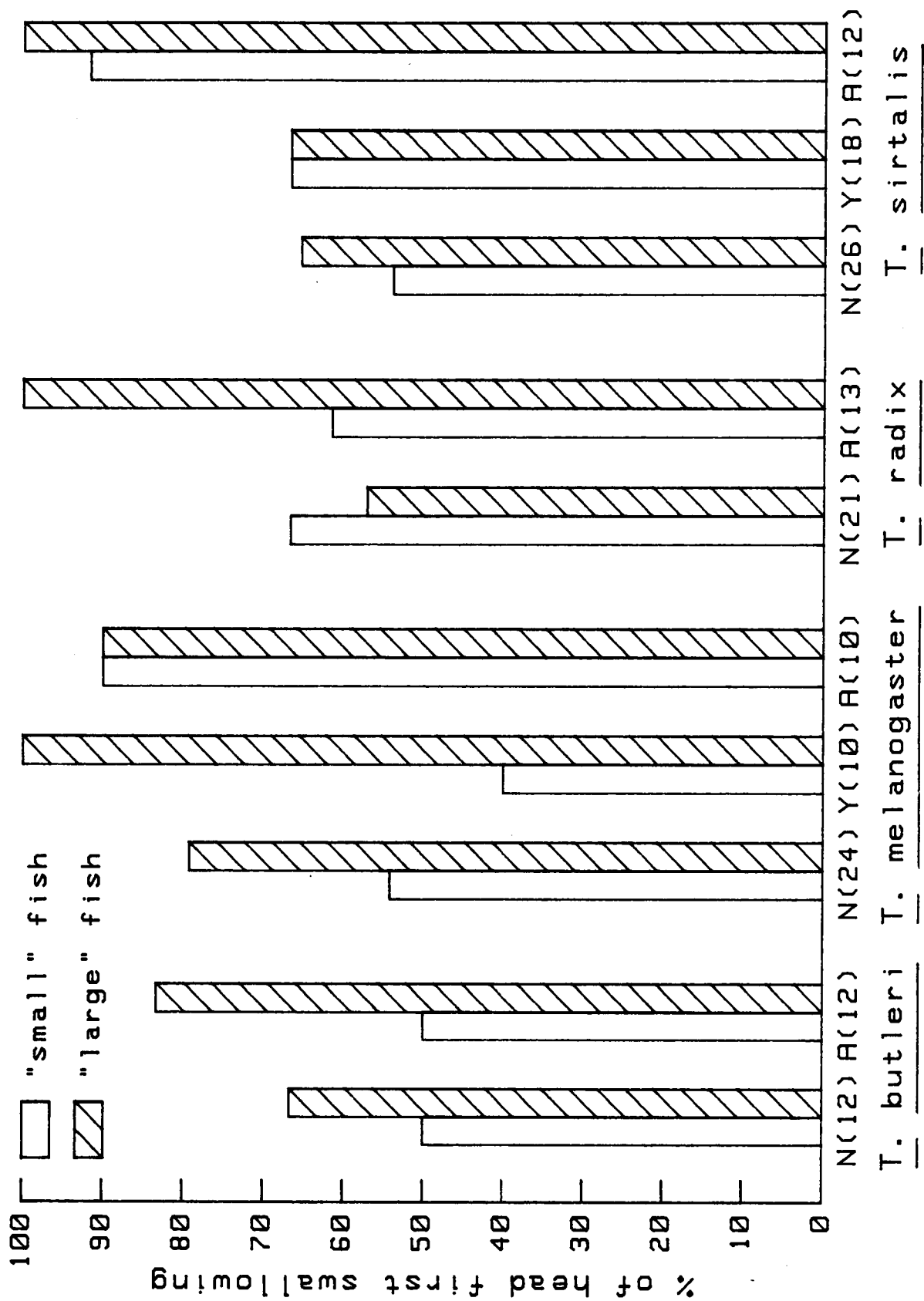


FIGURE 12

Thamnophis melanogaster showed a tendency for head first ingestion in both sizes of prey. In brief, adults of the four species showed preference ( $p < .10$ ) for head first ingestion when the fish was large.

Another G-test (also adjusted for Williams' correction) was calculated to determine whether there were significantly more head first swallowing when the fish was large than when it was small (Table 7). Newborns showed no significant difference except for a preference in I. melanogaster ( $p = .07$ ). Yearling I. melanogaster and adult I. radix showed significantly more head first ingestion when the fish was large. The rest did not show any significant differences although I. butleri showed a preference ( $p = .09$ ) for head first ingestion when the fish was large. Thamnophis melanogaster and I. sirtalis preferred head first swallowing whether the fish was large or small, which explains why there was no significant difference in these two species.

Summarizing, newborns seemed to be less selective in ingestion site when compared to yearlings and adults. Experience and maturation of adults might explain this difference.

### 3. Within species and across age classes

A G-test was calculated to determine whether there were any differences within species and across age classes with respect to capture location and swallow site of a small or a large fish (Table 8). With respect to head first capture, only I. melanogaster showed a significant difference between newborns, yearlings, and adults, on a small fish, whereas I. radix and I. sirtalis showed a significant difference on a large fish (I. melanogaster having a p value of .07).

Referring to swallow site, I. melanogaster and I. sirtalis showed significant differences between age classes with respect to a small fish whereas I. butleri and I. radix did not. With respect to large prey I. radix and I. sirtalis showed a significant difference for head first ingestion between the different age groups.

The pattern shown in Table 8 is not clear except that with small fish (capture and swallow sites) I. butleri and I. radix are more similar as opposed to the other two species. On the other hand, with large fish (capture and swallow sites) I. butleri differs from the other three species.

TABLE 8 - G-test for Goodness of Fit for differences  
WITHIN SPECIES and ACROSS AGE CLASSES of  
Thamnophis with respect to the site of  
capture and the site of swallowing of either  
a small or a large fish.

|                        | n  | df | small fish |      | large fish |      |
|------------------------|----|----|------------|------|------------|------|
|                        |    |    | G          | p    | G          | p    |
| CAPTURE LOCATION       |    |    |            |      |            |      |
| <u>I. butleri</u>      | 24 | 2  | .22        | .89  | 2.89       | .24  |
| <u>I. melanogaster</u> | 44 | 4  | 14.00      | .007 | 8.63       | .07  |
| <u>I. radix</u>        | 34 | 2  | .63        | .73  | 9.33       | .01  |
| <u>I. sirtalis</u>     | 56 | 4  | 6.82       | .15  | 12.22      | .02  |
| SWALLOWING SITE        |    |    |            |      |            |      |
| <u>I. butleri</u>      | 24 | 1  | 0          | 1    | .90        | .34  |
| <u>I. melanogaster</u> | 44 | 2  | 6.47       | .04  | 3.99       | .14  |
| <u>I. radix</u>        | 34 | 1  | .09        | .76  | 10.62      | .001 |
| <u>I. sirtalis</u>     | 56 | 2  | 6.06       | .05  | 8.63       | .01  |

#### 4. Within age classes and across species

A G-test was performed to detect differences within age classes and across species with respect to capture location and swallow site of a small and large fish (Table 9). Adults showed significant preference for head first capture and head first ingestion when the fish was small whereas yearlings showed it only with respect to swallow site and on large fish. This strengthens the finding that there are differences across species but these are to be found mostly in the adult stage.

### C. STATISTICAL ANALYSIS OF HANDLING AND SWALLOWING LATENCIES

The medians, first, and third quartiles of the handling and swallowing latencies for the four species and three age classes of Thamnophis are shown in Tables 10 and 11 respectively. Since the distribution of these variables was not normal, medians were preferred to means. Graphic representations are shown in Figures 13 to 16.

