70-14,426

PRESTON, William Burton, 1937-
THE COMPARATIVE ECOLOGY OF TWO WATER SNAKES, _NATRIX RHOMBIFERA_ AND _NATRIX ERYTHROGASTER_, IN OKLAHOMA.

The University of Oklahoma, Ph.D., 1970
Zoology

University Microfilms, Inc., Ann Arbor, Michigan

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

THE COMPARATIVE ECOLOGY OF TWO WATER SNAKES, *NATRIX RHOMBIFERA* AND *NATRIX ERYTHROGASTER*, IN OKLAHOMA

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

WILLIAM BURTON PRESTON

Norman, Oklahoma

1970

THE COMPARATIVE ECOLOGY OF TWO WATER SNAKES,

NATRIX RHOMBIFERA AND *NATRIX ERYTHROGASTER*,

IN OKLAHOMA

APPROVED BY

DISSERTATION COMMITTEE

ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. Charles C. Carpenter, as my advisor, for his guidance in selecting the problem, for guidance and suggestions during the study, and for the use of his facilities. In addition to Dr. Carpenter I wish to thank the other members of my advisory committee, Drs. Elroy L. Rice, Howard B. Haines, and J. Keever Greer for the critical reading of the manuscript.

For their interest, help, and encouragement I wish to thank my fellow students and many friends throughout Oklahoma.

Special thanks are due my wife, Willetta, for her help in reading and typing the manuscript, and in the field work.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

THE COMPARATIVE ECOLOGY OF TWO WATER SNAKES, *NATRIX RHOMBIFERA* AND *NATRIX ERYTHROGASTER*, IN OKLAHOMA

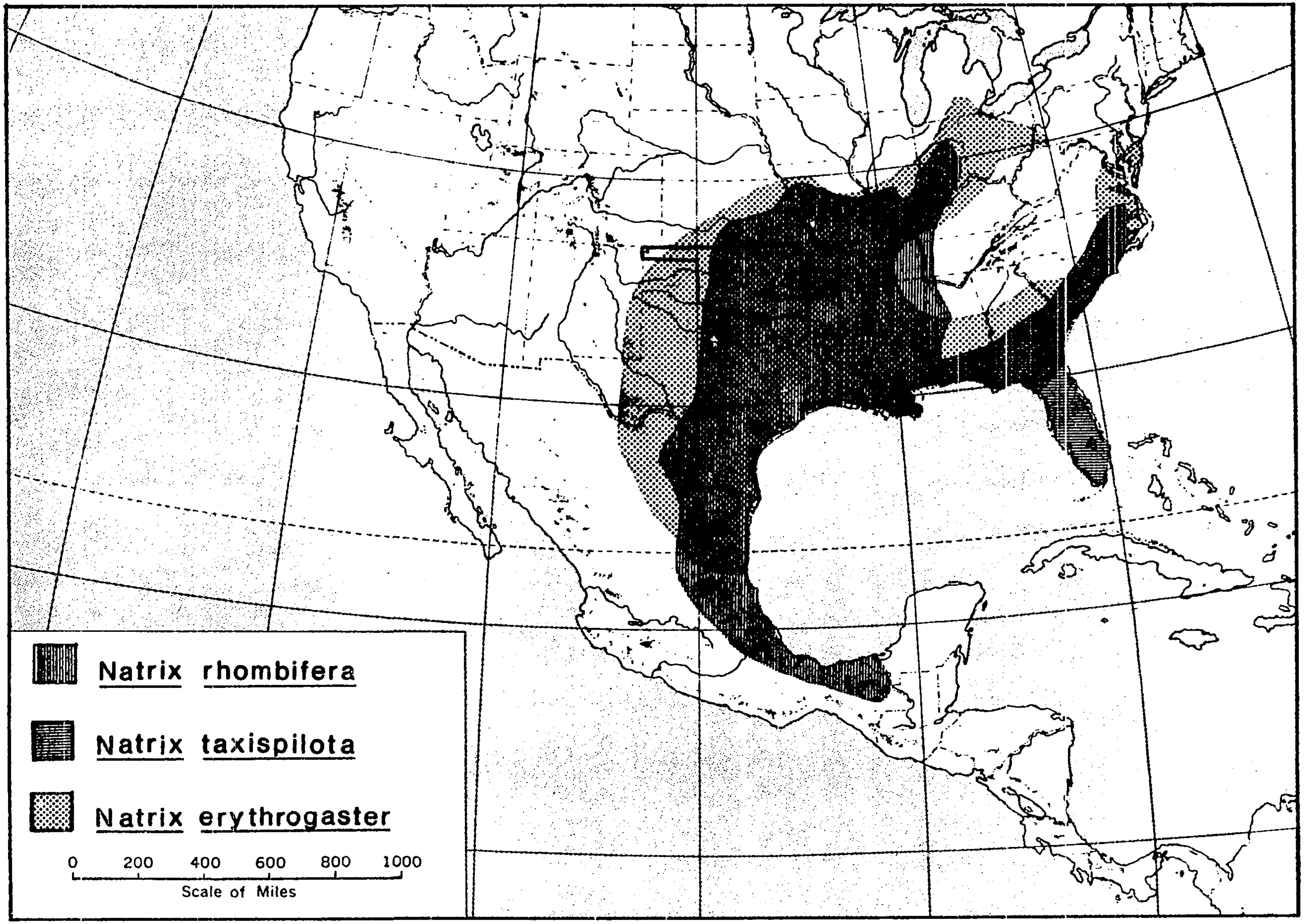
CHAPTER I

INTRODUCTION

The term, "ecological niche" is commonly defined by ecologists as the role of the organism in the ecosystem. Elton (1939), in 1927, was the first to use "niche" in this functional sense. Gause (1934), working with protozoa, had shown that two closely related species cannot occupy the same culture. This led to the competitive exclusion principle, which, put into its simplest form, states that "Complete competitors cannot coexist" (Hardin, 1960). This implies that two species cannot occupy the same ecological niche. To do so would result in competition, ending, according to the principle, with the elimination of one of the two species.

In Oklahoma seven forms of water snakes of the genus *Natrix* are known to occur. Two of these, the diamond-backed water snake (*Natrix rhombifera*) and the plain-bellied water snake (*Natrix erythrogaster*), are sympatric over much of their geographic range (Figure 1). *Natrix erythrogaster* ranges from Delaware in the east to eastern New Mexico in the west (Conant, 1955), thus ranging farther east and farther west

Figure 1. Geographic range of *Natrix rhombifera*, *Natrix taxispilota*, and *Natrix erythrogaster*. After Conant (1958); Smith (1956); Smith and Taylor (1945); and Wright and Wright (1957).


Natrix rhombifera
Natrix taxispilota
Natrix erythrogaster
0 200 400 600 800 1000
Scale of Miles

than does N. rhombifera. The former species ranges also farther north than does the latter (Figure 1). In altitudinal distribution N. rhombifera ranges from sea level to 2,000 feet (Wright and Wright, 1957). Natrix erythrogaster ranges from sea level to 6,700 feet in Mexico (Stebbins, 1966).

The range of N. erythrogaster shown in Figure 1 includes four subspecies, two of which occur in Oklahoma. Natrix erythrogaster transversa (Hallowell) occurs over most of the state and N. e. flavigaster Conant occurs in the southeastern part of the state. For the purpose of the present study, however, these will not be differentiated and will both be referred to as Natrix erythrogaster, for in southeastern Oklahoma these two forms are difficult to distinguish due to apparent interbreeding (Conant, 1949).

Natrix rhombifera is represented by two subspecies in Figure 1, one of which, Natrix rhombifera rhombifera (Hallowell), occurs in Oklahoma. The geographic range of N. taxispilota is illustrated in Figure 1 because Cliburn (1956) presents evidence to show that N. rhombifera can be regarded as a subspecies of N. taxispilota. If this is so the geographic distributions of N. taxispilota and N. erythrogaster are quite similar. However in the present study the writer retains the taxonomy given by Wright and Wright (1957) and by Conant (1958), maintaining the usage of "Natrix rhombifera".

Both N. rhombifera and N. erythrogaster are commonly observed in the same lake or pond. According to the competitive exclusion principle, these two species, in order to coexist must occupy different ecological niches. There must be some degree of ecological differentiation in order to reduce competition between the two species. The possibility exists, of course, that these two species are competing and their existence together is on a temporary basis only; however it is more probable that differences in niche requirements exist, lessening competition and permitting them to occupy the same general habitat.

There has been a limited amount of research carried out on the ecology or on some aspect of the ecology of each of these two species (Cagle, 1937; Diener, 1957; Laughlin, 1959; Greding, 1964; Sisk and McCoy, 1964; Bowers, 1966), however to the writer's knowledge, no comparative study of these two snakes has been undertaken.

To determine the complete ecological niche of an animal would be impractical as our techniques are insufficiently sophisticated to determine the more subtle aspects of the ecological niche. With this in mind, it is the purpose of the present study to determine the ecological separation, if such exists, between these two species where they occur in the same lakes or ponds in Oklahoma.

CHAPTER II

METHODS

The Study Areas

An attempt was made to select study areas that were relatively free from human disturbance. Areas in the vicinity of Norman, Oklahoma, were preferred but excursions were also made in search of study areas elsewhere in the state. Data were collected on snakes encountered during these excursions.

The choice of study areas was governed primarily by accessibility and by abundance of snakes. Three main study areas were selected. Two of these were in Cleveland County; Hospital Lake in Norman, and Smith Lake in the Lexington Game Management Area. The third, in McCurtain County, was a lake in the Kulli Recreation Area in the Oachita National Forest, southeast of Idabel. Other areas studied were three ponds near Wanette, Pottawatomie County, and to a lesser extent, two lakes on Central State Hospital property on 24th Avenue East in Norman.

Hospital Lake is located in the northeast quarter of Section 20, Township 9 North, Range 2 West, Norman Quadrangle. The lake is old, and when full covers 14 acres. In the summer of 1965, when this study was begun, the water level was very low. A gradual increase in the level has occurred, the lake attaining its highest level early in the summer of 1969. The earthen dam is located at the west end of the lake and is covered with many rocks and concrete blocks. The dam cover is grassy, with thickets of Prunus angustifolia, and is bordered at the water's edge with saplings of Salix nigra and Populus deltoides, with these species actually standing in the water in the summer of 1969. At the east end of the lake, particularly in the areas designated by the writer as the northeast arm and the east arm, are more groves of Salix and Populus saplings. The remainder of the shoreline is mainly grassy or bare soil.

Twenty to 30 feet east of the lake is a smaller lake or pond, 1.5 to 2 acres in area, which will be referred to as the small lake. The earthen dam of this lake is on the northwest side and is faced with many concrete blocks. Mature Salix and Populus trees border the dam as well as much of the shoreline. During high water, a small trickle of water flows from this lake into the larger lake.

Smith Lake is located in the southeast quarter of Section 19, Township 7 North, Range 1 East, Eason Quadrangle. This lake, originally constructed about 1935, became silted in and was drained and completely dry for several years. The present lake, which is 7 acres in area when full, was rebuilt in 1956. In 1965 and 1966 the water level was relatively constant, very low in 1967 and very high in 1968 and 1969. The earthen dam, at the south end of the lake, is faced with sandstone rocks. Mature trees, mainly Salix, with some Ulmus and Populus, border the dam. At the north end of the lake lies oak forest, with Salix near the water's edge. The remainder of the shoreline is mainly open with mixed areas of grass and bare soil.

Kulli Lake is located in the southeast quarter of Section 30, Township 8 South, Range 25 East, Haworth Quadrangle. The lake was constructed in 1944 and when full is 7 acres in area. In 1965 the water level was very low but increased every year until the summer of 1968, when the level was exceedingly high, flooding several picnic tables. The level remained high in 1969. The earthen dam, at the west end of the lake, is covered with grass. Whereas most of the shoreline is grassy with areas of bare soil, woodland surrounds the east end of the lake, the shore here bordered with high grass. In the picnic and camping areas, which constitute most of the shoreline, the grass is kept short by mowing.

Each of the three ponds near Wanette, Pottawatomie County, is approximately 1.5 to 2 acres in area. One, designated by the writer as the Stone Dam Pond, lies in the northeast quarter of Section 19, Township 6 North, Range 3 East, Wanette Quadrangle. The dam is of earth, but is faced with stone forming a vertical wall affording many crevices in which snakes may seclude themselves. Mature _Salix_, _Celtis_, _Ulmus_, and _Juniperus_ trees border the dam, which is located at the south end of the pond. The remainder of the shore is primarily grassy or bare soil.

About 20 feet to the east of this pond lies another, designated as the Small Pond, with the dam at the west end and running at right angles to the stone dam. A few mature _Salix_ trees border the dam, th rest of the shore being grassy or of bare soil.

In the northwest quarter of Section 19 lies the third pond, Snag Pond, so called because of the many standing dead trees in the water. An earthen dam, grass-covered and with a few *Salix* trees, bounds the west end of the pond. Along the entire south shore is oak woodland and along the north shore are a few *Salix* trees. The remainder of the shore is grassy.

In Norman, on 24th Avenue East are two small lakes that were studied to a lesser extent. The east lake, 6 acres in area, lies on the east side of the road, in the northwest quarter of Section 27, Township 9 North, Range 2 West. The lake was constructed in 1952 or 1953. At the east end is the earthen dam. The west end is very shallow and weedy, with a few trees. The remainder of the shore is a mixture of grassy areas and bare soil.

The west lake lies to the west of the road in the northwest quarter of Section 28. This lake is 13 acres in area and was constructed in 1953 or 1954. An earthen dam impounds the lake on the east end and concrete blocks face the dam. There are a few trees along the dam and a few scattered near the southwest end of the lake. The remainder of the shore is grassy or of bare soil.

Where creeks were encountered, they were investigated but not extensively.

Capture and Processing of Snakes

Methods of Capture

Early in the study an attempt was made at trapping using the type of funnel trap designed by Fitch (1960). This attempt was made on private property five miles east of Norman and was discontinued after the traps were vandalized. It was assumed that if traps were vandalized on private property trapping would be impractical in more public areas such as Hospital Lake.

Snakes were found by searching along the shores of the lakes and ponds and by turning over driftwood. Pillstrom Tongs (Pillstrom, 1954) were used quite satisfactorily in catching the snakes, even while moving and in the water. Hospital Lake was patrolled during daylight hours, with some night excursions in 1968. Smith Lake was patrolled mainly at night with occasional day trips. Kulli Lake was patrolled almost entirely at night. The Wanette ponds were patrolled during the day only and the lakes on 24th Avenue in Norman were patrolled both day and night.

Processing

At the point of each capture the air temperature at a height of 3 feet was taken as well as the temperature of the substrate on which the snake was lying or the water temperature if appropriate. Also, a number of cloacal temperatures were taken, particularly in 1968 and 1969. Earlier in the study, when several snakes were collected during a night patrol around the shore they were put into a bag together and processed later and then released all at once at the same location. Cloacal temperatures were not taken under these conditions. By this method larger numbers could be collected during an evening. Later it was felt that better data could be obtained by processing the snakes as they were captured and releasing them at once although fewer could be taken in an evening by this latter method.

Snout-vent and tail length were recorded for each snake. Sexing was done after the method of Schaefer (1934) and marking after the method of Blanchard and Finster (1933). Before weighing, the snake was forced to regurgitate any food. Snakes were weighed in a pre-weighed cloth bag using a spring scale. Gravid females were recorded. Ecdysis, scars or other unusual marks such as stub tails were noted also.

The activity of the snake at the time of capture as well as its behaviour on release was recorded.

Sight Records

Frequently snakes were seen that could not be approached, or attempts to capture failed. All ecological data were recorded for these sight records and the snake's activity was noted also.

CHAPTER III

RESULTS

Numbers

The total number of snakes of the genus *Natrix* captured or seen, including recaptures, during the course of the study was 527, of which 306 were *Natrix rhombifera*, 164 were *N. erythrogaster*, 48 *N. grahami*, 7 *N. sipedon confluens*, and 2 *N. s. pleuralis*. Overall, *N. rhombifera* appeared to be twice as abundant as *N. erythrogaster*. Brown (1950) states that *N. e. transversa* is one of the most common water snakes to be found in Texas, and that *N. rhombifera* is about as plentiful as this species throughout the eastern half of the state. Diener (1957) found *N. erythrogaster* to be twice as abundant as *N. rhombifera* in Kansas. Greding (1964) collected 14 *N. e. flavigaster* to 20 *N. rhombifera* in Hunt County, Texas. Strecker (1915) refers to *Tropidonotus sipedon transversus* Hallowell (*N. e. transversa*) as the common water snake of Texas. Cagle (1937) states in his study at Reelfoot Lake, Tennessee, that two thirds of the snakes captured were *N. rhombifera*. Of 37 snakes collected in Lake McAlester, Pittsburg County, Oklahoma, 23 were *N. taxispilota* (*N. rhombifera*) and 4 were *N. erythrogaster* (Laughlin 1959). It appears, from the results of the present study, that *N. rhombifera* is the most abundant water snake in Oklahoma.