#### 1. Within species and within age classes

A Wilcoxon matched-pairs signed-ranks two-tailed test was used to determine whether there were any differences among species and among age classes with respect to the

TABLE 9 - G-test for Goodness of Fit for differences  
 WITHIN AGE CLASSES and ACROSS SPECIES of  
Thamnophis with respect to the site of  
 capture and the site of swallowing of either  
 a small or a large fish.

|                  | n  | df | small fish |     | large fish |     |
|------------------|----|----|------------|-----|------------|-----|
|                  |    |    | G          | p   | G          | p   |
| CAPTURE LOCATION |    |    |            |     |            |     |
| Newborns         | 83 | 6  | 4.53       | .61 | 2.57       | .86 |
| Yearlings        | 28 | 2  | 1.64       | .47 | 3.97       | .14 |
| Adults           | 47 | 6  | 13.54      | .04 | 9.34       | .16 |
| SWALLOWING SITE  |    |    |            |     |            |     |
| Newborns         | 83 | 3  | 1.24       | .74 | 2.65       | .45 |
| Yearlings        | 28 | 1  | 1.87       | .17 | 6.18       | .01 |
| Adults           | 47 | 3  | 8.09       | .04 | 5.00       | .17 |

TABLE 10 - Medians, first and third quartiles of the HANDLING LATENCIES (in seconds) for four species and three age classes of Thamnophis tested on a small fish (S) and on a large fish (L). These values are shown graphically in Figures 13 and 14.

|                        | n  | S/L | Median | Q1   | Q3     |
|------------------------|----|-----|--------|------|--------|
| NEWBORNS               |    |     |        |      |        |
| <u>I. butleri</u>      | 12 | S   | 10.5   | 0    | 37.75  |
|                        | 12 | L   | 89.5   | 63.5 | 192.75 |
| <u>I. melanogaster</u> | 24 | S   | 6.5    | 0    | 41.25  |
|                        | 24 | L   | 60     | 2.5  | 150    |
| <u>I. radix</u>        | 21 | S   | 35     | 5.5  | 77.5   |
|                        | 21 | L   | 120    | 0    | 185    |
| <u>I. sirtalis</u>     | 26 | S   | 13.5   | 0    | 45.25  |
|                        | 26 | L   | 62.5   | 7.5  | 165    |
| YEARLINGS              |    |     |        |      |        |
| <u>I. melanogaster</u> | 10 | S   | 25.5   | 9.25 | 44     |
|                        | 10 | L   | 11     | 0    | 45     |
| <u>I. sirtalis</u>     | 18 | S   | 30.5   | 8    | 95.5   |
|                        | 18 | L   | 95     | 43   | 372.5  |
| ADULTS                 |    |     |        |      |        |
| <u>I. butleri</u>      | 12 | S   | 8      | 0    | 40.25  |
|                        | 12 | L   | 240    | 240  | 240    |
| <u>I. melanogaster</u> | 5  | S   | 0      | 0    | 5.5    |
|                        | 5  | L   | 13     | 6    | 58.5   |
| <u>I. radix</u>        | 13 | S   | 18     | 0    | 33     |
|                        | 13 | L   | 25     | 0    | 46     |
| <u>I. sirtalis</u>     | 12 | S   | 0      | 0    | 29     |
|                        | 12 | L   | 2.5    | 0    | 24.25  |

TABLE 11 - Medians, first and third quartiles of the SWALLOWING LATENCIES (in seconds) for four species and three age classes of Thamnophis tested on a small fish (S) and on a large fish (L). These values are shown graphically in Figures 15 and 16.

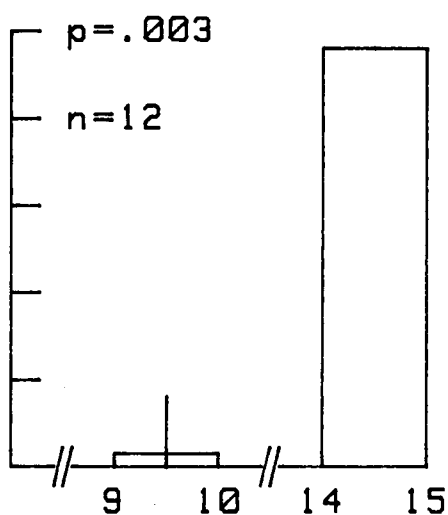
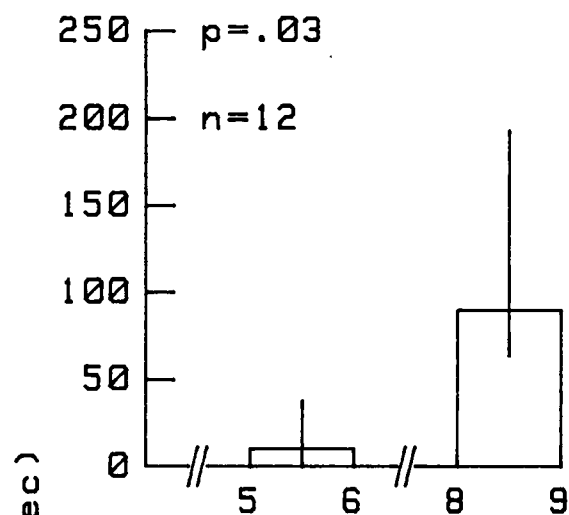
|                        | n  | S/L | Median | Q1     | Q3     |
|------------------------|----|-----|--------|--------|--------|
| NEWBORNS               |    |     |        |        |        |
| <u>I. butleri</u>      | 12 | S   | 62.5   | 51     | 115    |
|                        | 12 | L   | 561    | 195    | 928.75 |
| <u>I. melanogaster</u> | 24 | S   | 45.5   | 17.5   | 81.75  |
|                        | 24 | L   | 310    | 220    | 682.5  |
| <u>I. radix</u>        | 21 | S   | 38     | 20.5   | 119.5  |
|                        | 21 | L   | 590    | 367.5  | 1100   |
| <u>I. sirtalis</u>     | 26 | S   | 36.5   | 19     | 64     |
|                        | 26 | L   | 507.5  | 195    | 697.5  |
| YEARLINGS              |    |     |        |        |        |
| <u>I. melanogaster</u> | 10 | S   | 33     | 25.75  | 36     |
|                        | 10 | L   | 200    | 148.75 | 305    |
| <u>I. sirtalis</u>     | 18 | S   | 34     | 19     | 61.75  |
|                        | 18 | L   | 270    | 138.75 | 346.25 |
| ADULTS                 |    |     |        |        |        |
| <u>I. butleri</u>      | 12 | S   | 39.5   | 25.25  | 64     |
|                        | 12 | L   | 425    | 241.5  | 795    |
| <u>I. melanogaster</u> | 5  | S   | 14     | 9.5    | 52     |
|                        | 5  | L   | 83     | 56     | 97.5   |
| <u>I. radix</u>        | 13 | S   | 21     | 13.5   | 32     |
|                        | 13 | L   | 1000   | 534    | 1725   |
| <u>I. sirtalis</u>     | 12 | S   | 27.5   | 11.75  | 44     |
|                        | 12 | L   | 462    | 310    | 1237.5 |

FIGURE 13 - Graphic representations for newborn and adult Thamnophis butleri and T. radix of the medians (first and third quartiles being represented by a vertical line) of the HANDLING latencies (in seconds) for a small fish (S) and for a large fish (L), fish width given in millimeters. In the top left corner of each graph the p value for a two-tailed test (Wilcoxon matched-pairs signed-ranks test) is given as well as the number of pairs used that did not have any ties.-

# NEWBORNS

# ADULTS

## T. butleri



## T. radix

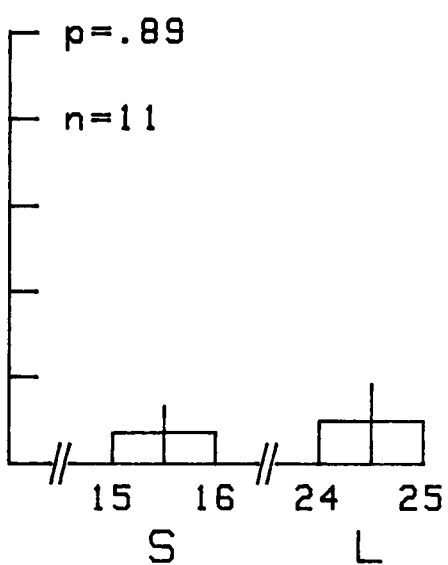
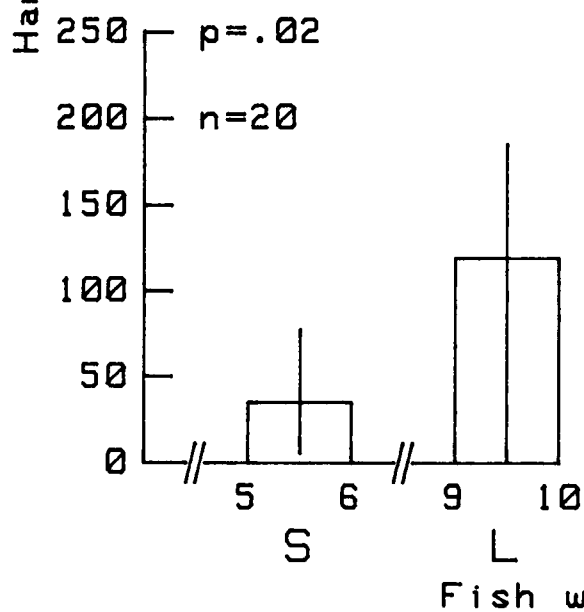


FIGURE 13

FIGURE 14 - Graphic representations for newborn, yearling, and adult Thamnophis melanogaster and T. sirtalis of the medians (first and third quartiles being represented by a vertical line) of the HANDLING latencies (in seconds) for a small fish (S) and for a large fish (L), fish width given in millimeters. In the top left corner of each graph the p value for a two-tailed test (Wilcoxon matched-pairs signed-ranks test) is given as well as the number of pairs used that did not have any ties.

# NEWBORNS    YEARLINGS    ADULTS

## T. melanogaster

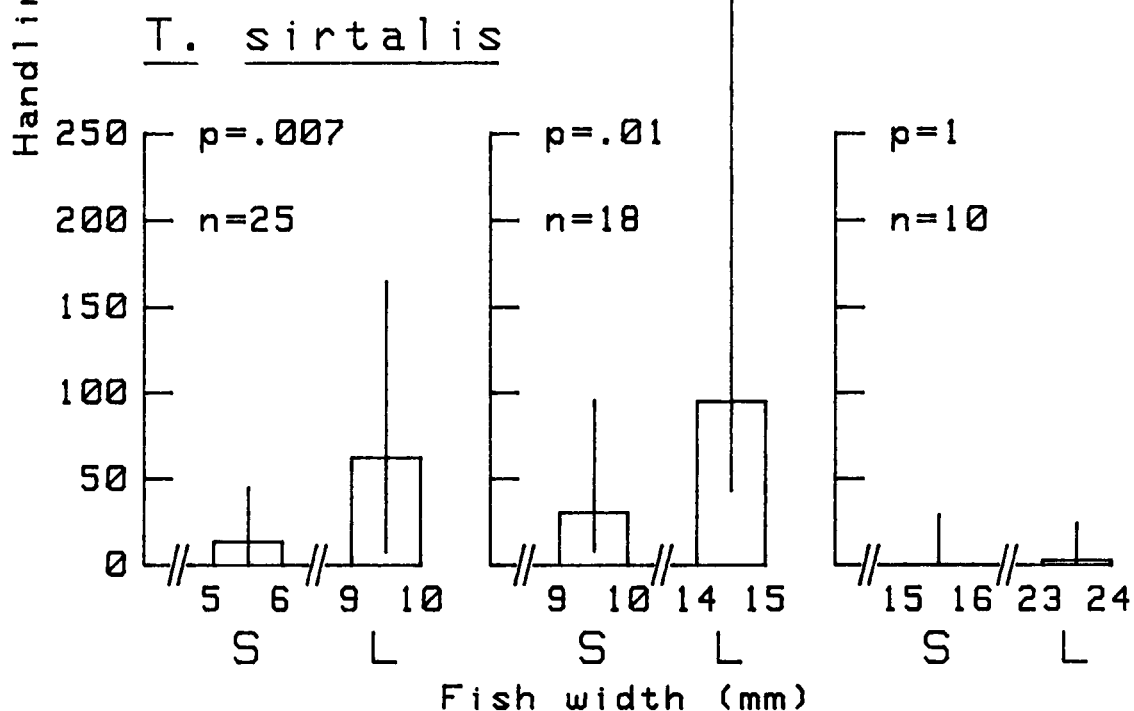
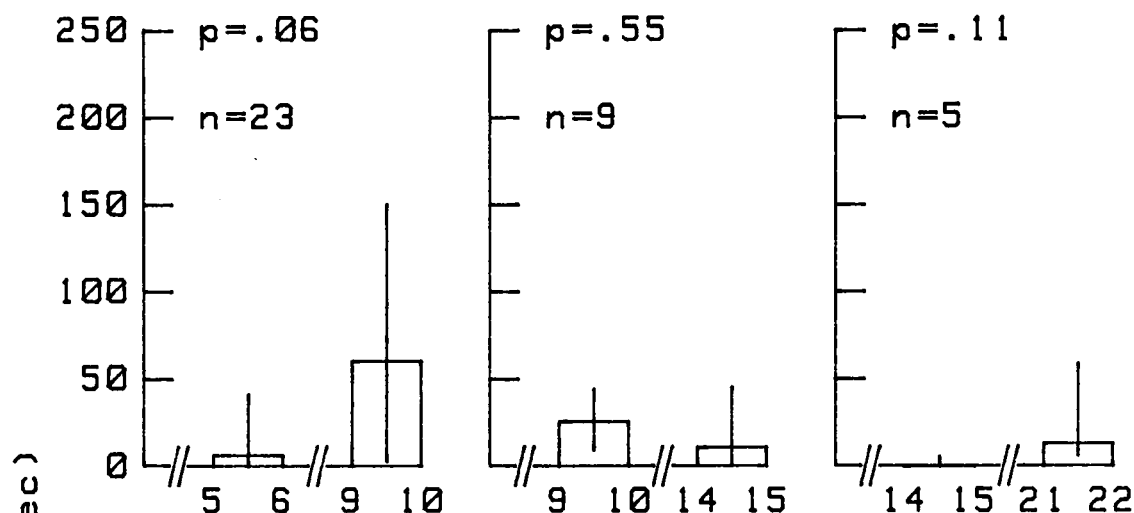


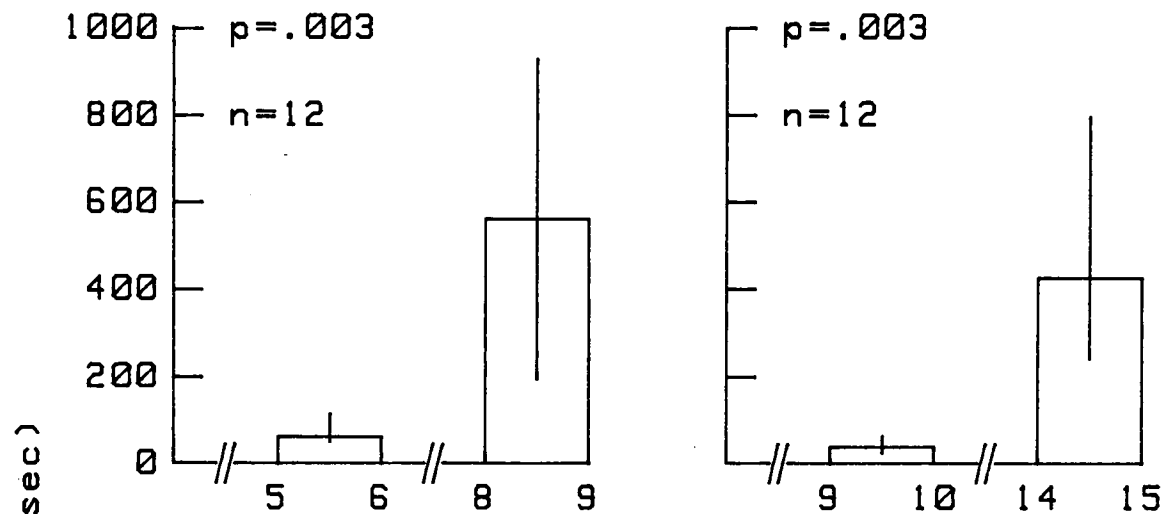
FIGURE 14

FIGURE 15 - Graphic representations for newborn and adult Thamnophis butleri and T. radix of the medians (first and third quartiles being represented by a vertical line) of the SWALLOWING latencies (in seconds) for a small fish (S) and for a large fish (L), fish width given in millimeters. In the top left corner of each graph the p value for a two-tailed test (Wilcoxon matched-pairs signed-ranks test) is given as well as the number of pairs used that did not have any ties.