In Table I the numbers of the two species are presented according to study area. These data represent all records for the five years of the study. Since the amount of time spent in each of the study areas varied, the table serves to provide an indication of the relative abundance of the two species in each study area only. Table I reveals that Natrix rhombifera is the most abundant snake in every area except the larger of the two Hospital Lakes. If these two lakes are combined as one study area, which is expedient in that the snakes undoubtedly move from one lake to the other due to their close proximity, Natrix rhombifera is more numerous but the ratio is smaller.

The largest sample taken for any one day, August 6, 1966, at the Kulli Recreation Area in McCurtain County, including sight records, involved 51 snakes, 41 of which were N. rhombifera, 7 N. erythrogaster, and 3 N. sipedon confluens.

In Table II the relative abundance of the two species is compared in each study area for each year. In the two Hospital Lakes both species occurred in approximately a one-to-one ratio in 1965. N. erythrogaster was most abundant in the following two years and then N. rhombifera became more numerous. In Smith Lake the trend was reversed, while in Kulli Lake N. rhombifera remained the most abundant species throughout the course of the study. These phenomena will be discussed below.

Size, Growth and Longevity

Size

Comparative data on the size of the adult snakes is presented

Table I. Numbers of snakes captured (including recaptures) and seen only, according to locality and sex.

Locality	*Natrix rhombifera*					*Natrix erythrogaster*				
	seen	M	F	T	%	seen	M	F	T	%
Hospital L.:										
large	33	16	8	57	47.9	27	10	27	64	52.1
small	21	4	1	26	70.3	9	-	2	11	29.7
Smith L.:	27	11	7	45	63.4	15	7	4	26	36.6
Wanette area:										
Stone Dam	14	1	1	16	51.6	15	-	-	15	48.4
Small	8	1	-	9	75.0	2	1	-	3	25.0
Snag	1	-	-	1	20.0	4	-	-	4	80.0
Kulli L.:	38	31	37	106	84.1	7	4	9	20	15.9
Misc.:	23	10	13	46	68.7	6	7	8	21	31.3
TOTALS	165	74	67	306	65.1	85	29	50	164	34.9

Table II. Numbers of *Natrix rhombifera* (*N.r.*) and *Natrix erythrogaster* (*N.e.*) seen or captured (including recaptures) in different study areas according to year.

	1965				1966				1967				1968				1969			
	N.r.	%	*N.e.*	%	*N.r.*	%	*N.e.*	%	*N.r.*	%	*N.e.*	%	*N.r.*	%	*N.e.*	%	*N.r.*	%	*N.e.*	%
Hospital L.																				
large	7	50.0	7	50.0	7	41.2	10	58.8	1	6.7	14	93.3	29	55.8	23	44.2	13	56.5	10	43.5
small	-	-	1		-	-	-	-	1	50.0	1	50.0	7	63.6	4	36.4	18	78.3	5	21.7
Total	7	46.7	8	53.3	7	41.2	10	58.8	2	11.8	15	88.2	36	57.1	27	42.9	31	67.4	15	32.6
Smith L.	26	81.3	6	18.7	14	53.8	12	46.2	3	50.0	3	50.0	1	50.0	1	50.0	1	20.0	4	80.0
Wanette																				
Stone Dam					5	83.3	1	16.7	4		-	-	1		-	-	6	30.0	14	70.0
Small P.		not studied					dry		3		-	-	2		-	-	4	57.1	3	42.9
Snag P.					-	-	1		1	33.3	2	66.7	-	-	-	-	-		1	
Kulli L.	7	77.8	2	22.2	57	85.1	10	14.9	16	80.0	4	20.0	8	80.0	2	20.0	19	90.5	2	9.5

in Table III. The two species are of comparable size, the females in both tending to be larger.

According to Wright and Wright (1957) male N. rhombifera breed at 72.2 to 119 cm and the females at 82 to 145 cm. It is assumed that these figures represent total length. It is the preference of the writer to use snout-vent length as a basis for comparison of size and growth since a great many of the snakes examined during the course of the study had stub tails.

Betz (1963) states that females require at least 2.5 years to attain sexual maturity. Data obtained in the present study indicate that at this age the females are 63 to 68 cm in snout-vent length (Figure 2).

Wright and Wright (1957) give the breeding size of N. erythrogaster males and females as 72.4 to 103.7 and 86.5 to 133.5 cm respectively.

In Table IV, size data are presented for newborn snakes. There appears to be little difference in length between the young of either species. Data obtained in the present study indicate no difference in size between the sexes, however Franklin (1944) found that in Natrix taxispilota, newborn males tend to be larger than females. He points out that this trend is reversed in the adults. This supports the above observation made by the writer.

In Figure 4 both sexes of the two species are compared with respect to size classes, in 5 cm intervals. The histograms for the females of both species are somewhat similar in that there is a preponderance of individuals in the smaller size classes. The males also

Table III. Size of adult water snakes (*Natrix*). Total length is indicated by T; snout-vent length by s.

Species	No.	Sex	Range (cm)	Mean		Authority
N. rhombifera			76.2-121.9		T	Conant (1958)
			81.3-170.2		T	Wright and Wright (1957)
	27	M	61.5-88.4	72.1	s	Present study
	17	M	82.2-108.3	93.1	T	
	23	F	62.7-118.9	86.4	s	
	16	F	79.0-146.9	106.9	T	
N. erythrogaster			76.2-121.9		T	Conant (1958)
			45.7-171.5		T	Wright and Wright (1957)
	12	M	55.5-82.8	72.2	s	Present study
	9	M	71.9-106.8	92.9	T	
	12	F	66.5-95.6	84.5	s	
	10	F	84.0-121.0	103.5	T	

Figure 2. *Natrix rhombifera*. Snout-vent length plotted against month of capture. The time of capture is plotted to the nearest two weeks. Circles represent females and dots, males. The vertical line represents the range and the crossbar the mean of 60 newborn young. The means of the males and females were the same.

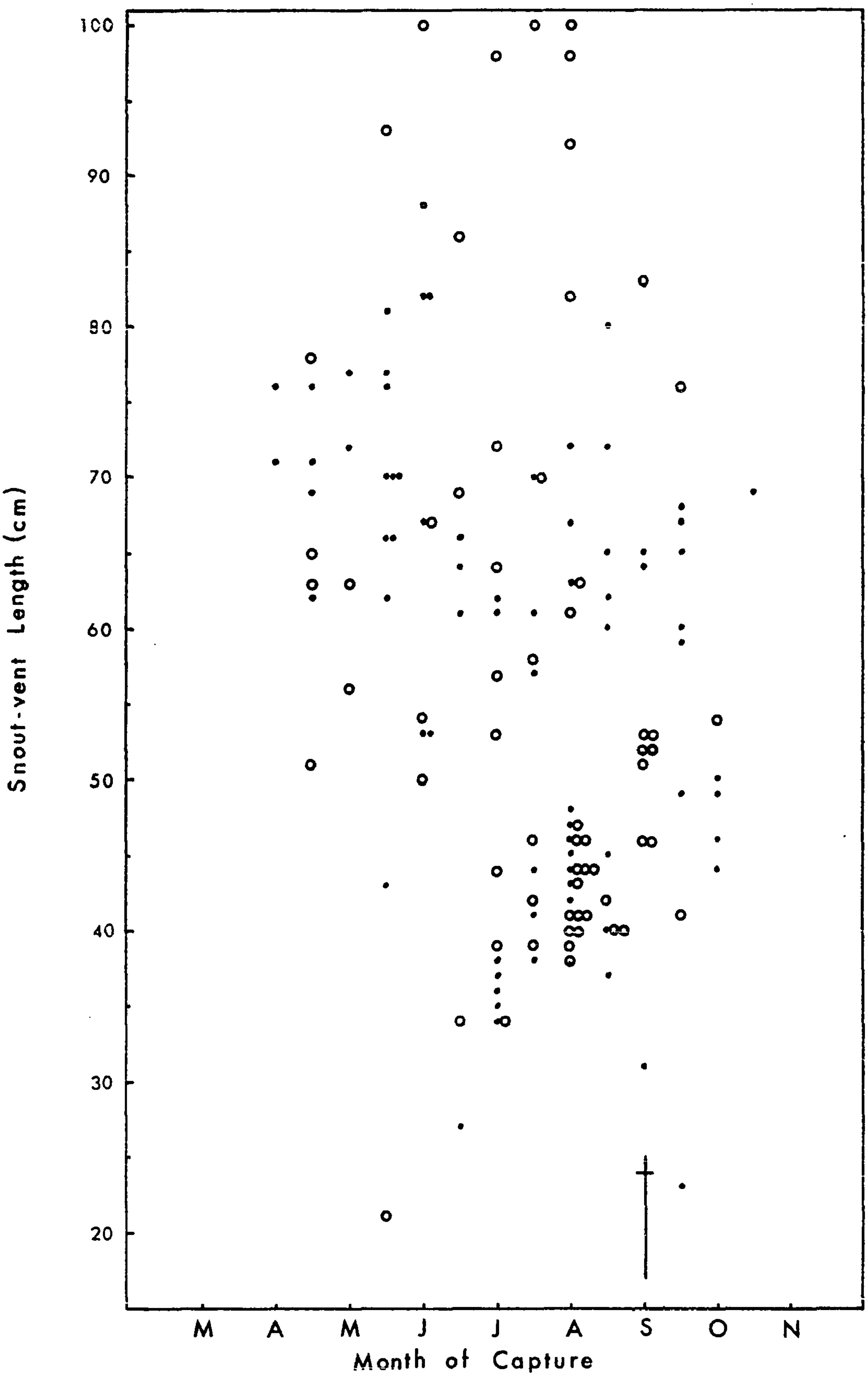

100
90
80
70
60
50
40
30
20
Snout-vent Length (cm)
M
A
M
J
J
A
S
O
N
Month of Capture

Figure 3. _Natrix erythrogaster_. Snout-vent length plotted against month of capture. The time of capture is plotted to the nearest two weeks. Circles represent females and dots, males.

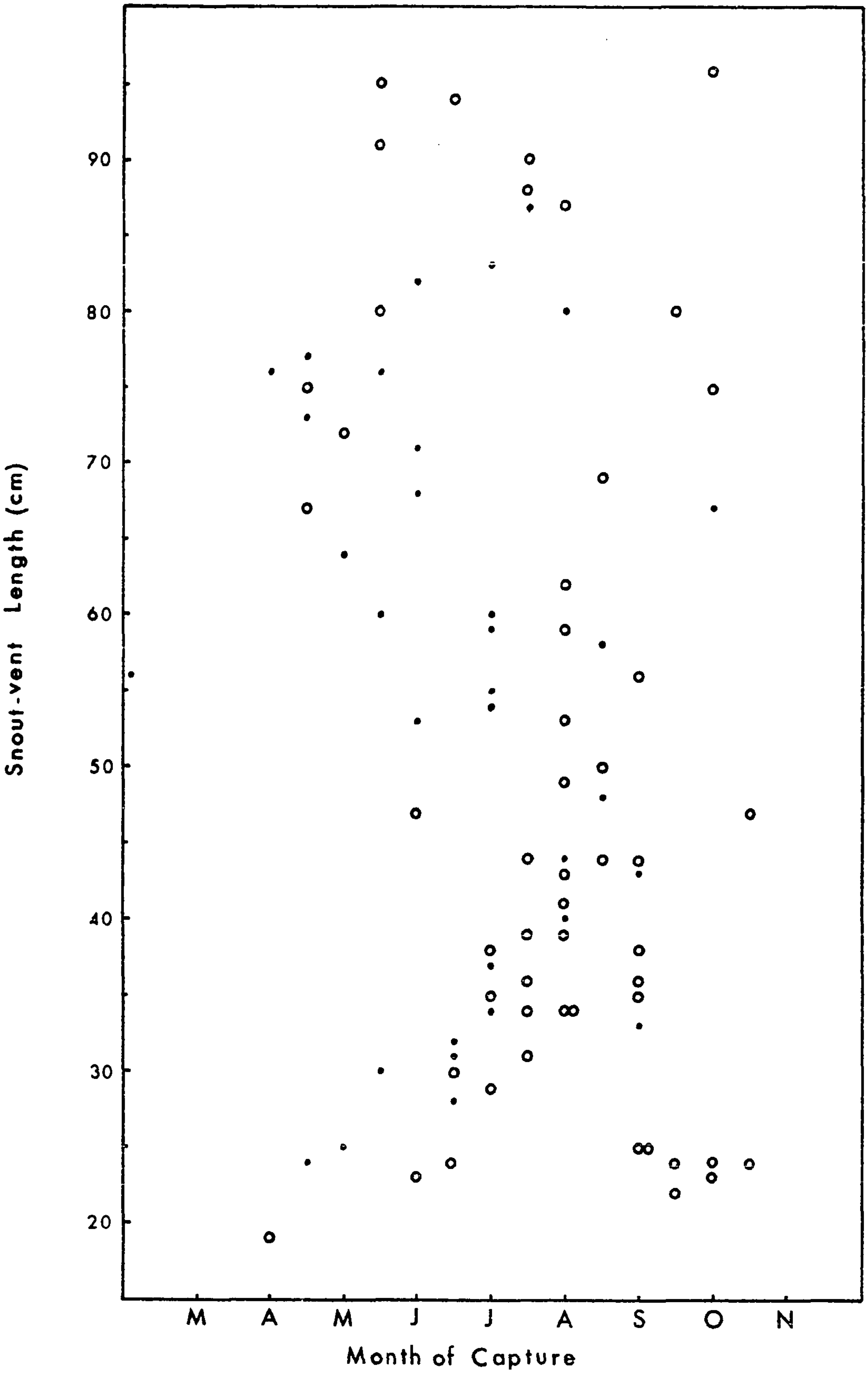

Snout-vent Length (cm)
90
80
70
60
50
40
30
20
M
A
M
J
J
A
S
O
N
Month of Capture

Table IV. Size of newborn water snakes (Natrix). Total length is indicated by T; snout-vent length by s.

Species	No.	Sex	Range (cm)	Mean		Authority
N. rhombifera	34	F	16.5-25.2	23.6	s	Present study
	33	F	27.5-32.4	30.6	T	
	26	M	17.0-25.3	23.9	s	
	26	M	22.8-33.4	31.5	T	
	25		20.3-24.6	22.7	T	Kennedy (1964)
N. taxispilota	21	F	17.9-24.6	23.85		Franklin (1944)
	13	M	23.8-25.9	25.18		
	21	F	23.6-25.2	24.25		
	16	M	24.6-25.8	25.17		
	22	F	19.0-25.1	24.11		
	18	M	20.0-26.8	25.06		
N. e. transversa	7	F	22.3-24.8	23.8	s	Present study
	7	F	28.7-32.8	31.3	T	
			19.0-25.3		T	Anderson (1965)
			21.9-26.4			Conant (1933)

show some similarity in that there are two peaks of distribution, one toward each end of the histogram. The females exhibit a greater size range than do the males of either species, with *N. rhombifera* females showing the greatest. Overall, these histograms reveal no great difference between the two species.

In Figures 5, 6, and 7 comparisons are made between weight and body length. In the males no difference can be noted visually between the two species in the relationship between weight and length. In the females, however, *N. rhombifera* shows a tendency toward a greater weight for a given size. *Natrix rhombifera* females tend to be heavier than the males, whereas there appears to be little difference in weight between the sexes in *N. erythrogaster*. Carpenter (1953a) found no difference between sexes in *Thamnophis sirtalis* and *T. butleri* regarding the length-weight relationship.

Growth

When snout-vent length is plotted against date of capture (Figures 2 and 3), snakes of the same age tend to be grouped. These age-size groups are discernible up to about 2 years of age. Beyond this age, due to differential growth rates, the pattern tends to become scattered due to overlapping age groups.

Growth curves were obtained by plotting the mean snout-vent length for each size group against each growing month (Figures 8 and 9). Due to a greater number of captures, the growth curve of *N. rhombifera* can be traced farther than that of *N. erythrogaster*, 2 years and 10 months, and 2 years respectively.

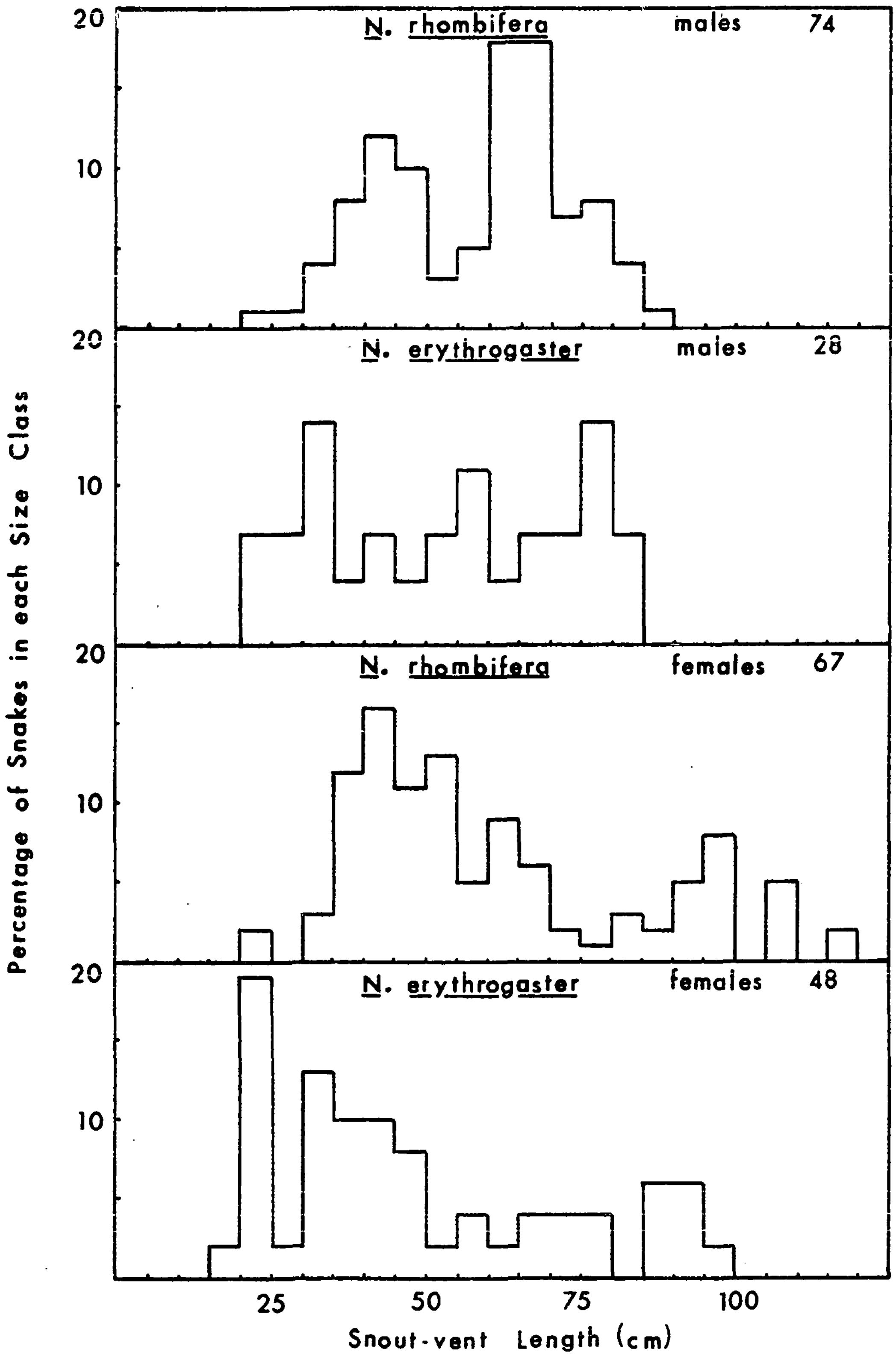


Figure 4. Size distribution in Natrix rhombifera and Natrix erythrogaster. Includes snakes from all study areas.

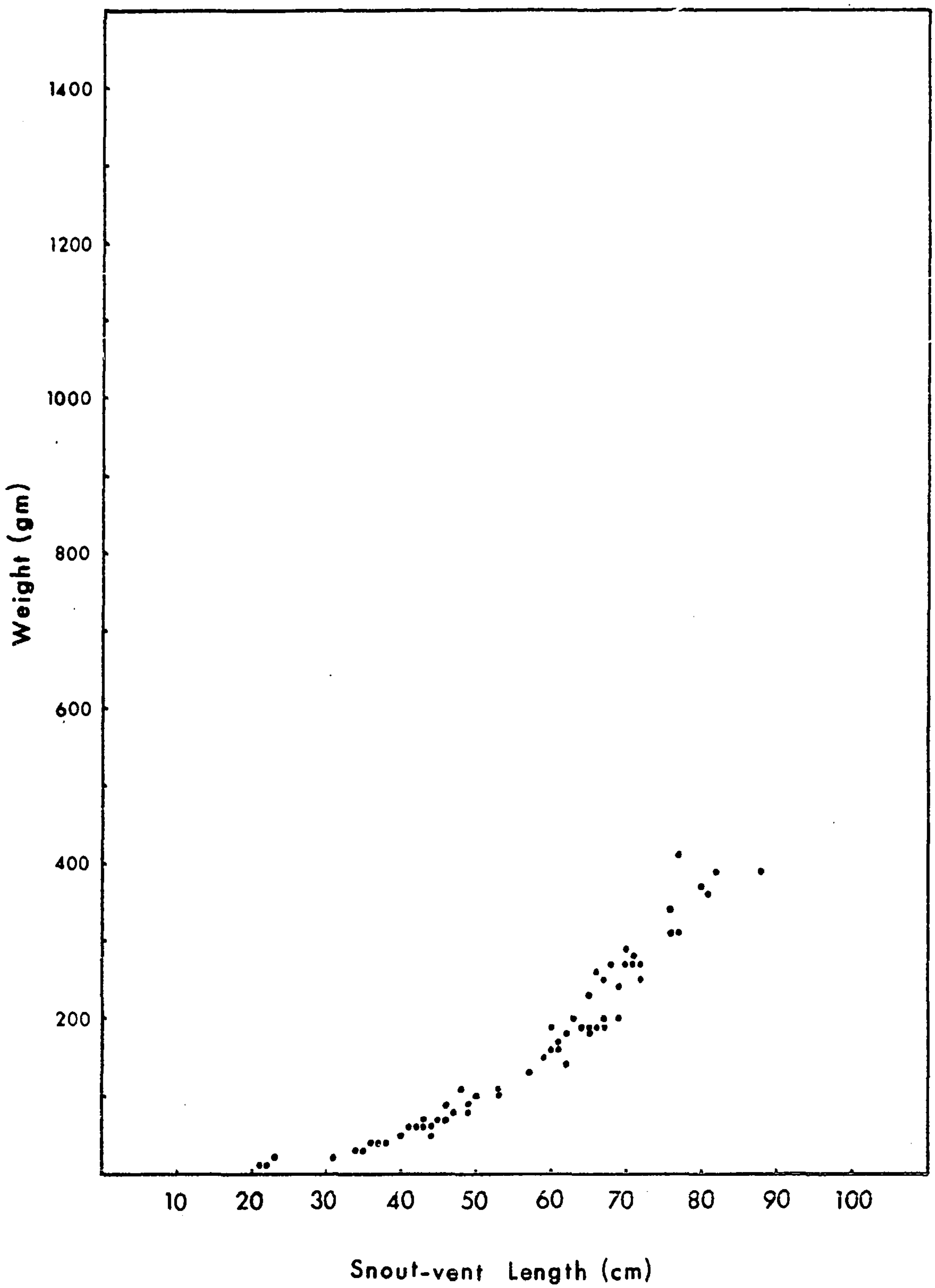


Figure 5. Natrix rhombifera males. Weight-length relationship.

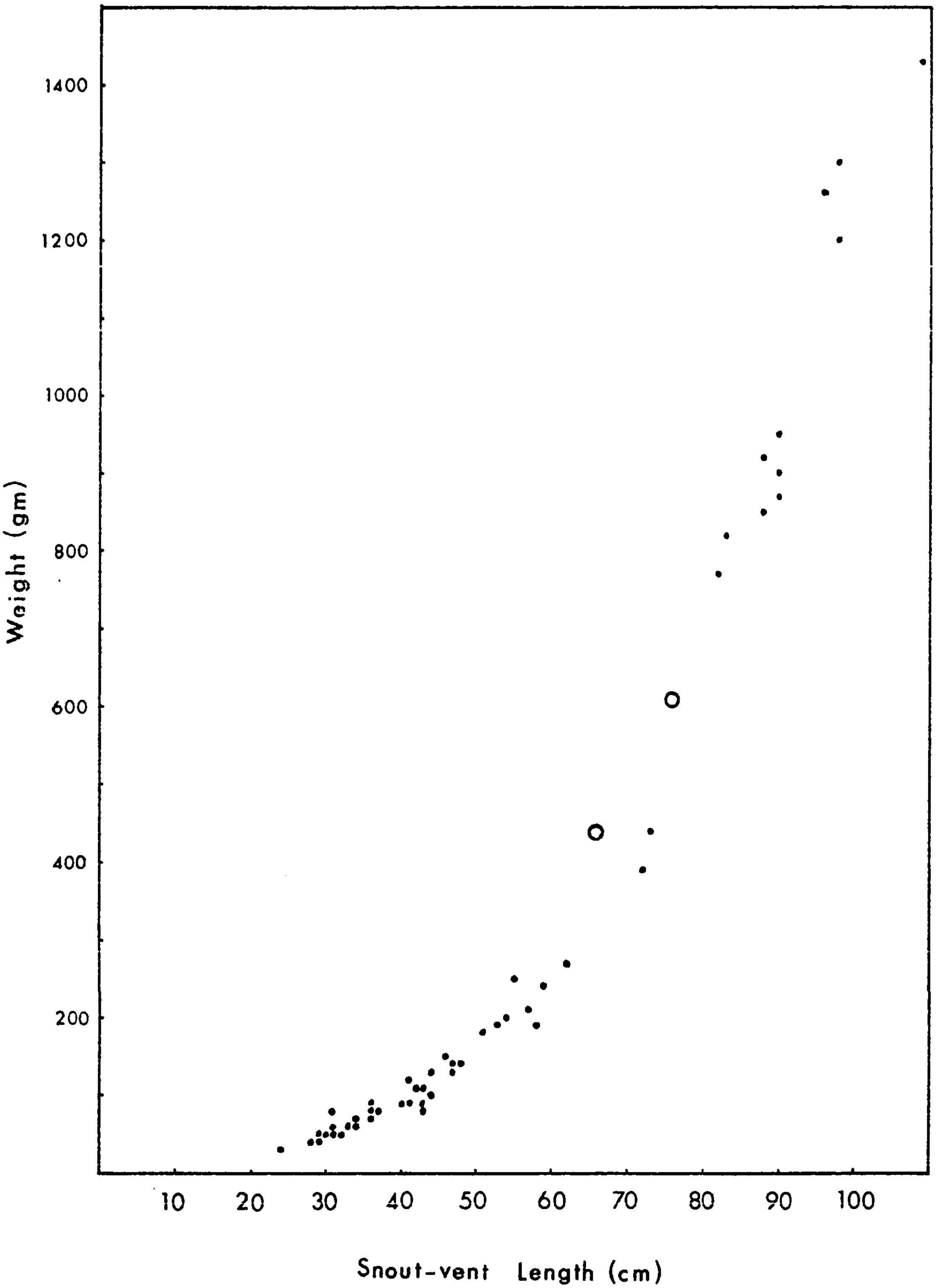


Figure 6. Natrix rhombifera females. Weight-length relationship. Circles represent gravid females.

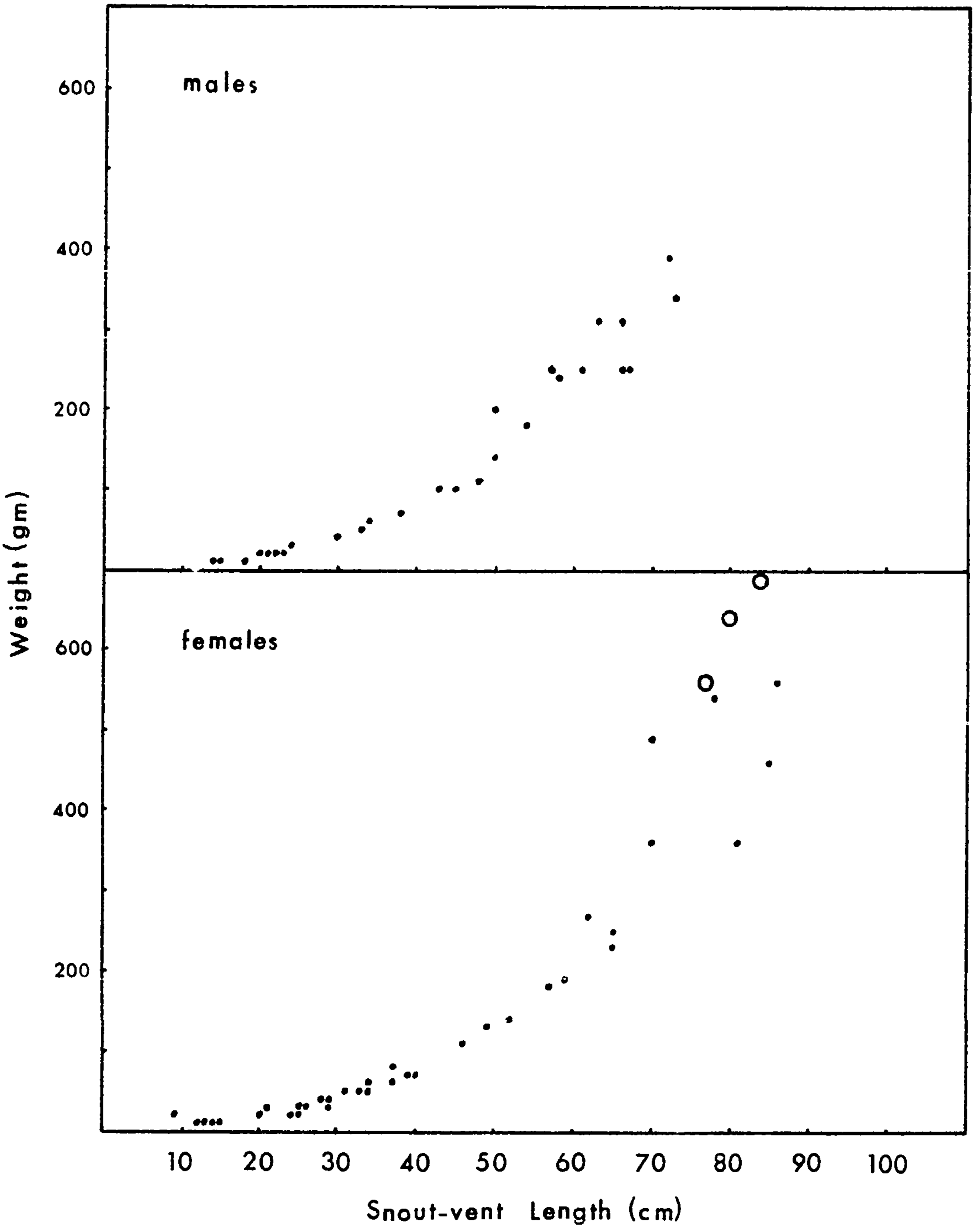


Figure 7. Natrix erythrogaster males and females. Weight-length relationship. Circles represent gravid females.