# NEWBORNS

# ADULTS

## T. butleri



## T. radix

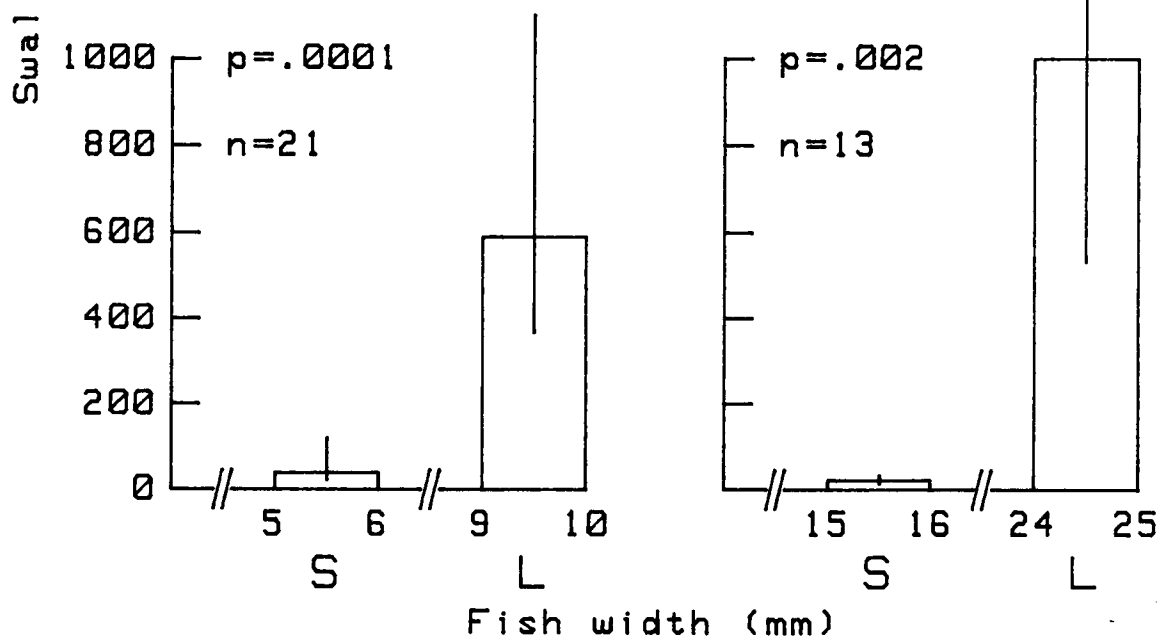
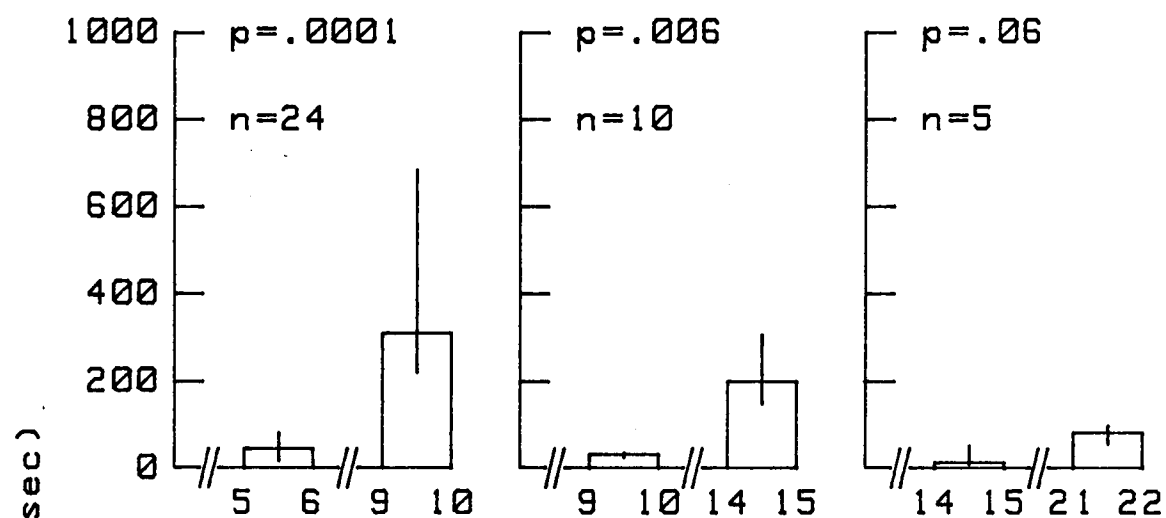


FIGURE 15

FIGURE 16 - Graphic representations for newborn, yearling, and adult Thamnophis melanogaster and T. sirtalis of the medians (first and third quartiles being represented by a vertical line) of the SWALLOWING latencies (in seconds) for a small fish (S) and for a large fish (L), fish width given in millimeters. In the top left corner of each graph the p value for a two-tailed test (Wilcoxon matched-pairs signed-ranks test) is given as well as the number of pairs used that did not have any ties.

# NEWBORNS    YEARLINGS    ADULTS

## T. melanogaster



## T. sirtalis

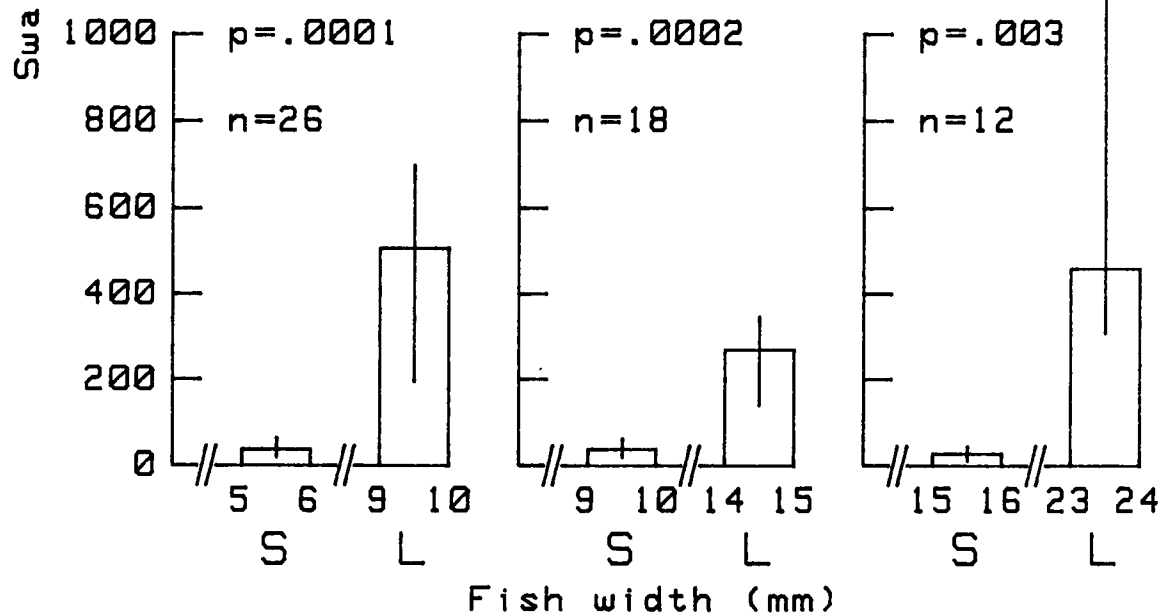


FIGURE 16

handling and swallowing latency of a small versus a large fish (Table 12, and Figures 13 to 16). Except for adult I. melanogaster, which was slightly over the .05 level, all species and age classes showed a very significant difference in swallowing latency, taking more time to ingest a large fish than a small one. This variable clearly depended directly on the size of the fish.