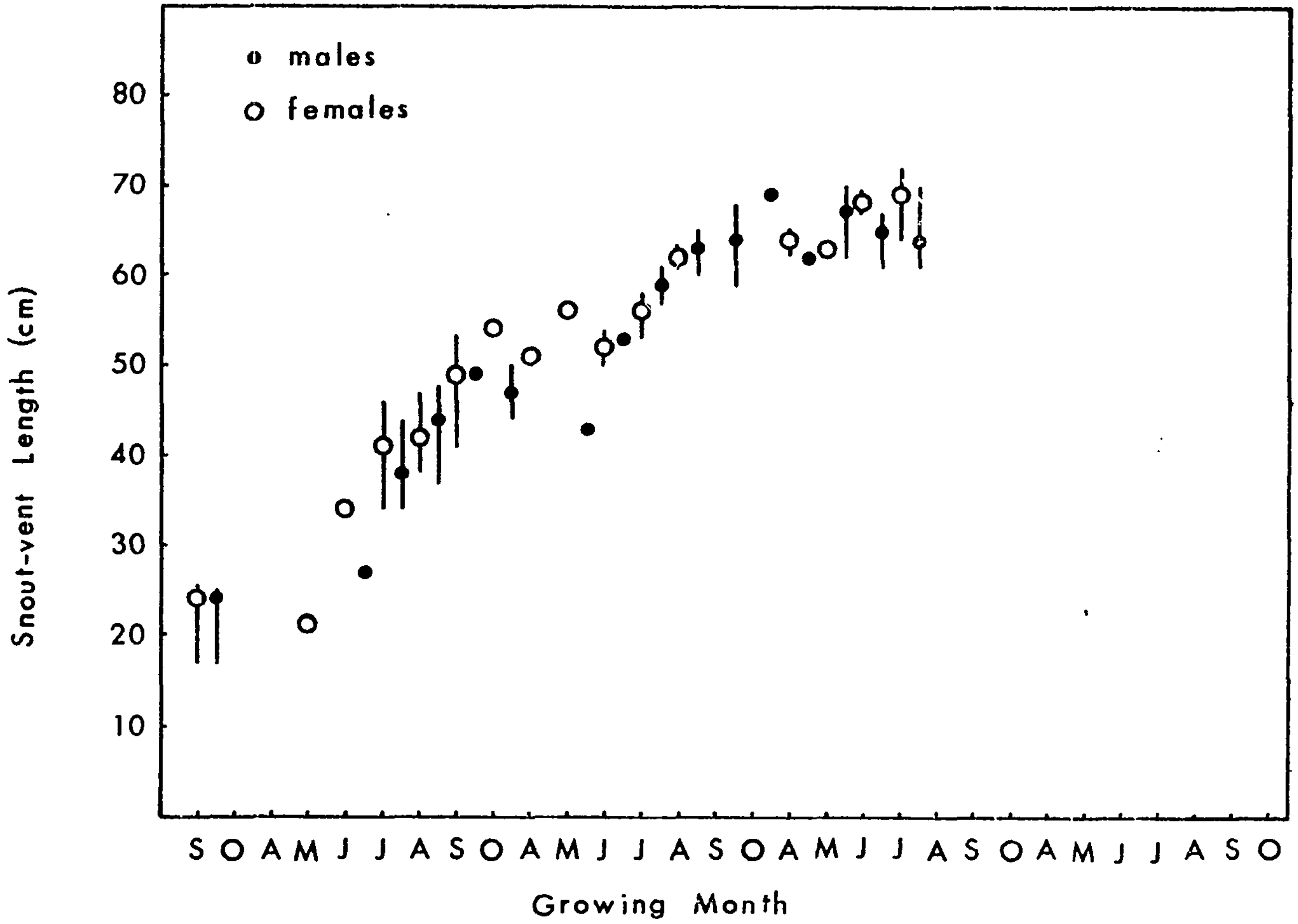


Figure 8. Mean snout-vent length plotted against month of capture for <u>Natrix rhombifera</u>. The vertical lines represent range.

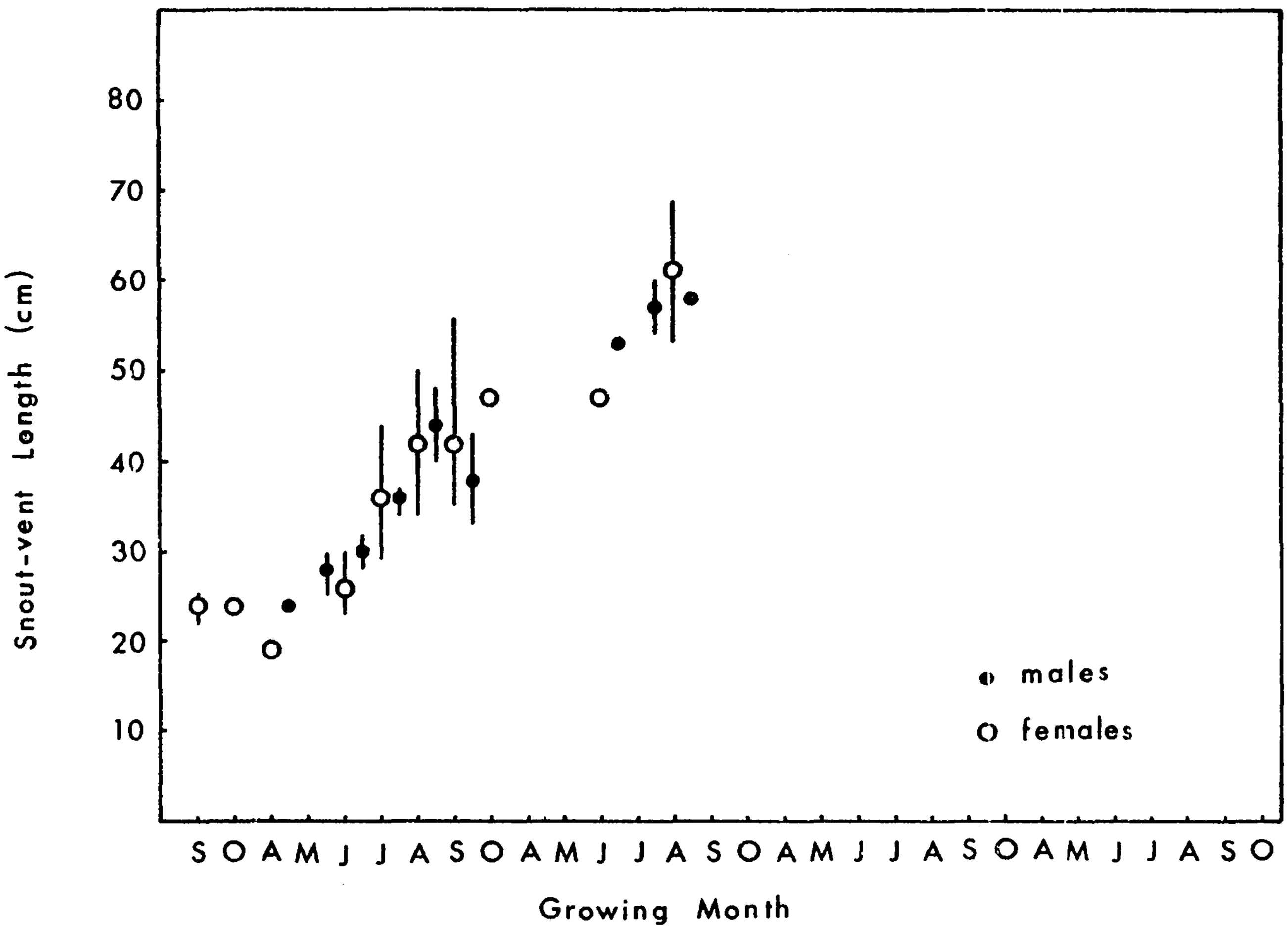


Figure 9. Mean snout-vent length plotted against month of capture for *Natrix erythrogaster*. The vertical lines represent range.

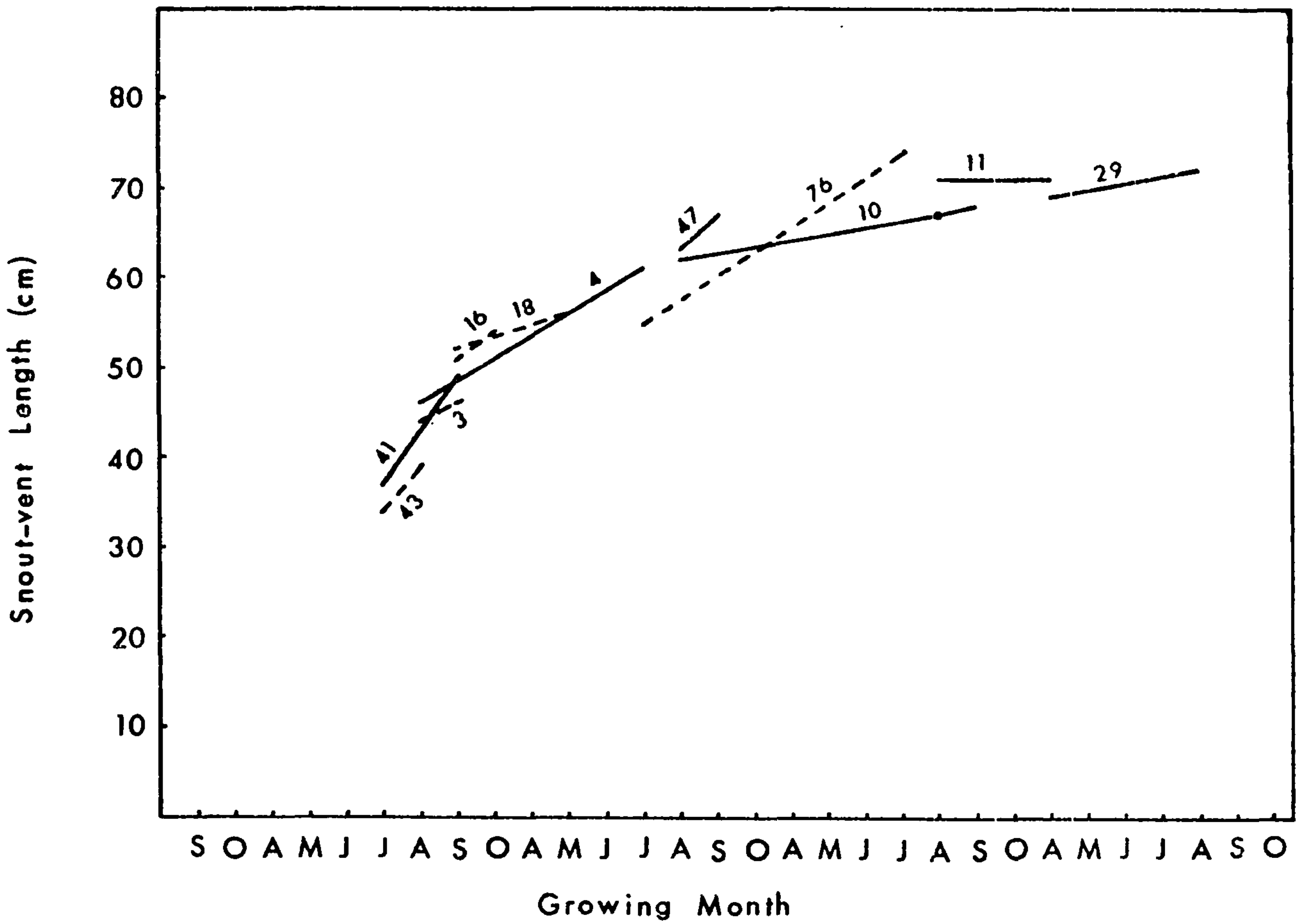


Figure 10. Natrix rhombifera. Growth, based on recaptures. The dashed lines represent females, and the solid lines males. The numbers are identification numbers assigned to individual snakes.

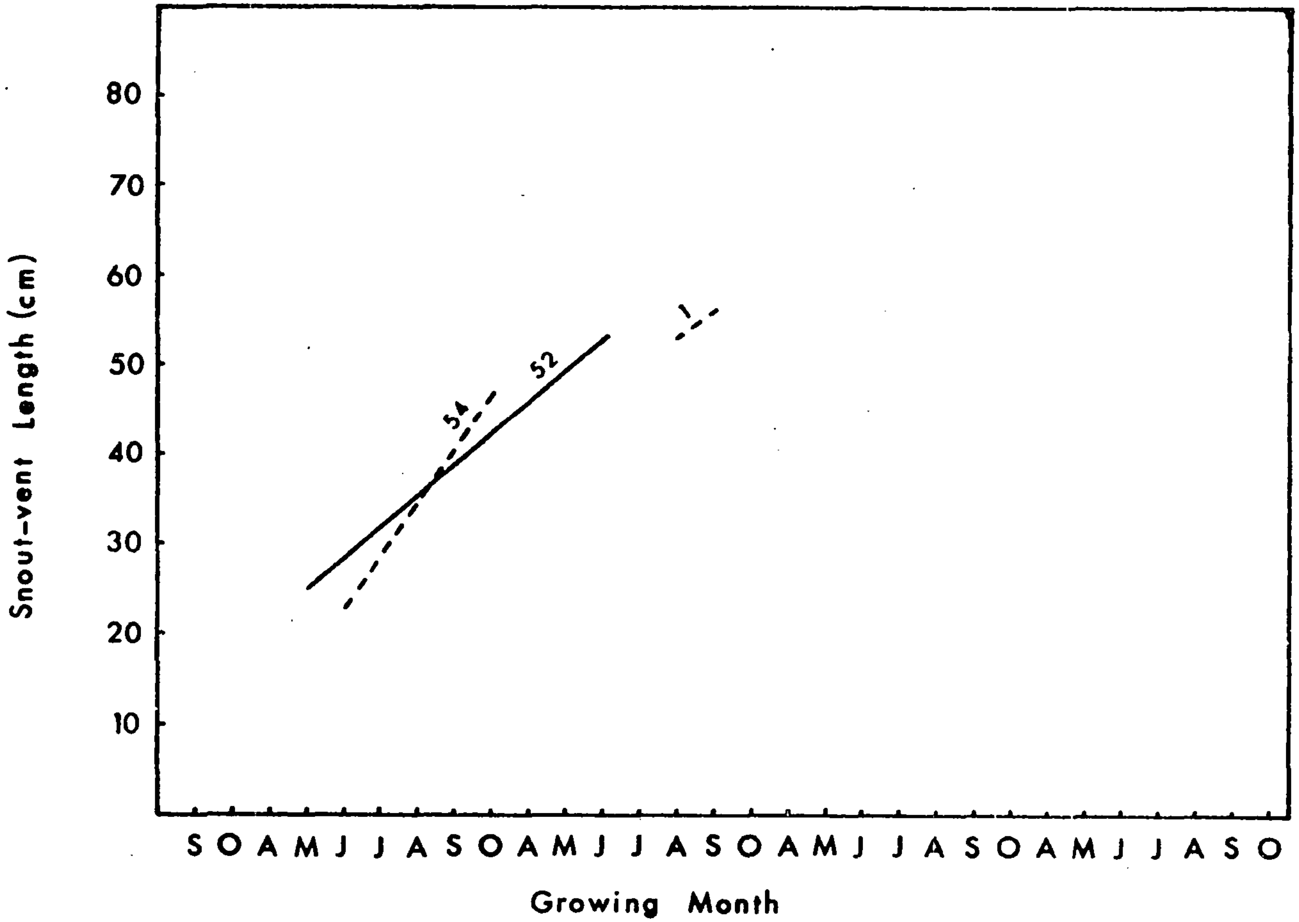


Figure 11. Natrix erythrogaster. Growth, based on recaptures. The dashed lines represent females, and the solid lines males. The numbers are identification numbers assigned to individual snakes.

These growth curves are supported by individual growth records of recaptured snakes (Figures 10 and 11) arranged in order of increasing age. These growth curves are very similar to those presented by Fukada (1961), for several species in Japan.

Numerical values for growth rates, expressed in centimeters per day, are presented in Table V. It should be pointed out, however, that recaptures may not provide entirely accurate data on growth rates in that some snakes are prone to stunting due to the effects of handling. Fitch (1949) found this to be so in Crotalus viridis oreganus, the evidence being mainly in weight losses. In the present study weight loss was evident in some males. It is interesting to note that Fickess (1962) observed histological changes and increase in weight of the adrenals in N. rhombifera subjected to stress.

Comparing the average growth rates on the basis of percent increase in body length per day with the age class (Table VI) it is evident that the younger snakes of both sexes tend to grow more rapidly than do the older snakes. Although the evidence is very scanty, the same trend can be seen in both species.

There is no difference in growth rates between males and females evident in Figures 8, 9, 10, and 11. However the numerical data (Table VI) present some evidence, though scanty, that the growth rate of females is greater than that for males. The mean growth rate for 10 males is .11 percent per day and that for 6 females is .18 percent per day. It was noted earlier that N. rhombifera females tended to grow larger than males, hence one would expect their growth rate to be greater. It may be that the growth rates are similar up to 3

Table V. Growth rates, based on recaptures. The growth period is set arbitrarily from April to October inclusive. Last column of figures: % snout-vent length per day, based on original length.

Date Capture	Recapt.	Sex	Approx. Age (yr.)	Growth Period (days)	Length* L_1 (cm)	L_2	Incr.	cm/d	%/d
Natrix rhombifera									
11/8/65	6/7/66	M	1	178	46.1	60.8	14.7	.083	.18
21/8/65	16/4/66	M	2+	87	71.7	71.2	-	-	-
21/8/65	6/8/66	M	2	199	62.1	66.7	4.6	.023	.04
	17/9/66	M	3	42		68.2	1.5	.036	.05
1/9/65	17/9/66	M	2	16	64.1	64.9	.8	.050	.08
17/9/65	25/9/65	M	2	8	59.1	59.5	.4	.050	.09
16/4/66	6/8/66	M	2+	112	68.6	72.3	3.7	.033	.05
9/7/66	17/9/66	M	1-	70	36.8	48.5	11.7	.167	.45
6/8/66	17/9/66	M	2	42	63.3	67.3	4.0	.095	.15
15/4/69	14/5/69	M	2+	29	76.0	76.8	.8	.028	.04
11/8/65	10/9/65	F	1	30	43.9	45.9	2.0	.067	.15
1/9/65	10/10/65	F	1	39	51.4	54.1	2.7	.069	.13
9/9/65	11/5/66	F	1	93	51.7	56.3	4.6	.049	.10
9/7/66	19/7/67	F	2+	224	97.8	100.3	2.5	.011	.01
9/7/66	6/8/66	F	1-	28	34.3	39.2	4.9	.175	.51
1/7/67	2/7/68	F	2	215	53.0	72.3	19.3	.090	.17
Natrix erythrogaster									
1/5/68	9/6/69	M	1-	253	24.7	52.6	27.9	.110	.45
6/8/65	10/9/65	F	2	35	52.9	55.6	2.7	.077	.15
3/6/68	29/10/68	F	1-	148	22.8	46.9	24.1	.163	.71

*L_1 represents initial length and L_2, the length at recapture.

Table VI. Comparisons of average growth rate, in percent snout-vent length per day, with age.

Species	Sex	Approx. Age (yr.)	No.	%/day (mean)
Natrix rhombifera	M	2+	4	.04
	M	2	4	.09
	M	1 or less	2	.32
	F	2+	1	.01
	F	2	1	.17
	F	1 or less	4	.22
Natrix erythrogaster	M	1-	1	.45
	F	2-	1	.15
	F	1-	1	.71

years of age and diverge after that time. From the data obtained in the present study it was not possible to trace growth curves beyond 3 years. Fitch (1960) found a rather abrupt divergence in the growth of copperheads (Agkistrodon contortrix) beyond 4 years, the males growing faster.

Many authors have observed that the females of the species studied grew at a faster rate than did the males (Carpenter, 1952b: Thamnophis sirtalis, T. sauritus, T. butleri; Fitch, 1963a: Coluber constrictor, 1965: Thamnophis sirtalis; Fukada, 1959: Natrix tigrina tigrina; Heyrend and Call, 1951: Crotalus viridis lutosus; Platt, 1969: Heterodon platyrhinos, H. nasicus; Raney and Roecker, 1947: Natrix septemvittata, N. sipedon sipedon; Volsøe, 1944: Vipera berus). In some species it has been observed that males grow faster than females (Fitch, 1960: Agkistrodon contortrix; Fitch, 1963b: Elaphe obsoleta; Fukada, 1960: Elaphe quadrivirgata; Heyrend and Call, 1951: Masticophis taeniatus taeniatus). Burkett (1966) was unable to note any dimorphism in growth rate in Agkistrodon piscivorus.

Based on Figures 8, 9, 10, and 11, no difference in growth rates is evident between N. rhombifera and N. erythrogaster.

Longevity

Longevity data are obtained mainly from captive snakes. However, marking experiments carried out over a long period, such as that done by Fitch (1949) may give some indication of the life span. It may be expected that snakes in captivity, under optimum conditions would tend to live to a greater age. Fitch's observations of wild rattlesnakes, however, tend to agree with those published by Perkins (1955) and Shaw (1962) for captive snakes.

Mertens (1964) records a longevity of 15 years and 28 days for the offspring of an integrade Natrix natrix astreptophora x schweizeri male and a Natrix tessellata female hatched in captivity. Conant and Hudson (1949) give the longevity of N. e. trasversa as 4 years and 3 months and that of N. e. erythrogaster as 8 years and 10 months. Flower (1925) gives the longevity for 6 N. rhombifera as ranging from 2 years, 8 months and 15 days to 7 years, 7 months and 7 days.

If the growth curve presented in Figure 8 is reasonably accurate, the life span of N. rhombifera must extend considerably beyond 4 years if an adult body length of over 100 cm is to be attained, as was the case for several females encountered in the present study. It is likely that the life spans of these two species are somewhat similar to those of species of similar size as presented by Perkins, and by Shaw, with a life span ranging somewhere between 10 and 20 years.

Reproduction

Sex Ratios

It may at first seem reasonable that the most accurate sex ratios would be obtained by taking a large sample in a particular area during a limited time. However, due to the possibility that one sex may for some reason be more active under a certain set of conditions, more than one such sample would be required, preferably several. In practice, small samples taken in different areas, in sufficient number should reveal the true sex ratio since in a species with a one-to-one sex ratio, the probability of capturing one of either sex would be .5. This method was used in the present study.

In the present study, Natrix rhombifera showed no significant difference between the expected one-to-one male-female ratio and the observed ratio of 74 males to 67 females (Table I). Sixty young N. rhombifera born at the Oklahoma City Zoo had a sex ratio of 34 females to 26 males. There is no significant difference from an expected one-to-one ratio. In N. erythrogaster a sex ratio of 29 males to 50 females differed significantly from an expected one-to-one ratio. This sex ratio is probably an artifact of small sample size.

Mating and Courtship

Very few observations were made on courtship activities hence the writer must rely to some extent upon the observations of others. Only two instances of copulation were recorded, one for each species. Louis Bussjaeger, of the University of Oklahoma, collected a copulating pair of N. erythrogaster in April 1967, in McCurtain County. The pair was collected in daylight in a culvert. In the second instance, Rick Collins, also of the University of Oklahoma, observed a copulating pair of N. rhombifera at night, May 29, 1969, in Cleveland County.

On May 16, 1969 the writer observed two N. rhombifera escaping into the water. One of these could be identified as a female by the shorter, narrower tail when it emerged on a tree limb near the shore. The second, a male, was captured a few minutes later. It was actively searching the area where the two were last seen together. Evidently courtship had been in progress when the two snakes were disturbed.

On April 30, 1969 three N. erythrogaster were observed swimming actively about in shallow water. They appeared to pursue one another periodically. As it approached shore, one, a male, was captured. This may have been courtship activity as the snakes did not appear to be searching for food. Tinkle and Liner (1955) observed similar behavior in Natrix sipedon confluens and concluded that "These aggregations are probably preliminary to mating."

According to Diener (1957), N. erythrogaster mates in early April and throughout May in the southern part of its range. He observed mating in Arkansas on May 20. Franklin (1944) states that the breeding season for N. taxispilota in Florida is during the latter part of May. Hurter (1911) referring to N. rhombifera in Missouri, states, "Middle of April I found this rather vicious looking snake already mated, lying on the branches of small trees and shrubs ,...". The breeding period appears to be about the same for both species.

According to Betz (1963) the gestation period for N. rhombifera is approximately three months in duration. A snake mating at the end of May, as observed in the present study, would then give birth in the latter part of August or the first part of September, which agrees with observations discussed below.

Young

The time of birth for both species appears to be in the fall or late summer. A summary of birth dates of water snakes is presented in Table VII.

In the present study new young of N. erythrogaster were found in the field September 14, 26 and October 3 and 19. A new young N.

rhombifera was found by the writer on September 14, 1965 and another was examined September 18, 1969.

Data on numbers of young born, embryos or eggs found in female *Natrix* are summarized in Table VIII.

Published data on the size of females and number of young born or embryos or ova found are presented in Table IX. If the number of young is compared with the size of the females (Figure 12) some degree of correlation is evident, the larger snakes tending to produce more young.

As stated earlier maturity is reached by *N. rhombifera* females at two and one half years of age (Betz, 1963). Data obtained in the present study indicate that at this age the females would be at least 60 cm in snout-vent length (Figure 1). Wright and Wright (1957) give the size of breeding females as ranging from 82 to 145 cm in total length. Examination of Table X will reveal that relatively few of the mature females were gravid at the same time. It will be noted that of 11 females captured at Kulli Lake in 1966 none was gravid. It should be pointed out that most of these were collected in August, about one month prior to parturition. It may be that females, when gravid, tend to seclude themselves and would hence be less susceptible to capture. Carpenter (1953b) noted such a tendency in *Thamnophis*. In 1968 two of 7 were gravid and in 1969 none of 6. On the average, 8 percent (range: 0 to 28.6 percent) of the *N. rhombifera* were found to be gravid. From the same table it will be noted that relatively few mature *N. erythrogaster* females were gravid, the average being 20 percent, with a range of 0 to 50 percent. Rahn (1942) suggested a bienneal repro-

Table VII. Birth dates of young water snakes (*Natrix*).

Species	Date	Locality	Authority
N. rhombifera	Aug. & Sept.		Smith (1956)
	Sept. 3, 10, Aug. 27	Tennessee	Cagle (1937)
	Sept. 2, 3, 8	Oklahoma	Oklahoma City Zoo
	Sept. 9, Oct. 5	Missouri	Anderson (1965)
	Aug. to Nov. 8		Wright and Wright (1957)
	Nov. 3	Texas	Kennedy (1964)
N. taxispilota	Aug. to Sept.	Florida	Franklin (1944)
N. erythrogaster	late Aug.	Oklahoma	Carpenter (1958)
	Sept. 15, 19, 20, 21, Oct. 2	Missouri	Anderson (1965)
	Sept. 30, Oct. 10, 14	Ohio	Conant (1938)
	Sept. & Oct.		Smith (1956)
	late Aug. to Oct.		Wright and Wright (1957)

Table VIII. Numbers of young, eggs, or embryos observed in Natrix.

Species	Young	Embr.	Eggs	Authority
N. rhombifera	8-62	-	-	Anderson (1965)
	-	30	-	Cagle (1937)
	-	42	-	
	-	30	-	
	-	28	-	
	-	31	-	
	-	26	-	
	-	31	-	
	-	22	-	
	-	28	-	
	-	18	-	
	-	41	-	
	-	32	-	
	17	-	-	
	18	-	-	
	13	-	-	
	-	17	-	Carpenter (1958)
	62	-	-	Guidry (1953)
	26(1 dead)	4	-	Kennedy (1964)
	18-62	-	-	Wright and Wright (1957)
	-	-	10	Present study
	-	14	-	
N. taxispilota	30-40	-	-	Franklin (1944)
N. e. transversa	8	-	-	Anderson (1965)
	22	-	-	
	22	-	-	
	11	-	-	
	13	-	-	
	22	-	-	
	14	-	-	
	17	-	-	Carpenter (1958)
	-	16	-	
	"about 12"	-	-	Diener (1957)
	15-21	-	-	Wright and Wright (1957)
	-	-	6	Present study
	-	-	14	
	-	32	-	Carpenter (unpubl. data)
N. e. erythrogaster	-	-	28	Cagle (1942)

Table IX. Size of females and number of eggs, embryos or young observed in Natrix. Stub-tail is indicated by (st.).

Species	Length (cm)	No. eggs, emb., yng.	Authority
N. rhombifera	124.0	30	Cagle (1937)
	132.5	42	
	112.5	30	
	110.5	28	
	122.6	31	
	95.0	26	
	110.5	31	
	102.5	22	
	110.0	28	
	85.0	18	
	122.6	41	
	111.3	32	
	121.2	17	
	101.0	18	
	111.9	13	
	103.3	17	Carpenter (1958)
	176.3	30	Kennedy (1964)
	95.5	14	Present study
	104.3 (st.)	10	
N. taxispilota	124.5	34	Franklin (1944)
	128.5	37	
N. e. erythrogaster	111.4	14	Conant (1938)
	123.8	27	
N. e. transversa	101.3	16	Carpenter (1958)
	144.5	32	Carpenter (unpubl.)
	107.3	6	Present study
	116.4	14	

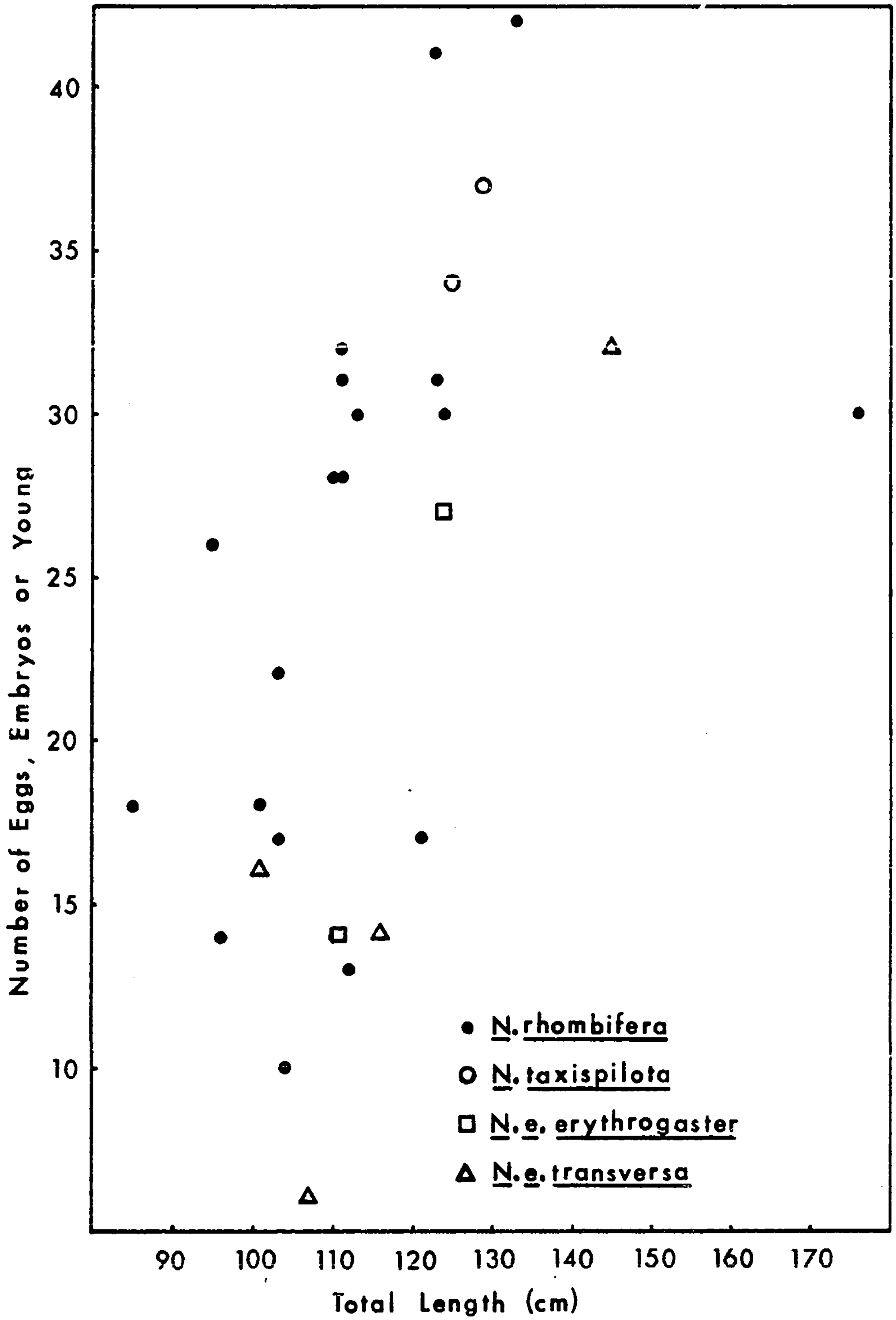


Figure 12. Relationship between length of female and number or potential number of offspring. Three species are represented.

Table X. Numbers of gravid mature females observed. Females 60 cm in snout-vent length are assumed to be mature.

Study Area	1965		1966		1967		1968		1969	
	MF	G	MF	G	MF	G	MF	G	MF	G
Natrix rhombifera										
Hospital L.	1	-	-	-	-	-	2	2	-	-
Smith L.	-	-	-	-	-	-	-	-	-	-
Kulli L.	-	-	10	-	1	-	1	-	2	-
Other	-	-	1	-	-	-	4	-	4	-
Total	1	-	11	-	1	-	7	2	6	-
Natrix erythrogaster										
Hospital L.	-	-	-	-	-	-	3	2	1	-
Smith L.	-	-	-	-	-	-	-	-	-	-
Kulli L.	1	-	3	-	1	-	-	-	1	1
Other	-	-	-	-	2	-	2	-	-	-
Total	1	-	3	-	3	-	5	2	2	1

ductive cycle for *Crotalus viridis viridis* in Wyoming, based on the fact that he found two stages of mature females in approximately equal numbers, those with large ovaries, with motile sperm in the reproductive tract, and those with small ovaries and with no sperm. Volsøe (1944) in studies on *Vipera*, found a biennial cycle in northern Europe and an annual cycle in the south. Klauber (1956) believed northern rattlesnakes to have a biennial reproductive cycle and the southern rattlesnakes to have an annual cycle but admitted insufficient evidence. Fitch (1949) found a biennial cycle in *Crotalus viridis oreganus* in California.

In the present study, the fact that relatively few mature females were gravid at any one time leads the writer to suspect a biennial cycle in both of the species studied. One would expect approximately one half of the mature females to contain large ova or embryos at a given time in a biennial cycle. However considerably less than half, on the average, were observed in this condition. In snakes such as rattlesnakes, that congregate in large numbers for hibernation, a more representative sample of the population can be obtained, particularly on spring emergence. It is likely that in the present study many gravid females were missed, perhaps, as suggested earlier, due to a greater tendency toward seclusion.