Referring to handling latency, there was a significant difference in handling time (taking more time to handle a large fish than a small one) in newborn and adult I. butleri, in newborn I. radix and in newborn and yearling I. sirtalis. The rest were non-significant except for newborn I. melanogaster which were close to .05 level ( $p = .06$ ). Therefore, all newborns, including a clear tendency for I. melanogaster, showed a significant increase in handling time when the fish was large. However, except for adult I. butleri, the adult species showed no significant difference in handling time whether the fish was large or small. Yearling I. melanogaster showed no significant difference whereas yearling I. sirtalis did.

These results seem to support the hypothesis that the fish specialist, I. melanogaster, will not take significantly more time to handle a larger prey (although it will to ingest it) because it is more efficient and quicker

TABLE 12 - Differences by species and by age class of Thamnophis (using the Wilcoxon matched-pairs signed-ranks two-tailed test, T) with respect to HANDLING and SWALLOWING LATENCIES of small and large fish (n being the number of pairs with no ties). Also see Figures 13 to 16.

|                        | Handling latency |    |      | Swallowing latency |   |       |
|------------------------|------------------|----|------|--------------------|---|-------|
|                        | n                | T  | p    | n                  | T | p     |
| <u>I. butleri</u>      |                  |    |      |                    |   |       |
| Newborns               | 12               | 10 | .03  | 12                 | 0 | .003  |
| Adults                 | 12               | 0  | .003 | 12                 | 0 | .003  |
| <u>I. melanogaster</u> |                  |    |      |                    |   |       |
| Newborns               | 23               | 75 | .06  | 24                 | 0 | .0001 |
| Yearlings              | 9                | 33 | .55  | 10                 | 0 | .006  |
| Adults                 | 5                | 1  | .11  | 5                  | 0 | .06   |
| <u>I. radix</u>        |                  |    |      |                    |   |       |
| Newborns               | 20               | 44 | .02  | 21                 | 0 | .0001 |
| Adults                 | 11               | 31 | .89  | 13                 | 0 | .002  |
| <u>I. sirtalis</u>     |                  |    |      |                    |   |       |
| Newborns               | 25               | 62 | .007 | 26                 | 0 | .0001 |
| Yearlings              | 18               | 29 | .01  | 18                 | 0 | .0002 |
| Adults                 | 10               | 27 | 1    | 12                 | 0 | .003  |

in handling a species-specific prey whatever its size within certain limits. On the other hand, newborn and adult I. butleri, an earthworm specialist, take significantly more time to handle a large fish. These snakes showed a lack of efficiency when confronted with large prey, as described in section A, this chapter.

Thamnophis radix and I. sirtalis, the two generalist species in this study, showed significant differences in the young but not in the adults. This also seems to support the hypothesis that a generalist would have a genetically more "open" behavior program (Mayr, 1974) meaning that newborns would be less efficient with new or larger prey. With experience/maturation they would "learn" how to deal with a regularly encountered prey and would therefore become more and more efficient in handling it. As adults they might become as efficient as a fish specialist on fish if that were their usual prey. Moreover, it is suggested that their behavior program might be "closing" with experience, and efficiency could be gained at the price of flexibility (Gass, 1985). In sum, newborns of these two species would be the real generalists.

## 2. Within species and across age classes

A Mann-Whitney U-Test was used for I. butleri and I. radix and a Kruskal-Wallis one way analysis of

variance test was used for I. melanogaster and I. sirtalis to determine whether there were any differences between age classes within species with respect to handling and swallowing latencies on small and large fish (Table 13).

Referring to handling time and the large fish situation, all species showed significant differences between young and adults except for I. melanogaster. This is in accordance with the findings from the previous section, where newborn I. radix and I. sirtalis showed less efficiency than adults in handling larger prey. The significant result obtained for I. butleri might be due to the particular circumstance of having to use for the adults of this species a handling time that considered dropping and grabbing the fish (see section on Methods and section A, this chapter).

Thamnophis melanogaster showed no significant difference between young and adults also in accordance to what would be expected in a fish specialist. However, a significant difference was obtained for handling time of a small fish. This result is unexplained at this point except that, as in many of the other previous tests, this species stands out as behaving differently from the other three. The rest of the species showed no significant difference between young and adults in handling time of a small fish.

TABLE 13 - Differences WITHIN SPECIES and ACROSS AGE CLASSES for four species of Ithamnophis with respect to handling and swallowing latencies on small and large fish. The Mann-Whitney U-Test (z approximation) was used for I. butleri and I. radix (newborns and adults) while the Kruskal-Wallis test one way analysis of variance (chisquare approximation, df = 2) was used for I. melanogaster and I. sirtalis (newborns, yearlings and adults).

|                        |    | small fish |       |        | large fish |       |         |
|------------------------|----|------------|-------|--------|------------|-------|---------|
|                        | n  | z          | chisq | (p)    | z          | chisq | (p)     |
| HANDLING LATENCY       |    |            |       |        |            |       |         |
| <u>I. butleri</u>      | 24 | .21        |       | (.83)  | 3.85       |       | (.0001) |
| <u>I. melanogaster</u> | 44 |            | 7.13  | (.03)  |            | 4.65  | (.10)   |
| <u>I. radix</u>        | 34 | 1.94       |       | (.16)  | 4.61       |       | (.03)   |
| <u>I. sirtalis</u>     | 56 |            | 4.55  | (.10)  |            | 13.04 | (.001)  |
| SWALLOWING LATENCY     |    |            |       |        |            |       |         |
| <u>I. butleri</u>      | 24 | 2.6        |       | (.009) | .35        |       | (.73)   |
| <u>I. melanogaster</u> | 44 |            | 5.59  | (.06)  |            | 24.07 | (.0001) |
| <u>I. radix</u>        | 34 | 4.83       |       | (.03)  | 1.91       |       | (.17)   |
| <u>I. sirtalis</u>     | 56 |            | 1.04  | (.59)  |            | 8.76  | (.01)   |

With respect to swallowing latency (Table 13)

I. butleri and I. radix showed significant differences between newborns and adults in swallowing time of a small fish whereas there was no significant difference in swallowing time of a large fish. The other two species showed the reverse: not significant on a small fish (although I. melanogaster is close with  $p = .06$ ) and significant on a large fish. These results show an interesting relationship between, on the one hand, I. butleri and I. radix, and on the other, I. melanogaster and I. sirtalis. This relationship will also be seen with results of another test shown in the last section of this chapter.

### 3. Within age classes and across species

A Mann-Whitney U-Test was used for yearling I. melanogaster and I. sirtalis and a Kruskal-Wallis one way analysis of variance test was used for newborns and adults of the four species of Thamnophis to determine whether there were any differences within age classes and across species with respect to handling and swallowing time on a small and a large fish (Table 14).

Referring to handling latency and small fish, none of the three age classes had any significant difference. The four species behaved very similarly within an age class

TABLE 14 - Differences WITHIN AGE CLASSES and ACROSS SPECIES for four species of Thamnophis with respect to handling and swallowing latencies on small and large fish. The Mann-Whitney U-Test (z approximation) was used for yearlings (T. melanogaster and T. sirtalis) whereas the Kruskal-Wallis one way analysis of variance (chisquare approximation, df = 3) was used for newborns and adults (four species of Thamnophis).

|                    |    | small fish |       |       | large fish |       |         |
|--------------------|----|------------|-------|-------|------------|-------|---------|
|                    | n  | z          | chisq | (p)   | z          | chisq | (p)     |
| HANDLING LATENCY   |    |            |       |       |            |       |         |
| Newborns           | 83 |            | 3.90  | (.27) |            | 1.06  | (.79)   |
| Yearlings          | 28 | .41        |       | (.68) | 2.82       |       | (.005)  |
| Adults             | 47 |            | 4.72  | (.19) |            | 28.01 | (.0001) |
| SWALLOWING LATENCY |    |            |       |       |            |       |         |
| Newborns           | 83 |            | 6.54  | (.09) |            | 5.60  | (.13)   |
| Yearlings          | 28 | .24        |       | (.81) | .60        |       | (.55)   |
| Adults             | 47 |            | 7.20  | (.07) |            | 27.22 | (.0001) |

with respect to the handling time of a small fish. This is in accordance with the many general and anecdotal accounts of snakes capturing and ingesting prey in a similar manner (see Introduction). Nevertheless, when considering handling latency of a large fish, yearlings and adults showed significant differences while newborns did not. It was the large prey that helped identify differences. Newborns seemed to be similar across species, but with age, some of the species (or all) showed significant differences in handling time of a large fish. To determine which species differ, other tests were performed. These will be explained in the last section of this chapter.