Mortality

Very little data on mortality appears to be available for snakes in general. It is to be expected, perhaps, that mortality is highest in the young snakes. Fitch (1949) estimated that only one quarter of the newborn young Crotalus viridis oreganus survived by the end of the first year. This was believed to be due mainly to low availability of food of the proper size. This is expected, perhaps, in a species relying mainly upon endotherms as prey. In the present study the question of availability of proper-sized food for young Natrix was less important in that fish and frogs appeared to be generally abundant in a variety of sizes. Nevertheless mortality in the young is probably much higher than that in the adults in that the young are more susceptible to predation.

Excluding snakes found dead on the road, during the course of the present study, 10 N. rhombifera and 3 N. erythrogaster were found dead (Table XI). If these numbers are compared with the numbers of snakes captured the percentages are 7.09 for N. rhombifera and 3.80 for N. erythrogaster. No significant difference was found between the two species.

Four of the 10 N. rhombifera were caught on fish lines. Fish was used as bait in at least one case. Guidry (1953) states that this species is caught frequently by anglers on their lines. It is to be expected, of course, that a fish-eating snake would be frequently caught on fish lines when minnows are used as bait. One N. rhombifera was shot by an angler who believed it to be a "water moccasin".

Not recorded as a case of mortality was a N. erythrogaster captured by Harold Cleveland, of the University of Oklahoma, in the presence of the writer on February 10, 1966. The snake was basking on dry grass at the water's edge. It died in captivity a few hours later. It is possible that the snake had emerged too soon from hibernation and

Table XI. Mortality of Natrix in the study areas.

	Natrix rhombifera					Natrix erythrogaster					
Year	Hosp.	Smith	Kulli	Misc.	T.	Hosp.	Smith	Kulli	Misc.	T.	G.T.
1965	2	3	-	1	6	-	1	1	-	2	8
1966	-	1	-	-	1	-	-	-	-	-	1
1967	-	-	-	-	-	-	-	-	-	-	-
1968	1	-	-	-	1	1	-	-	-	1	2
1969	1	-	1	-	2	-	-	-	-	-	2
Total	4	4	1	1	10	1	1	1	-	3	13

had received cold damage, being already ill when captured.

It was noted that many individuals of both species had stub-tails. Diener (1957) suggests that turtles may be partly responsible. In Table XII, N. rhombifera and N. erythrogaster are compared with respect to the presence or absence of stub-tails. The writer could demonstrate no significant difference between the two species in this respect. It would seem then that either species and either sex of each of the two species is equally prone to tail amputation.

Food Habits

Since snakes that are active are those most likely to be seen and captured, the proportion of snakes containing food is expected to be relatively low. It is the hungry snakes, or those searching for mates, that would tend to be most active. Those that have fed are likely to be more secretive while digesting the meal. In the present study, of 142 N. rhombifera examined, 25 (17.6 percent) contained food. Eleven of 79 (13.9 percent) N. erythrogaster examined contained food. In these determinations only captured snakes were used. Sight records were used, however, in determining the relative numbers of kinds of prey taken by the two species.

Other writers have recorded much higher percentages of snakes containing food. For N. rhombifera Bowers (1966) found 72.3 percent; Greding (1964), 30 percent; Laughlin (1959), 39.1 percent and Sisk and McCoy (1964), 76.6 percent. Greding (1964) found 28.6 percent of the N. e. flavigaster examined by him to contain food. It must be pointed out, however, that the above figures were obtained by opening stomachs

Table XII. Percentages of snakes with stub-tails from each study area.

	Natrix rhombifera			*Natrix erythrogaster*		
	M	F	T	M	F	T
Hospital L.	40.0	22.2	34.5	10.0	6.7	7.3
Kulli L.	19.4	10.8	14.7	25.0	22.2	23.1
Smith L.	-	-	-	16.7	50.0	30.0
Others	25.0	20.0	22.2	20.0	16.7	18.2
Totals	23.0	13.2	18.3	18.5	14.3	14.7

rather than by forced regurgitation. It is to be expected that small remains of food items could easily be missed by the writer's method.

Many authors discussing food habits of the two species under investigation make no statement on food preferences other than that both species feed upon frogs and fish (Anderson, 1965; Guidry, 1953; Raun, 1965; Smith, 1956; Stebbins, 1966; Strecker, 1927; Wright and Wright, 1957). Crayfish are often included in the diet of N. erythrogaster. The results obtained in the present study are presented in Table XIII. These data include sight records, that is, snakes seen with a frog or a fish in the mouth. Natrix rhombifera appeared to show a strong preference for fish, 88.89 percent of those with food containing fish. A significant difference in food preference could be demonstrated, favouring fish. The only other food item recorded for this species was tadpoles, making up the remaining 11.11 percent.

Natrix erythrogaster, on the other hand, seemed to prefer amphibians, most of which were adult frogs. However no significant difference in food preference of frogs over fish could be demonstrated.

Other writers have found evidence for similar food preferences in these two species. Cagle (1937) found 20 stomachs of N. rhombifera to contain 17 fish, 11 plus frogs and one turtle. Of 9 stomachs of N. taxispilota (N. rhombifera) examined by Laughlin (1959) all contained fish. Examination of 49 stomachs of this species by Sisk and McCoy (1964) revealed fish in 46 and amphibians in 6.

Bowers (1966) found amphibians in more stomachs than contained fish but goes on to point out that in the sample from a small lake only fish were found, while the sample from the minnow ponds contained more

Table XIII. Food records. Each record represents one snake. The number of sight records included in the total is represented by s.

	Amphibian			Fish	Crayfish
	Frog	Tadpole	Total		
Natrix rhombifera	-	3	3	24 (2s)	-
percent	-	11.11	11.11	88.89	-
Natrix erythrogaster	8 (1s)	1	9	3 (1s)	1
percent	61.54	7.69	69.23	23.08	7.69

anurans than fish by volume. It may be that the fish in the minnow ponds were too small to be utilized as food by adult N. rhombifera, hence a heavier utilization of anurans.

Diener (1957), in Kansas, found N. erythrogaster to be mainly a frog eater. Carpenter (1958) recorded a crayfish as a food item from this species, in addition to two more that had eaten fish. He also recorded a large Rana pipiens eaten by a N. rhombifera. One crayfish was found in a N. erythrogaster in the present study (Table IV). In this investigation, of 3 fish found as food items in N. erythrogaster, one was a Lepomis on a stringer and in another case a snake was observed going off a bank into the water with a fish in its mouth. It may well be that the snake found the fish dead on the bank, as the writer often found fish discarded by fishermen along the shores of ponds. Carpenter (unpubl. data) in 1968 found fish in 4 of 8 N. erythrogaster. One contained remains of a frog in addition to a fish.

During the course of the present study the writer had occasion to observe three instances in which a N. erythrogaster had just captured a frog. In one case a Rana pipiens, disturbed by the writer, jumped into the water and was seized by a snake lying under thick vegetation in shallow water. On another occasion, a half grown Rana catesbeiana was seized, as it jumped into the water, by a large N. erythrogaster partly concealed in water vegetation. In the third case distress calls of Rana catesbeiana were heard coming from shrubbery on the shore near the water's edge. Investigation revealed that the frog was in the jaws of a N. erythrogaster. On yet another occasion a swimming N. erythrogaster was observed to strike at and miss a frog as it jumped into the water. One afternoon in early June 1966, the writer observed a *N. erythrogaster* for fifteen minutes as it swam back and forth along the shoreline appearing to be actively searching. That snake may have been searching for a mate.

Two of the sight records for *N. rhombifera* were snakes seen with fish in their mouths. One *N. rhombifera* was captured at night with a live bullhead catfish held headfirst in its mouth. Feeding behaviour was observed only once in this species. A very young individual was observed in shallow water at night swimming in a circular motion and was seen to snap at small fish. Other authors (Bowers, 1966; Evans, 1942) have reported similar behaviour in this and in other species. The writer observed a *N. rhombifera* in daylight swimming in shallow water near shore with head under water, surfacing periodically.

It is the belief of the writer that food records collected over a long time period, as in the present study, are more likely to be an accurate indication of food preference than those collected from a large sample taken in a limited time period such as one night, as in the case of some of the reports cited earlier. Such cases may indicate a particular preference merely because that particular prey species is particularly available at that time. An example would be fish trapped in a drying puddle. Burghardt (1968) has shown that the newborn of 3 species of *Natrix* exhibited a difference in chemical preference. *Natrix s. sipedon* responded only to fish and amphibian extracts, and *N. grahami* and *N. septemvittata* only to crayfish extracts. Similar tests performed on *N. rhombifera* and *N. erythrogaster* may indicate a difference in chemical preference.

Habitat

The name "water snake" suggests an aquatic snake and most North American Natrix are aquatic to some extent. Diener (1957) comments that N. rhombifera are more aquatic than N. erythrogaster. When the present data for the two species are compared with respect to whether they were seen or captured in or out of the water, N. rhombifera appears to be the most aquatic (Table XIV). Observations made on snakes out of the water include those basking on the shore, basking in trees, and found under objects along the shore. Natrix erythrogaster was seen or captured as often out as in the water. Conant (1934, 1938) found N. e. erythrogaster as far as 200 yards from water.

The position in the habitat where each snake was observed or captured (other than in or out of water) indicates that both species were observed more frequently in areas of vegetational cover than in areas bare of vegetation (Table XV). This is to be expected in that snakes in general tend to be secretive.

Natrix rhombifera frequented trees more often than N. erythrogaster, and occasionally occurred as high as 10 feet above the water. The limbs on which the snakes basked generally overhung the water. Often, individual trees appeared to be preferred. Carr (1940) comments that N. taxispilota is the most arboreal water snake in Florida and that he has seen them 25 feet above the water.

On only two occasions was N. erythrogaster observed in trees, and then close to the water line.

Natrix erythrogaster was found more frequently under objects such as boards, logs, rocks, dead leaves and litter than was N. rhombifera.

Table XIV. Snakes observed in or out of water.

	Natrix rhombifera		*Natrix erythrogaster*	
	Number	Percent	Number	Percent
In water	195	67.01	79	50.64
Out of water	96	32.99	77	49.36
Totals	291	100	156	100

Table XV. Where snakes were observed in the habitat.

	Natrix rhombifera		*Natrix erythrogaster*	
	Number	Percent	Number	Percent
Cover (vegetation)	62	38.99	50	40.00
No cover	42	26.42	28	22.40
In stream	2	1.26	-	-
On object in water	8	5.03	2	1.60
In tree or shrub	19	11.95	2	1.60
Under objects	23	14.47	39	31.20
On pavement (road)	3	1.89	4	3.20
Total	159		125	

It may be that the latter species tends more to seclude itself in holes and therefore is not so readily observed in this situation.

The relative abundance of the two species may change with time in a given lake as indicated at Hospital Lake (Table II). It may well be that this apparent change in relative abundance is merely an artifact of small sample size. However in Hospital Lake there has been a change in the habitat with respect to water level. The lake was extremely low in 1965, the water level gradually increasing until spring 1969, when it was highest.

The change in abundance, on the other hand, may be fortuitous, depending upon a tendency to wander. This will be discussed below.

Associated Species

Predators

The only observed results of predation were those snakes found killed by humans, already discussed under mortality. In some instances these were unavoidably killed when caught on fish lines. However, other predators were observed in the study areas.

Racoon tracks were frequently seen along the shores. It is possible that these may prey to some extent upon the young snakes. Green herons (*Butorides virescens*) were commonly observed in the study areas, particularly at Hospital Lake. Yellow-crowned night herons (*Nyctanassa violacea*) and little blue herons (*Florida caerulea*) were less frequent. It is unlikely that any of these birds would feed on any but the smallest snakes.

It is possible that large snapping turtles (*Chelydra serpentina*) may occasionally prey upon the younger snakes. Many adults of both species are stub-tailed and it has been suggested that turtles may, at least in part be responsible (Diener 1957). Burkett (1966) reports two samples of 46 cottonmouths (*Agkistrodon piscivorus*) which contained remains of *N. erythrogaster* and one an unidentified *Natrix*. Of the areas studied, cottonmouths were seen only at Kulli Lake. McGrew (1963) found 8 juvenile *N. rhombifera* in the stomach of a channel catfish (*Ictalurus punctatus*).

Competitors

Any species utilizing fish or frogs as food could be regarded as competing with the two snakes in question. The three predatory birds previously discussed may in this respect be regarded as competitors as well as predators. However each of these birds has a varied diet, probably more so than the two snakes, hence competition would tend to be reduced. The only observations of utilization of the same food as *Natrix* recorded by the writer include *Coluber constrictor* and *Thamnophis proximus*, both observed eating leopard frogs (*Rana pipiens*). These two species were often seen at Hospital Lake and at the Wanette study area.

Other snakes observed in the study areas include *Natrix grahami* and *Opheodrys aestivus* at Hospital Lake, *Sistrurus miliarius* and *Agkistrodon contortrix* at Smith Lake, *Elaphe obsoleta* in the Wanette study area, and *Natrix sipedon confluens* and *Agkistrodon piscivorus* at Kulli Lake.

Prey

In addition to those discussed under food habits, several other species of frogs were abundant in the study areas. Acris crepitans was abundant in all study areas and was recorded as food in several young N. erythrogaster. In Kulli Lake, in addition to the species mentioned above, Rana clamitans, Hyla versicolor, Microhyla carolinensis and Bufo woodhousei fowleri x velatus were abundant, particularly during their respective breeding seasons.

A few other species of uncertain ecological relationship to Natrix were observed in the study areas. Muskrats (Ondatra zibethicus) were frequently seen in Hospital Lake. Old burrows of this species could possibly be used as hiding places or perhaps as hibernacula. Turtles of several species but mainly Pseudemys and Chelydra were abundant in most areas. Kinosternon flavescens were occasionally observed in Hospital Lake and Kinosternon subrubrum appeared to be common in Kulli Lake. Young turtles could possibly be utilized as food by Natrix. Lizards of the species Lygosoma laterale, Crotaphytus collaris, and Phrynosoma cornutum were commonly observed along the shores of Hospital Lake. The former two species, especially the second, were frequently under boards. These could possibly fall prey to Natrix.

Temperature Relations

The cloacal temperatures of 33 N. rhombifera were compared with those of 24 N. erythrogaster (Figure 13). The mean cloacal temperature obtained for N. rhombifera was 27.46 C, with a range of 19.3 to 32.0 C and that for N. erythrogaster was 26.45 C, with a range of 22.0 to 32.0 C.

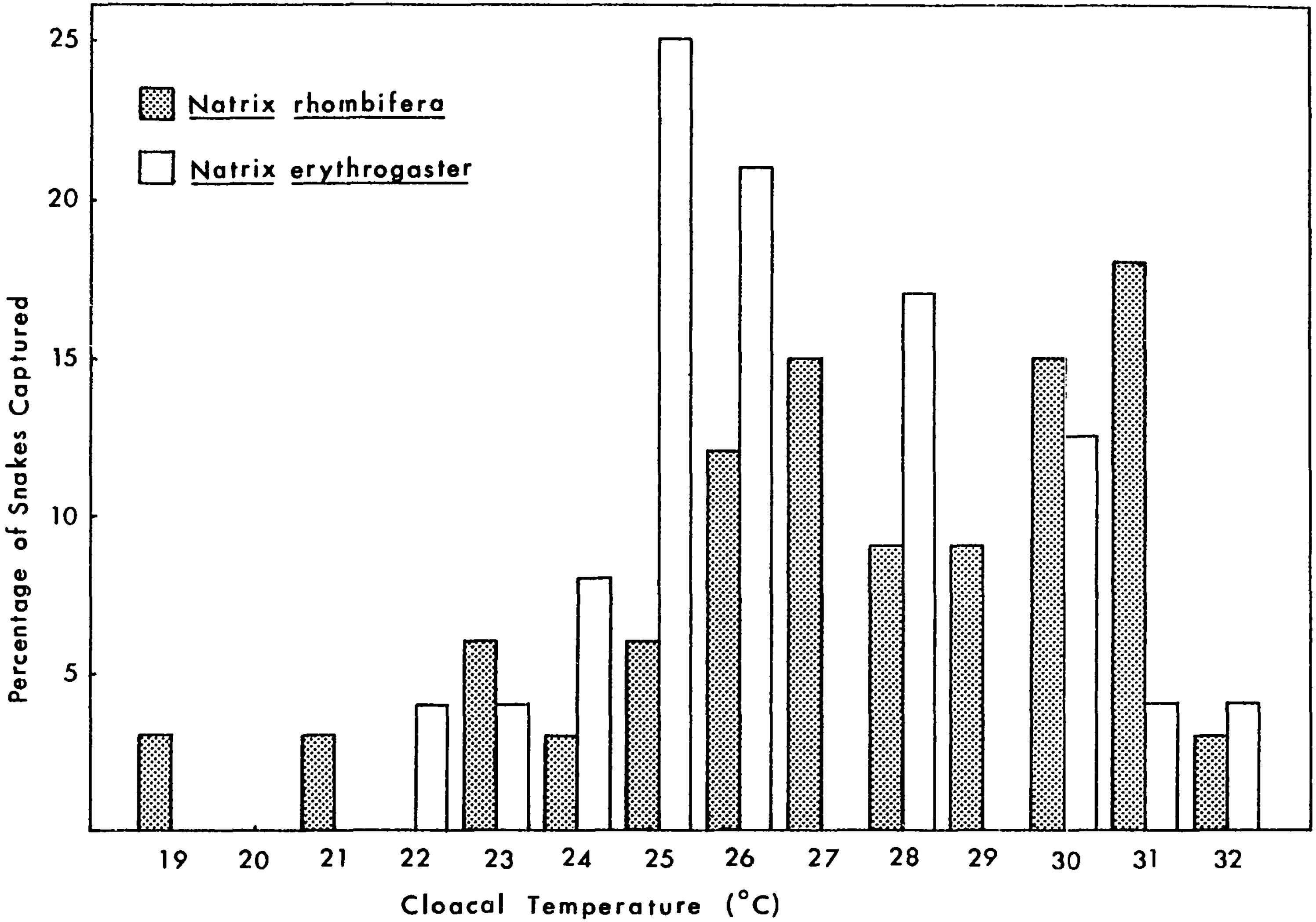


Figure 13. Cloacal temperature in relation to percentage of the number of both active and inactive snakes captured.

There is a significant difference between the two. These data, however, include apparently inactive as well as active snakes. Further comparison was made using data from active snakes only (Figure 14). Snakes basking when first seen, or hiding under objects were assumed to be inactive and were omitted from this figure. For 21 active *N. rhombifera* the mean cloacal temperature was 28.51 C, with a range of 24.0 to 31.0 C and for 14 active *N. erythrogaster* was 27.02 C, with a range of 22.0 to 32.0 C. Here no significant difference could be demonstrated. However, *N. rhombifera* apparently prefers a slightly higher body temperature than does *N. erythrogaster*.

Brattstrom (1965) cited a mean of 26.9 C, with a range of 25.8 to 29.8 C for 6 *N. rhombifera* and a mean of 29.0 C for 4 *N. erythrogaster*. It is likely that his samples were too small to give an accurate indication of the preferred body temperature.

Again using data from active snakes only, captured in the water, the two species were compared. Nineteen *N. rhombifera* had a mean cloacal temperature of 28.73 C, with a range of 24.0 to 30.5 C. The mean air temperature was 24.85 C, with a range of 17.6 to 27.3 C and that of the water was 29.67 C, with a range of 24.6 to 32.2 C. Fourteen *N. erythrogaster* had a mean cloacal temperature of 27.02 C, with a range of 22.0 to 32.0 C. The mean air temperature was 26.04 C, with a range of 22.4 to 29.2 C and the mean water temperature was 27.73 C, with a range of 22.3 to 31.8 C. Since the snakes were in the water when captured it is the water temperature that should be considered as the most important of the environmental temperatures. It is noted that the cloacal temperatures of snakes captured in the

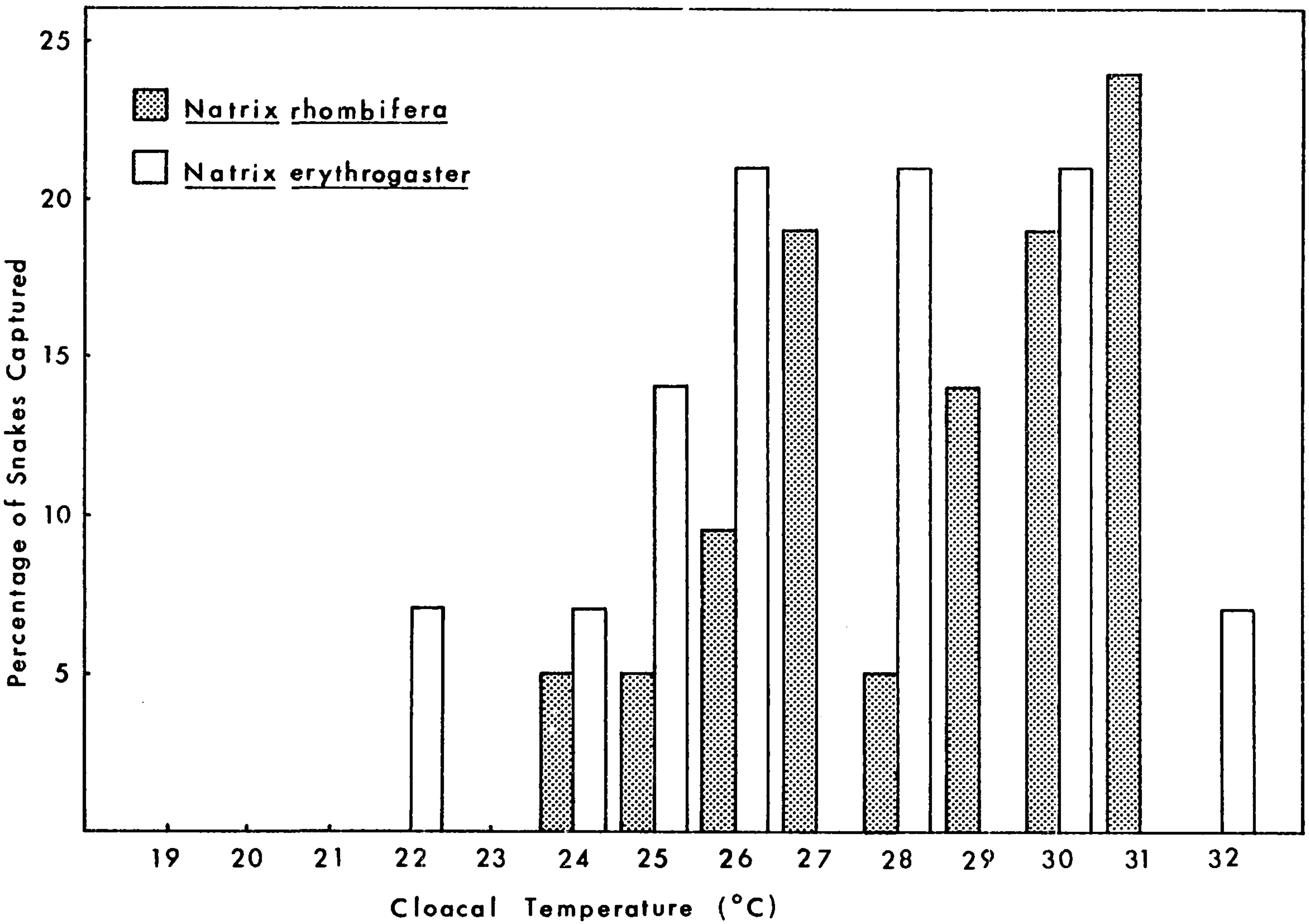


Figure 14. Cloacal temperature in relation to the percentage of the number of active snakes captured.

water are nearer to the water temperatures than to the air temperatures (Table XIV).

Activity Periods

Wright and Wright (1957) cite the seasonal activity period of N. e. transversa as beginning as early as March 24 in Kansas and extending as late as November 26 in Texas, and that of N. rhombifera as extending from March 24 to September 23. One individual of N. erythrogaster was seen by the writer on February 10, 1966. Diener (1957) observed this species first in the middle of March, 1955 and 1956.

One N. rhombifera was captured by the writer as late as November 5 in Cleveland County. Both species may temporarily emerge from hibernation to bask during warm winter days, however in the strict sense, this could hardly be regarded as part of the activity period. Neill (1948) reports that rising water in Georgia will bring out N. taxispilota in numbers to bask on tree branches, regardless of the temperature. After having "thawed out" they disappear.

The seasonal activity period for the two species in central Oklahoma appears to begin in early to mid April and ends mid to late October, depending upon the weather.

After emerging from hibernation the snakes appear to be diurnal, spending most of their time basking. As the nights become warmer they become active at night. The writer has observed both species active at night as early as mid April and in late September in southeastern Oklahoma. On the basis of temperature relations discussed

Table XVI. Comparisons of cloacal and environmental temperatures. Temperatures are in degrees Celsius.

		No.	Mean	Range
Natrix rhombifera				
Active snakes, captured in water:				
	Cloacal	19	28.60	24.0 - 30.5
	Air	18	24.85	17.6 - 27.3
	Water	19	29.66	24.6 - 32.0
Inactive snakes (capt. mainly out of water):				
	Cloacal	12	25.77	19.3 - 32.0
	Air	12	24.57	17.9 - 29.8
	Water	10	26.40	20.0 - 32.0
	Substrate	8	25.14	20.1 - 33.2
All snakes:	Cloacal	33	27.46	19.3 - 32.0
Natrix erythrogaster				
Active snakes, captured in water:				
	Cloacal	14	27.02	22.0 - 32.0
	Air	14	26.04	22.4 - 29.2
	Water	14	27.73	22.3 - 31.8
Inactive snakes (capt. out of water):				
	Cloacal	10	25.76	22.8 - 31.0
	Air	9	26.70	22.3 - 29.9
	Water	7	28.16	19.9 - 33.6
	Substrate	9	25.30	22.6 - 28.8
All snakes:	Cloacal	24	26.45	22.0 - 32.0

previously it is to be expected that *N. erythrogaster* would tend to begin its activity period slightly before *N. rhombifera* and end it slightly later.

Analysis of capture and sight records seems to indicate that *N. erythrogaster* tends to be more diurnal than nocturnal, and the activity of *N. rhombifera* appears to be more or less equally disturbed between day and night. Of the *N. erythrogaster*, 69.81 percent were seen or captured during daylight as compared to 45.95 percent of the *N. rhombifera*.

Movements

Since in the early part of the study snakes captured at night were processed and released all at once at the same location, movement data were obtained from relatively few recaptures. These data are presented in Table XVII. Eight *N. rhombifera* moved an average of 637 feet, with a range of 0 to 1200 feet and 6 *N. erythrogaster*, an average of 483 feet, with a range of 0 to 900 feet. Analysis of variance revealed no significant difference between the two species with respect to distance moved.

When the sexes are considered separately, 3 female *N. rhombifera* moved an average distance of 331 feet, with a range of 0 to 600 feet and 5 males moved an average of 820 feet, with a range of 400 to 1200 feet. Four *N. erythrogaster* females move 525 feet on the average, with a range of 0 to 900 feet and 2 males moved an average of 400 feet, with a range of 0 to 800 feet. Fitch (1949) found that *Crotalus viridis oreganus* males in California tended to move greater distances

Table XVII. Distances moved by the snakes, arranged in order of increasing time interval. The hibernation period (Nov. to Mar. inclusive) is excluded from the number of active days.

Sex	Area	Time interval	Active Days	Distance (feet)
Natrix rhombifera				
M.	Hospital L.	May 29/68 - June 3/68 (dead)	5	400
M.	Hospital L.	Apr. 15/69 - May 14/69	29	1200
M	Kulli L.	Aug. 6/66 - Sept. 17/66	42	1000
M	Kulli L.	Aug. 6/66 - Sept. 17/66	42	1000
M	Kulli L.	July 9/66 - Sept. 17/66	70	500
F	Smith L.	Sept. 9/65 - May 11/66	93	0
F	Kulli L.	July 1/67 - July 2/68	215	600
F	Kulli L.	July 9/66 - July 19/67	224	400
Mean				637
Natrix erythrogaster				
M	Hospital L.	Apr. 17/68 - May 1/68	14	0
M	Hospital L.	May 1/69 - June 9/69	39	800
F	Hospital L.	Aug. 6/65 - Aug. 11/65	5	600
F	Hospital L.	Sept. 14/67 - Sept. 26/67	12	0
F	Hospital L.	Aug. 11/65 - Sept. 10/65	30	900
F	Hospital L.	June 3/68 - Oct. 29/68	148	600
Mean				483

than did the females. Preston (1964) made similar observations on the same species in British Columbia. This tendency has been observed also in a number of other species: Agkistrodon contortrix, (Fitch, 1960); Coluber constrictor, (Fitch, 1963a); Elaphe obsoleta, (Fitch, 1963b); Thamnophis sirtalis, (Fitch, 1965); Thamnophis sauritus, (Carpenter, 1952a). This greater wandering tendency in males is perhaps linked closely with the search for mates.

It was noted above that for Natrix erythrogaster the average distance moved by males was exceeded by that moved by females. In Figure 15 the snakes are classified according to size as well as to species. It will be noted that the larger snakes of both species tended to move greater distances on the average. The N. erythrogaster females recaptured belonged to a larger size class than did the males. Preston (1964) observed a similar relationship between size and distance moved in Crotalus viridis.

It may be expected that the distance travelled would tend to increase with increase in the time interval between captures. Such a tendency has been observed in Thamnophis (Carpenter, 1952a; Fitch, 1965). However, it has been demonstrated by many authors that snakes tend to remain in a limited area (Carpenter, 1952a; Fitch, 1949, 1960, 1963a, 1963b; Platt 1969; Preston, 1964; Stickel and Cope, 1947). Carpenter proposed the term "activity range" to refer to this area. The data obtained in the present study (Table XVII) indicate no conclusive evidence of a tendency in Natrix to travel greater distances with increase in time interval.

When the numbers of recaptures are compared on a percentage

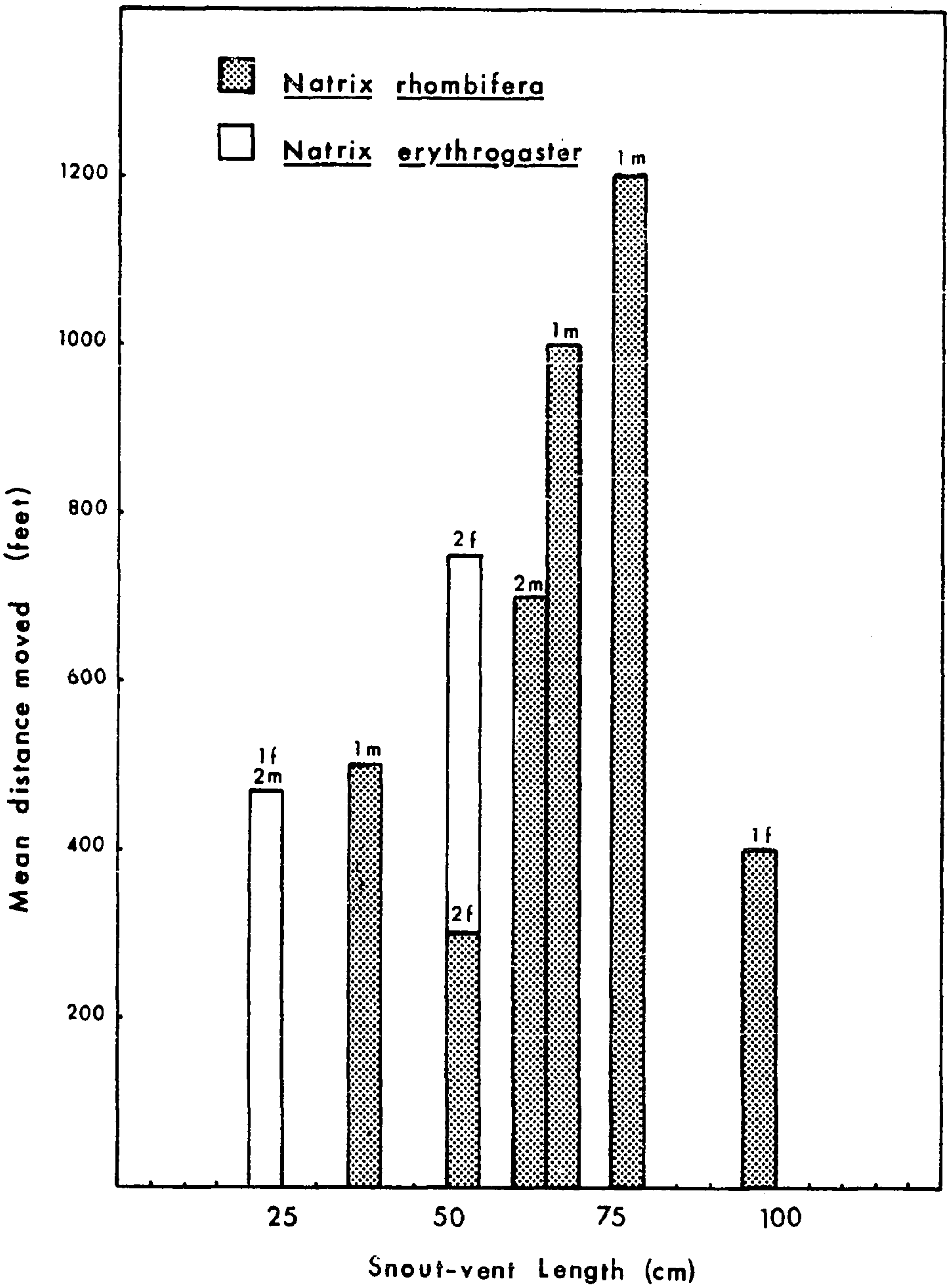


Figure 15. Relationship between distance travelled and size class. Males are represented by m, and females by f.

basis with those for other species (Table XVIII), it is evident that greater recapture success was attained when traps were used. The success of Preston (1964) and Woodbury (1951) may be attributed to the fact that most of the snakes were recaptured at the hibernating dens in both spring and fall.