With respect to swallowing time, the only significant difference was observed in adults for large fish. This shows a similar pattern as for handling latency, that the older the animals, the more different they will be from one another.

#### D. OVERALL STATISTICAL ANALYSIS

##### 1. Analysis of variance

An analysis of variance using the natural logarithms of handling, swallowing, and total latencies was performed to determine overall effects and interactions between the following factors:

- species: I. butleri, I. melanogaster,  
I. radix, and I. sirtalis,
- age: newborns, yearlings and adults,
- fish size: either small or large,
- capture location: head, middle or tail of fish (used  
in the models that consider handling and total latency),
- swallow site: head or tail of fish (used in the models  
that consider swallowing and total latency).

Results are shown in Table 15. Only those interactions that had a p value lower or equal to .15 were included. Any other interaction had a higher p value. The three overall models were very significant.

In the handling latency model, capture location and fish size were very significant. Significant interactions were found between species and fish size and between species, age, and fish size. In the swallowing latency model, fish size, age, and species were each very significant. Interactions that proved to be significant were between species and fish size, between species and age, and between species, age, and fish size. In the total latency model, fish size, age, and species were very significant as in the second model. Significant interactions were between species and fish size, and between species, age, and fish size as in the first model. In order to determine

TABLE 15 - Analysis of variance using natural logarithms of handling, swallowing and total latencies, considering overall effects and most significant interactions for four species of Thamnophis. Factors used were species, age, fish size, capture location and swallow site. Only those interactions that had a p value lower or equal to .15 were included. These were ranked from most significant to least significant.

|                                | df  | F      | p     |
|--------------------------------|-----|--------|-------|
| HANDLING LATENCY               |     |        |       |
| overall                        | 261 | 4.03   | .0001 |
| capture location               | 2   | 24.20  | .0001 |
| fish size                      | 1   | 10.89  | .001  |
| species*fish size              | 3   | 4.95   | .002  |
| species*age*fish size          | 4   | 2.68   | .03   |
| age*capture location           | 4   | 2.23   | .07   |
| species*age                    | 4   | 1.90   | .11   |
| species                        | 3   | 1.78   | .15   |
| SWALLOWING LATENCY             |     |        |       |
| overall                        | 279 | 26.39  | .0001 |
| fish size                      | 1   | 256.12 | .0001 |
| species*fish size              | 3   | 8.66   | .0001 |
| age                            | 2   | 8.74   | .0002 |
| species*age*fish size          | 4   | 5.17   | .0005 |
| species                        | 3   | 5.95   | .0006 |
| species*age                    | 4   | 3.49   | .008  |
| species*swallow site*fish size | 3   | 2.06   | .11   |
| TOTAL LATENCY                  |     |        |       |
| overall                        | 245 | 11.72  | .0001 |
| fish size                      | 1   | 195.30 | .0001 |
| age                            | 2   | 5.07   | .007  |
| species*age*fish size          | 4   | 3.54   | .008  |
| species                        | 3   | 3.91   | .009  |
| species*fish size              | 3   | 3.41   | .02   |
| species*age                    | 4   | 1.90   | .11   |
| capture location               | 2   | 2.05   | .13   |

where the differences were, a Tukey's studentized range test was performed.

## 2. Tukey's studentized range test for variability

Tukey's studentized range test for variability using the natural logarithms of handling, swallowing and total latencies was obtained to determine which factors differed significantly in an interaction. Significant interactions are shown in Table 16.

With respect to species the pair that differed consistently in the three models is I. butleri and I. melanogaster, the two specialists, but the former on earthworms and the latter on fish. In the second and third model, I. radix differed significantly from I. melanogaster and from I. sirtalis. This makes I. butleri and I. radix more similar to each other than to the other two species as was shown in a previous section. This gives support to the idea of I. butleri originating from I. radix (Burghardt, 1967, Carpenter, 1952).

Only in the total latency model was I. melanogaster significantly different from all the other three species, clearly setting it apart. Thamnophis melanogaster took significantly less time to handle and swallow (total latency) fish than the other three species which is in accordance with its specialization on fish.

TABLE 16 - Tukey's studentized range test for variability with respect to the natural logarithms of handling, swallowing and total latencies for four species of Ithamnophis. Factors compared were species, age, fish size, capture location and swallow site.

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FACTORS COMPARED (p < .05)

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| for HANDLING LATENCY |                   | greater | > | smaller                |
|----------------------|-------------------|---------|---|------------------------|
| species              | <u>I. butleri</u> |         | > | <u>I. melanogaster</u> |
| age classes          | newborns          |         | > | adults                 |
|                      | yearlings         |         | > | adults                 |
| fish size            | large             |         | > | small                  |
| capture location     | middle            |         | > | tail                   |
|                      | middle            |         | > | head                   |

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for SWALLOWING LATENCY

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|              |                   |  |   |                        |
|--------------|-------------------|--|---|------------------------|
| species      | <u>I. butleri</u> |  | > | <u>I. melanogaster</u> |
|              | <u>I. radix</u>   |  | > | <u>I. melanogaster</u> |
|              | <u>I. radix</u>   |  | > | <u>I. sirtalis</u>     |
| age classes  | newborns          |  | > | adults                 |
|              | newborns          |  | > | yearlings              |
| fish size    | large             |  | > | small                  |
| swallow site | head              |  | > | tail                   |

---

for TOTAL LATENCY

---

|                  |                    |  |   |                        |
|------------------|--------------------|--|---|------------------------|
| species          | <u>I. butleri</u>  |  | > | <u>I. melanogaster</u> |
|                  | <u>I. radix</u>    |  | > | <u>I. melanogaster</u> |
|                  | <u>I. sirtalis</u> |  | > | <u>I. melanogaster</u> |
|                  | <u>I. radix</u>    |  | > | <u>I. sirtalis</u>     |
| age classes      | newborns           |  | > | yearlings              |
|                  | newborns           |  | > | adults                 |
| fish size        | large              |  | > | small                  |
| capture location |                    |  | - |                        |
| swallow site     | head               |  | > | tail                   |

---

Referring to age classes, adults took significantly less time than newborns and yearlings in the first model, and took less time than newborns in the second and third models. Yearlings were significantly different from adults (taking more time to handle fish than adults) but not from newborns in the first model whereas they were significantly different from newborns (taking less time than newborns) but were not different from adults in the second and third models. This clearly puts newborns and adults in different categories with yearlings in an in-between stage. These results seem to strengthen previous ones that there is a developmental factor involved, probably based on maturational/experiential processes, that might explain these differences.

Fish size was significantly different in all three models, large fish taking more time than small fish to be handled and swallowed. This has proved to be an important variable in the observation of the feeding behavior of the snakes as it has often helped contrast differences and non-differences between factors.

Capture location in the first model showed significant differences between midbody capture of the fish and tail and between midbody and the head. If the fish was caught by the middle it took significantly more time to handle and arrive at the head or tail than if it were directly caught at the

head or at the tail. This implies that a snake would have the tendency of ingesting a fish by the end that is closest to where it is caught. In the total latency model, this factor is non-significant.