No significant difference in recaptures could be demonstrated between the two species of Natrix. The low incidence of recaptures in both species may be due to movement from one lake or pond to another outside the study area. The writer is convinced that this frequently happens. In the spring of 1969 a great many N. erythrogaster were observed on the same day along the dam of the Stone Pond in the Wanette study area. Later, during the summer few were seen, N. rhombifera being the more commonly observed species. This causes the writer to wonder if N. erythrogaster, being somewhat less aquatic than the other, tends to wander farther. One N. rhombifera moved a distance of 1200 feet, from the large Hospital Lake to the small lake. However, these lakes are immediately adjacent, being separated by only a dam. Movement between the two is undoubtedly a common occurrence. Tinkle (1957) referring to Thamnophis sauritus, states, "The major factor responsible for the paucity of recaptures is considered to be extensive movement of the snakes." Carpenter (1952a) presents evidence to the contrary, that movement by this species, and two others studied by him, is limited.

Table XVIII. Percentage of Natrix recaptured compared to that for other species. X indicates that trapping methods were used. No. includes total of captures and recaptures.

Species	No.	Rec.	%	Tr.	Authority
Natrix rhombifera	122*	16	13.1		Present study
Natrix erythrogaster	67*	6	9.0		Present study
Crotalus viridis oreganus	1010	78	7.7		Fitch (1949)
Crotalus viridis lutosus	2010	1080	53.7	x	Woodbury (1951)
Masticophis taeniatus taeniatus	1075	443	41.1	x	
Coluber constrictor mormon	155	28	18.1	x	
Pituophis catenifer deserticola	40	4	10.0	x	
Thamnophis sauritus proximus	31	8	25.8		Tinkle (1957)
Agkistrodon contortrix	2018	486	24.1	x	Fitch (1960)
Coluber constrictor	1688	668	39.6	x	Fitch (1963a)
	467	106	22.7	x	
Elaphe obsoleta obsoleta	516	157	43.7	x	Fitch (1963b)
Crotalus viridis oreganus	222	123	55.4	x	Preston (1964)
Thamnophis sirtalis	1354	257	19.0	x	Fitch (1965)
	812	151	18.6	x	
Heterodon nasicus	314	73	23.2	x	Platt (1969)
Heterodon platyrhinos	144	20	13.9	x	

Carpenter (pers. comm.) had about 25 percent recapture of each of Thamnophis sirtalis, T. sauritus and T. butleri.

*excluding snakes found dead or retained in captivity, and therefore not available for recapture.

CHAPTER IV

DISCUSSION AND CONCLUSIONS

The primary object of the present study was to demonstrate an ecological difference, if such existed, between *Natrix rhombifera* and *Natrix erythrogaster* where they occur together in lakes and ponds in Oklahoma. Of the factors investigated, food preferences, degree of aquatic tendencies, and temperature tolerance appear to be the most important in separating the two species ecologically.

Natrix erythrogaster tends to be less aquatic than does *N. rhombifera*. Observations of other authors support the evidence obtained in the present study. The more terrestrial habit of this snake may help to explain why it ranges farther west in distribution than does *N. rhombifera*. The western part of Oklahoma, for example, is more arid than the eastern part, due to lower precipitation.

However, the western distribution of *N. erythrogaster* could be explained also by a tolerance of lower activity temperatures, since in the western part of its range this snake occurs on the high plains, which are noted for greater extremes of temperature. The more northern limit of distribution of *N. erythrogaster* and its occurrence at higher elevations has already been noted. It is most likely that tolerance of lower temperatures and more terrestrial habits act in conjunction to enable a more westward extension of the range of this species.

Food preferences may be closely linked with the occurrence of N. erythrogaster in more arid areas. Data obtained in the present study support the observations of others that N. erythrogaster is primarily a frog-eater. Frogs are less aquatic than fish, but must return to the water to breed. Breeding, however, can occur in isolated water sources inaccessible to fish, providing a source of food for a frog-eating snake, where there would be no food for a fish-eater. Natrix rhombifera, also, has been observed to eat frogs and tadpoles. In the Wanette study area, two of the ponds, the Stone Dam Pond and the Small Pond, contained no fish. Bullfrogs, however, were abundant, and N. rhombifera were frequently observed at these ponds, at least as often as N. erythrogaster. It is probably not food then that limits the distribution of N. rhombifera, but more likely narrower temperature preferences and more aquatic habit.

It is to be expected that a species occuring over a wider range and tending to be less restricted to water than another species would have a greater tendency to wander. Movement data, however, do not support this premise, perhaps because of insufficient recaptures. However investigations were not carried out at any great distance from water. There were some indications of greater wandering tendencies on the part of N. erythrogaster. A slightly lower percentage of recaptures for N. erythrogaster than for N. rhombifera may indicate more extensive movement on the part of the former species. Tinkle (1957) had suggested that a paucity of recaptures might be explained by extensive movements. Also a slightly greater percentage of N. erythrogaster than N. rhombifera found on the paved highways during road counts (Table XV) may lend support to greater wandering tendencies on the part of the former species.

Some authors have commented that N. erythrogaster is the most common water snake in Texas (Strecker, 1915; Brown, 1950). The present study revealed N. rhombifera to be much more abundant than N. erythrogaster in the areas studied in Oklahoma. Diener (1957) found N. erythrogaster more abundant than N. rhombifera in Kansas, near the limits of the range of both species. It is probable that both species are now more abundant than formerly, due to the building, and stocking with fish, of water impoundments. These impoundments also provide breeding places for amphibians, and habitat for crayfish. It is likely that both species of Natrix are not only more abundant but are more widely and evenly distributed than they were at the turn of the century. Viosca (1924) stated that "Both rhombifera and taxispilota have the same habits and habitats, that is open water courses, and their distribution is closely associated with southern coastal rivers, rhombifera extending in range farther inland along the Mississippi Valley."

The differences between the general ecological niches of the diamond-backed water snake (Natrix rhombifera) and the plain-bellied water snake (Natrix erythrogaster) can be summarized in the following way. Natrix rhombifera is primarily a fish-eating snake, which tends to be more aquatic than does N. erythrogaster. This aquatic habit is logical in view of the piscatorial food habits of this species. The arboreal tendencies of N. rhombifera may also be linked to its aquatic habits in that escape into the water is facilitated by a plunge from an overhanging tree limb. *Natrix erythrogaster* exhibits a lower temperature tolerance for activity than does *N. rhombifera*, which may explain in part the distributional differences in these two species, the former extending farther north and west in its range than does the latter.

Natrix erythrogaster exhibits a food preference for frogs, and tends to be more terrestrial and more diurnal than does *N. rhombifera*. It may be that *N. erythrogaster*, being more terrestrial than *N. rhombifera*, would have greater wandering tendencies than the latter. Evidence for this, however, was slight.

These differences in food preference, temperature tolerance and in aquatic tendencies appear significant and sufficient in separating ecologically these two sympatric water snakes in Oklahoma.

LITERATURE CITED

Anderson, P. 1965. The reptiles of Missouri. Univ. Missouri Press, Columbia. 330 p.

Betz, T. W. 1963. The gross ovarian morphology of the diamond-backed water snake, Natrix rhombifera, during the reproductive cycle. Copeia 1963(4):692-697.

Blanchard, F. N., and E. B. Finster. 1933. A method of marking living snakes for future recognition, with a discussion of some problems and results. Ecol. 14:334-347.

Bowers, J. H. 1966. Food habits of the diamond-backed water snake, Natrix rhombifera rhombifera, in Bowie and Red River Counties, Texas. Herp. 22(3):225-229.

Brattstrom, B. H. 1965. Body temperatures of reptiles. Amer. Midl. Natur. 73(2):376-422.

Brown, B. C. 1950. An annotated check list of the reptiles and amphibians of Texas. Baylor Univ. Press, Waco. 259 p.

Burghardt, G. M. 1968. Chemical preference studies on newborn snakes of three sympatric species of Natrix. Copeia 1968 (4):732-737.

Burkett, R. D. 1966. Natural history of the cottonmouth moccasin, Agkistrodon piscivorus, (Reptilia). Univ. Kansas Publ., Mus. Nat. Hist. 17(9):435-491.

Cagle, F. R. 1937. Notes on Natrix rhombifera as observed at Reelfoot Lake. J. Tennessee Acad. Sci. 12(2):179-185.

______. 1942. Herpetological fauna of Jackson and Union Counties, Illinois. Amer. Midl. Natur. 28(1):164-200.

Carpenter, C. C. 1952a. 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.

______. 1952b. Growth and maturity of the three species of Thamnophis in Michigan. Copeia 1952(4):237-243.

______. 1953a. Weight-length relationship of Michigan garter snakes. Michigan Acad. Sci., Arts and Let. 38:147-150.

______. 1953b. An ecological survey of the herpetofauna of the Grand Teton - Jackson Hole area of Wyoming. Copeia 1953(3):170-174.

______. 1958. Reproduction, young, eggs, and food of Oklahoma snakes. Herp. 14(2):113-115.

Carr, A. 1940. A contribution to the herpetology of Florida. Univ. Florida Publ., Biol. Sci. Ser. III (1).

Cliburn, J. W. 1956. The taxonomic relations of the water snakes Natrix taxispilota and rhombifera. Herp. 12:198-200.

Conant, R. 1934. The red-bellied water snake, Natrix sipedon erythrogaster Forster in Ohio. Ohio J. Sci. 34(1):21-30.

______. 1938. The reptiles of Ohio. Amer. Midl. Natur. 20(1):1-200.

______. 1949. Two new races of Natrix erythrogaster. Copeia 1949(1): 1-15.

______. 1955. Notes on Natrix erythrogaster from the eastern and western extremes of its range. Chi. Acad. Sci. Nat. Hist. Misc. (147):1-3.

______. 1958. A field guide to the reptiles and amphibians of the United States and Canada east of the 100th meridian. Houghton Mifflin Co., Boston. 366 p.

______., and R. G. Hudson. 1949. Longevity records for reptiles and amphibians in the Philadelphia Zoological Garden. Herp. 5:1-8.

Diener, R. A. 1957. An ecological study of the plain-bellied water snake. Herp. 13:203-211.

Elton, C. 1939. Animal ecology. The MacMillan C., New York. 209 p.

Evans, P. D. 1942. A method of fishing used by water snakes. Chi. Natur. 5(3):53-55.

Fickess, D. R. 1962. Adrenal response of the diamond-back water snake (Natrix rhombifera) to stress. Herp. 18(4):250-253.

Fitch, H. S. 1949. Study of snake populations in central California. Amer. Midl. Natur. 41:513-579.

______. 1960. Autecology of the copperhead. Univ. Kansas Publ. Mus. Nat. Hist. 13:85-288.

______. 1963a. Natural history of the racer Coluber constrictor. Univ. Kansas Publ. Mus. Nat. Hist. 15:351-468.

______. 1963b. Natural history of the black rat snake (Elaphe o. obsoleta) in Kansas. Copeia 1963(4):649-658.

______. 1965. An ecological study of the garter snake, Thamnophis sirtalis. Univ. Kansas Publ. Mus. Nat. Hist. 15:493-564.

Flower, S. S. 1925. Contributions to our knowledge of the duration of life in vertebrate animals. III. Reptiles. Proc. Zool. Soc. Lond. 1925, 2:911-981.

Franklin, M. A. 1944. Notes on the young of the brown water snake. Copeia 1944(4):250.

Fukada, H. 1959. Biological studies on the snakes VI. Growth and maturity of Natrix tigrina tigrina (Boie). Bull. Kyota Gakugei Univ., Ser. B(15):25-41.

______. 1960. Biological studies on the snakes VII. Growth and maturity of Elaphe quadrivirgata (Boie). Bull. Kyoto Gakugei Univ., Ser. B(16):6-21.

______. 1961. Biological studies on the snakes VIII. On the growth formulae of snakes and their applications to other reptiles. Bull. Kyoto Gakugei Univ. Ser. B(17):16-40.

Gause, G. F. 1934. The struggle for existence. The Williams and Wilkins Co., Baltimore. 163 p.

Greding, E. J. Jr. 1964. Food of Natrix in Hunt County, Texas. Southwest. Natur. 9(3):206.

Guidry, E. V. 1953. Herpetological notes from southeastern Texas. Herp. 9(1):49-56.

Hardin, G. 1960. The competitive exclusion principle. Sci. 131:1292-1297.

Heyrend, F. L., and A. Call. 1951. Growth and age in western striped racer and the Great Basin rattlesnake. Herp. 7(1):28-40.

Hurter, J. 1911. Herpetology of Missouri. Trans. St. Louis Acad. Sci. 20(5):59-274.

Kennedy, J. P. 1964. Natural history notes on some snakes of eastern Texas. Texas J. Sci. 16(2):210-215.

Klauber, L. M. 1956. Rattlesnakes: Their habits, life histories, and influence on mankind. Univ. California Press, Berkeley and Los Angeles. 2 vol., 1476 p.

Laughlin, H. E. 1959. Stomach contents of some aquatic snakes from Lake McAlester, Pittsburg County, Oklahoma. Texas J. Sci. 11(1):83-85.

McGrew, W. C. III. 1963. Channel catfish feeding on diamond-backed water snakes. Copeia 1963(1):178.

Mertens, R. 1964. A longevity record for a hybrid water snake. Herp. 20(2):134.

Neill, W. T. 1948. Hibernation of amphibians and reptiles in Richmond County, Georgia. Herp. (4):107-144.

Perkins, C. B. 1955. Longevity of snakes in captivity in the United States as of January 1, 1955. Copiea 1955(3):262.

Pillstrom, L. G. 1954. A device for the collection of amphibians and reptiles. Herp. 10:180.

Platt, D. R. 1969. Natural history of the hognose snakes Heterodon platyrhinos and heterondon nasicus. Univ. Kansas Publ. Mus. Nat. Hist. 18(4):253-420.

Preston, W. B. 1964. The importance of the facial pit of the northern pacific rattlesnake (Crotalus viridis oreganus) under natural conditions in southern British Columbia. Unpubl. M. Sc. Thesis, Univ. British Columbia, 64 p.

Raney, E. C. and R. M. Roecker. 1947. Food and growth of two species of water snakes from western New York. Copeia 1947(3):171-174.

Rahn, H. 1942. The reproductive cycle of the prairie rattler. Copeia 1942(4):233-240.

Raun, G. G. 1965. A guide to Texas snakes. Museum Notes No. 9. A publication of the Texas Memorial Museum.

Schaefer, W. H. 1934. Diagnosis of sex in snakes. Copeia 1934(4):181.

Shaw, C. E. 1962. Longevity of snakes in the United States as of January 1, 1962. Copeia 1962(2):438.

Sisk, M. E., and C. J. McCoy. 1964. Stomach contents of Natrix r. rhombifera (Reptilia: Serpentes) from an Oklahoma lake. Proc. Okla. Acad. Sci. 44:68-71.

Smith, H. M. 1956. Handbook of amphibians and reptiles of Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ. N. 9, 2nd Ed. 356 p.

______., and E. H. Taylor. 1945. An annotated checklist and key to the snakes of Mexico. Smithsonian Institution, U. S. Natl. Mus. Bull. 187. Wash. 239 p.

Stebbins, R. C. 1966. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston. 279 p.

Stickel, W. H., and J. B. Cope. 1947. The home range and wanderings of snakes. Copeia 1947(2):127-137.

Strecker, J. K. 1915. Reptiles and amphibians of Texas. Baylor Bulletin 18(4), Baylor Univ. Press, Waco. 82 p.

______. 1927. Observations on the food habits of Texas amphibians and reptiles. Copeia 1927(162):6-9.

Tinkle, D. W. 1957. Ecology, maturation and reproduction of Thamnophis sauritus proximus. Ecol. 38:69-77.

______. and E. A. Liner. 1955. Behavior of Natrix in aggregations. Field and Lab. 23(3-4):84-87.

Viosca, P. Jr. 1924. A contribution to our knowledge of the water snakes. Copeia 1924(126):3-13.

Volsøe, H. 1944. Structure and seasonal variation of the male reproductive organs in Vipera berus (L.) Spolia Zool. Mus. Hauniensis V. Reprint., Copenhagen. p. 1-172.

Woodbury, A. M. 1951. Symposium: A snake den in Tooele County, Utah. Introduction - A ten-year study. Herp. 7(1):4-14.

Wright, A. H., and A. A. Wright. 1957. Handbook of snakes. Comstock Publishing Associates, Ithaca. 2 vol., 1105 p.