Swallow site was significant in both the swallow latency model and the total latency model. Snakes took more time to swallow fish head first than tail first which would contradict reports that it should be the reverse (e.g. Diefenbach and Emslie, 1971). However, this result might have been affected by the fact that small and large fish data were pooled together in this analysis (e.g. there were few tail first swallowing when the fish was large). Nevertheless, a difference might exist due to morphological differences between rodents and fish. Observing snakes feeding on large fish, they were slower going over the middle part of the body than going over the head or tail sections. A study comparing feeding behavior of snakes on different types of prey would be needed and might reveal different tactics depending on the type of prey.

## CHAPTER IV

### CONCLUSIONS

Feeding behavior in the four species of Thamnophis follows a sequential pattern of grabbing a fish, often by its midbody, determining one end, reorienting to that end, and ingesting the prey. How a snake determines the head or tail of a fish is unknown. However, that they are capable of doing so is attested by the many head first ingestions observed in this study. Head first ingestion was clearly related to the size of the prey.

In spite of the overall similarities in feeding behavior in the four species of Thamnophis, the statistical analysis of the data established significant differences between juveniles and adults, and between the fish specialist, I. melanogaster, and the three other species.

Several aspects of this study need to be emphasized:

1. The general feeding behavior in the four species is similar: a snake captures a fish, determines one end, preferably the head if the prey is large, goes to that end and swallows. However, when this behavior is examined more closely, differences appear.

2. An important difference is seen between the young and adults. Adults are in general more efficient and quicker than newborns in handling fish. They also strike more often at the prey's head than the newborns. This could imply that a developmental process is involved allowing for maturation and experience to affect the snakes' feeding behavior.
3. Within species, newborn I. radix and I. sirtalis are significantly less efficient handling large fish compared to handling small fish than their adult counterparts. The other two species do not show such a difference between newborns and adults. It could imply that I. radix and I. sirtalis are subject to greater developmental changes and have a more "open" behavior program. They might, therefore be more prone to adapt and will show more flexibility to changing circumstances than the other two species. (However, it is possible that with age and with increased efficiency, there might be a loss in flexibility, with a consequent "closing" of the behavior program. This would be an interesting aspect on which to do further research).
4. Results from the previous point seem to be connected to differences between the generalists (I. radix and I. sirtalis), the specialist on fish (I. melanogaster), and the specialist on

earthworm (I. butleri). The generalists show differences between newborns and adults whereas, in the fish specialist, newborns resemble adults in their efficiency in handling fish. In the earthworm specialist, newborns resemble adults in their inefficiency to handle fish.

5. I. butleri and I. radix seem more similar with respect to the behaviors studied than to either of the other two species, giving support to the idea that the former originated from the latter.
6. I. melanogaster is quicker and more efficient when handling fish than the other species studied. This strengthens the notion that this species is the fish specialist of the group.

Although the present study would benefit from a more controlled approach (such as using only one species of fish and varying its size), it does allow for determining differences and similarities across species and age classes. Similar studies using other species would be highly desirable and worthwhile.

LITERATURE CITED

#### LITERATURE CITED

- Arnold, S. J. 1978. Some effects of early experience on feeding responses in the common garter snake, Thamnophis sirtalis. Anim. Behav., 26:455-462.
- Arnold, S. J. 1981. The Microevolution of Feeding Behavior. In: Foraging Behavior: Ecological, Ethological, and Psychological Approaches (A. C. Kamil and T. D. Sargent, Eds.). Garland STPM Press, New York and London, pp. 409-453.
- Bellairs, A. 1970. The Life of Reptiles. Vol. I, Universe Books, New York City.
- Bolles, F. 1890. Barred owls in captivity. Auk 7: 101-114.
- Breen, J. F. 1974. Encyclopedia of Reptiles and Amphibians. T. F. H. Publications, Inc. Ltd.
- Burghardt, G. M. 1966. Stimulus control of the prey attack response in naive garter snakes. Psychon. Sci., 4:37-38.
- Burghardt, G. M. 1967. Chemical-cue preferences of inexperienced snakes: comparative aspects. Science, 157:718-721.
- Burghardt, G. M. 1968. Chemical preference studies on newborn snakes of three sympatric species of Natrix. Copeia, 1968:732-737.
- Burghardt, G. M. 1969. Comparative prey-attack studies in newborn snakes of the genus Thamnophis. Behaviour, 33:77-114.
- Burghardt, G. M. 1970a. Intraspecific geographical variation in chemical food cue preferences of newborn garter snakes (Thamnophis sirtalis). Behaviour, 36:246-257.
- Burghardt, G. M. 1970b. Chemical perception in reptiles. In: Communication by Chemical Signals (J. W. Johnston, Jr., D. G. Moulton and A. Turk, Eds.). Appleton-Century-Crofts, New York, pp. 241-308.

- Burghardt, G. M. 1975. Chemical prey preference polymorphism in newborn garter snakes *Thamnophis sirtalis*. Behaviour, 52:202-225.
- Burghardt, G. M. 1977a. Learning Processes in Reptiles. In: Biology of the Reptilia (C. Gans and D. W. Tinkle, Eds.). Academic Press, London, New York and San Francisco, 7:555-681.
- Burghardt, G. M. 1977b. Ontogeny of communication. In: How Animals Communicate (T. A. Sebeok, Ed.). Indiana Univ. Press, pp. 71-97.
- Burghardt, G. M. 1978. Behavioral ontogeny in reptiles: Whence, whither, and why? In: The Development of Behavior (G. M. Burghardt and M. Bekoff, Eds.). Garland, New York, pp. 149-174.
- Burghardt, G. M. 1980. Behavioral and stimulus correlates of vomeronasal functioning in reptiles: feeding, grouping, sex and tongue use. In: Chemical Signals. Vertebrate and Aquatic Invertebrates (D. Muller-Schwarze and R. M. Silverstein, Eds.). Plenum Press, New York and London, pp. 275-301.
- Burghardt, G. M., and D. Denny, 1983. Effects of prey movement and prey odor on feeding in garter snakes. Z. Tierpsychol., 62:329-347.
- Burghardt, G. M., and E. H. Hess, 1968. Factors influencing the chemical release of prey attack in newborn snakes. J. Comp. Physiol. Psychol., 66:289-295.
- Burghardt, G. M., and C. H. Pruitt, 1975. Role of the tongue and senses in feeding of naive and experienced garter snakes. Physiol. and Behav., 14:185-194.
- Carpenter, C. C. 1952. Comparative ecology of the common garter snake (*Thamnophis s. sirtalis*), the ribbon snake (*Thamnophis s. sauritus*), and Butler's garter snake (*Thamnophis butleri*) in mixed populations. Ecol. Monogr., 22: 235-258.
- Carr, A. 1971. The Reptiles. Time-Life Books, New York.

- Chiszar, D., and T. Carter, 1975. Reliability of individual differences between garter snakes (Thamnophis radix) during repeated exposures to an open field. Bull. Psychon. Soc., 5:507-509.
- Chiszar, D., T. Carter, L. Knight, L. Simonsen, and S. Taylor, 1976. Investigatory behavior in the plains garter snake (Thamnophis radix) and several additional species. Animal Learning and Behavior, 4:273-278.
- Conant, R. 1963. Semiaquatic snakes of the genus Thamnophis from the isolated drainage system of the Rio Nazas and adjacent areas in Mexico. Copeia, 1963:473-499.
- Conant, R. 1975. A Field Guide to Reptiles and Amphibians of Eastern/Central North America. Houghton Mifflin Company, Boston.
- Cooper, W. E. 1981. Head-first swallowing of large prey by a scincid lizard, Eumeces laticeps. J. Herp., 15:371-373.
- Cundall, D., and C. Gans, 1979. Feeding in water snakes: an electromyographic study. J. Exp. Zool., 209:189-207.
- Czaplicki, J. A., and R. H. Porter, 1974. Visual cues mediating the selection of goldfish (Carassius auratus) by 2 species of Natrix. J. Herp., 8:129-134.
- Diefenbach, C. O. and S. G. Emslie, 1971. Cues influencing the direction of prey ingestion of the japanese snake, Elaphe climacophora (Colubridae, Serpentes). Herpetologica, 27:461-466.
- Ditmars, R. 1936. The Reptiles of North America. Doubleday and Company, Inc. Garden City, New York.
- Drummond, H. M. 1979. Stimulus control of amphibious predation in the northern water snake (Nerodia s. sipedon). Z. Tierpsychol., 50:18-44.

- Drummond, H. M. 1980. Aquatic foraging in some new world natricine snakes: generalists and specialists and their behavioral evolution. Unpublished Doctoral Thesis. University of Tennessee, Knoxville.
- Drummond, H. 1983. Aquatic foraging in garter snakes: a comparison of specialists and generalists. *Behaviour*, 86:1-30.
- Drummond, H. 1985. The role of vision in the predatory behaviour of natricine snakes. *Anim. Behav.*, 33:206-215.
- Drummond, H. M., and G. M. Burghardt, 1983. Geographic variation in the foraging behavior of the garter snake, *Thamnophis elegans*. *Behav. Ecol. Sociobiol.*, 12: 43-48.
- Drummond, H. M., and C. Macias Garcia. Specialist and generalist compared: a field study of snake foraging. In preparation.
- Echternacht, A.C. 1977. *How Amphibians and Reptiles Live*. Elsevier-Phaidon, Oxford.
- Evans, P. D. 1942. A method of fishing used in water snakes. *Chicago Nat.*, 5:53:55
- Ewer, R. F. 1968. *Ethology of Mammals*. Logos Press, London.
- Fagen, R. 1982. Evolutionary issues in development of behavioral flexibility. *In: Perspectives in Ethology* (P. P. G. Bateson and P. H. Klopfer, Eds.). Plenum Press, New York and London, 5:365-383.
- Fitch, H. S. 1965. An ecological study of the garter snake, *Thamnophis sirtalis*. *Univ. Kansas Publ. Mus. Nat. Hist.*, Lawrence, 15:493-564.
- Fox, W. 1952. Notes on feeding habits of pacific coast garter snakes. *Herpetologica*, 8:4-8.
- Fuchs, J. L., and G. M. Burghardt, 1971. Effects of early feeding experience on the responses of garter snakes to food chemicals. *Learning and Motivation*, 2:271-279.

- Gass, C. L. 1985. Behavioral foundations of adaptation. In: Perspectives in Ethology (P. P. G. Bateson and P. H. Klopfer, Eds.). Plenum Press, New York and London, 6:63-107.
- Gove, D. 1971. The responses of ecologically dissimilar populations of the water snake, Natrix sipedon sipedon, to surface extracts of prey species, with observations on feeding and defense behaviors. Master Thesis. University of Tennessee, Knoxville.
- Gove, D. and G. M. Burghardt, 1975. Responses of ecologically dissimilar populations of the water snake Natrix s. sipedon to chemical cues from prey. J. Chem. Ecol., 1:25-40.
- Greene, H. W. 1976. Scale overlap, a directional sign stimulus for prey ingestion by ophiophagous snakes. Z. Tierpsychol., 41:113-120.
- Halloy, M. 1985a. Liophis poecilogurus (Wied). Supp. Rev. fr. Aquariol., 2:291.
- Halloy, M. 1985b. Note sur Liophis sagittifer (Jan, 1861). Rev. fr. Aquariol., 12:27-30.
- Herzog, H. A., and G. M. Burghardt, in press. Development of antipredator responses in snakes. III: Stability of individual and litter differences over the first year of life. Ethology.
- Kardong, K. U. 1975. Prey capture in the cottonmouth snake. J. Herp., 9:169-175.
- Klein, J. 1975. Headfirst prey ingestion by newborn Elaphe and Lampropeltis. Copeia, 1975:366.
- Krebs, J. 1973. Behavioral aspects of predation. In: Perspectives in Ethology. (P. P. G. Bateson and P. H. Klopfer, Eds.). Plenum Press. New York and London, 1:73-111.
- Kubie, J., and M. Halpern, 1975. Laboratory observations of trailing behavior in garter snakes. J. Comp. Physiol. Psychol., 89:667-674.

- Kubie, J., and M. Halpern, 1978. Garter snake trailing behavior: effects of varying prey-extract concentration and mode of prey-extract presentation. *J. Comp. Physiol. Psychol.*, 92:362-373.
- Leyhausen, P. 1979. *Cat Behavior*. Garland SIPM Press, New York and London (translated by B. A. Tonkin).
- Loop, M. S. 1974. The effect of relative prey size on the ingestion behavior of the bengal monitor, Varanus bengalensis (Sauria: Varanidae). *Herpetologica*, 30:123-127.
- Loop, M. S., and L. G. Bailey, 1972. The effect of relative prey size on the ingestion behavior of rodent-eating snakes. *Psychon. Sci.*, 21:189-190.
- Machlis, L., and P. W. D. Dodd, with J. C. Fentress. 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. *Z. Tierpsychol.*, 68:201-214.
- Mayr, E. 1974. Behavior programs and evolutionary strategies. *Am. Sci.*, 62:650-659.
- Mertens, R. 1960. *The World of Amphibians and Reptiles*. McGraw Hill Book Company, Inc., New York, London, and Toronto.
- Naulleau, G. 1964. Premières observations sur le comportement de chasse et de capture chez les vipères et les couleuvres. *La Terre et la Vie*, 1:54-76.
- Naulleau, G. 1966. La biologie et le comportement prédateur de Vipera aspis au laboratoire et dans la nature. Thèse, Université de Nancy, France.
- Oyama, S. 1982. A reformulation of the idea of maturation. *In: Perspectives in Ethology*. Plenum Press, New York and London, 5:101-131.
- Pope, C. H. 1960. *The Reptile World. A Natural History of the Snakes, Lizards, Turtles, and Crocodilians*. Alfred A. Knopf, New York.
- Queiroz de, A., and K. de Queiroz, 1987. Prey handling of Eumeces gilberti with comments on headfirst ingestion in Squamates. *J. Herp.*, 3:57-63.

- Schmidt, K. P., and R. F. Inger, 1957. Living Reptiles of the World. Hannover House, Garden City, New York.
- Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill Book Company, Inc., New York, Toronto, and London.
- Sokal, R. R., and F. J. Rohlf, 1981. Biometry: the Principles and Practice of Statistics in Biological Research, 2nd ed. W. H. Freeman and Company, San Francisco.
- Stebbins, R. C. 1966. A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin Company, Boston.
- Stoner, D. 1941. Feeding behavior of a water snake. Science, 94:307.
- Trapido, H. 1943. Observations of the feeding habits of some water snakes. Chicago Nat., 6:42.
- Voris, H. K., and M. W. Moffett, 1981. Size and proportion relationship between the beaked sea snake and its prey. Biotropica, 13:15-19.
- Wendelken, P. W. 1978. On prey-specific hunting behavior in the western ribbon snake, Thamnophis proximus (Reptilia, Serpentes, Colubridae). J. Herp., 12:577-578.
- Wilde, W. S. 1938. The role of jacobson's organ in the feeding reaction of the common garter snake, Thamnophis sirtalis sirtalis (Linn). J. Exp. Zool., 77:445-465.
- Wright, A. H., and A. A. Wright, 1957. Handbook of Snakes of the United States and Canada. Vol.II. Comstock Publishing Associates, Ithaca, New York.

## VITA

Monique Halloy de Grosse was born on 25 May, 1949, in Brussels, Belgium. She spent most of the next 12 years in Zaïre, returning periodically to Belgium. From 1961 to 1964, she lived in Belmont, Massachusetts, where she attended Junior High School. In 1964, she left for Argentina, where she lived most of the next 20 years. She finished high school in 1967 and obtained a degree in Psychology from the University of Tucumán, Argentina, in 1972. After working for two years in the Department of Psychology, she stopped altogether in order to take care of her two children. Once both were in school, she started studying again, taking courses in Zoology at the University of Tucumán. In 1985, she was accepted at the University of Tennessee, Knoxville, in a program that would allow her to pursue her new interest in animal behavior.