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BIOLOGICAL PRODUCTIVITY OF SNAKES OF THE PAWNEE SITE, 1970-1971

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TABLE OF CONTENTS

Page

ABSTRACT

An estimate of energy flow through snakes on the shortgrass prairie was provided by employing information from the literature, performing specific pilot studies in the laboratory, and determining species composition and some aspects of population dynamics in the field. During 1970 and 1971, 228 prairie garter snakes (*Thamnophis radix*), 33 prairie rattlesnakes (*Crotalus viridis*), 31 gopher snakes (*Pituophis catenifer*), and 17 western hognosed snakes (*Heterodon nasicus*) were collected, marked, weighed, measured, and released on the Pawnee Site of the U.S. IBP Grassland Biome. Of the 309 snakes released, 48 were recaptured at least once. The mean live weight of resident snakes of all dry-land species was found to be 84.3 g/ha during the summer months. A study plot near the only permanent water on the Pawnee Site was found to have a live weight summer biomass of *T. radix* of 1248 g/ha. Pilot studies measured respiration rates, excretion rates, and gross energy of snakes.

A model was developed showing energy input from prey species into snake populations and the subsequent major energy losses. This model will become one component of a complex series of models produced by the IBP Program, which will represent the major energy relationships within different trophic levels on the shortgrass prairie. The eventual result of the IBP effort will be the mathematical manipulation of selected factors in the ecosystem, leading to predictions about the effect of each factor on productivity in the Grassland Biome sites.

INTRODUCTION

This study has been developed as an integral part of the United States' contribution to the International Biological Program (IBP). The IBP was developed by the International Council of Scientific Unions as a worldwide, nongovernmental organization in which more than 70 countries are currently participating. In the United States the IBP has been sponsored by the National Academy of Sciences.

The overall purpose of the IBP is to examine the biological basis of productivity in human welfare. A major objective of the IBP is the organized worldwide study of organic production on the land, in fresh waters, and in the seas so that adequate estimates may be made of the potential yield of new, as well as existing, natural resources. In light of these objectives, it is proposed that an intensive study of the entire ecosystem be made in each of the following biomes--grassland, tundra, desert, coniferous forest, deciduous forest, and tropical forest.

The rationale behind the IBP ecosystem analysis was stated in the original proposal (Van Dyne, 1969):

> "There is an increasing human awareness of man's part in ecosystems and his influence on them. Traces of his pesticides can be found in living organisms throughout the world. Induced instability of ecosystems is an important cause of economic, political, and social disturbances. Conversely, man's attempts at solution of social problems frequently causes ecosystem disruption due to his own ignorance. The gravest problem facing man in a peaceful world is the establishment of a reasonable balance and harmony between a stabilized world population and the environmental resources upon which that population depends.
>
> In altering his environment in order to overcome its limitations for him, man learns that he often is faced with undesirable, as well as desirable, consequences of environmental change. In manipulating and managing his environment, seldom has he foreseen the full consequences of his action, whether

> advertent or inadvertent. Human populations are increasing at an unprecedented rate. Technological power is altering the environment at an increasing rate. Yet we have developed and are still in the process of developing much technology and scientific knowledge that will enable us to better perceive the influences of our management of ecosystems. While exploitation of ecosystems is still occurring throughout the world, the consequences are yet unknown. And we need to know the long-term effects, both losses and profits, resulting from ecosystem manipulation, such as the further shortening of food chains, as human populations continue to increase exponentially and impose greater stresses on our world resources. We need to know more about the structure and function of ecosystems.
>
> The functions of an ecosystem include transformation, circulation, and accumulation of matter and flow of energy through the medium of living organisms and their activities, and through natural physical processes. Some specific functional processes include photosynthesis, decomposition, herbivory, carnivory, soil formation, chemical finding, leaching, and nitrogen fixation. The ecosystem must be studied as a whole in order to understand the energy transformation, the hydrologic cycle, or cycles of carbon, nitrogen, phosphorus, or other elements. Thus, directly or indirectly, understanding ecosystems and the ecosystem concept is fundamental in the management of renewable resources such as forests, ranges, watersheds, fisheries, wildlife, and agricultural crops and stock. Cooperative studies on large-scale ecosystems are needed before existing theory can be applied fully to their management."

This study was done on the IBP Pawnee Site which is a 15,000-acre station on the shortgrass prairie and located 12 miles northeast of Nunn, Colorado. The purpose of the study was to determine the bioproductivity of snakes in the shortgrass prairie, as one phase of the total ecosystem analysis. Information was collected in the field during 1970 and 1971 on the species present, population densities, distributions, sex ratios, sizes, and growth rates of snakes on the shortgrass prairie. These data were correlated with laboratory studies done during the same period on reproduction, respiration, excretion, and fat storage in snakes. An energy flow model was developed from these field and laboratory studies. This model describes the ecological role of snakes in such a way that it can be incorporated as *one* of many different components into a systems analysis framework. This study makes a direct contribution to the understanding of energy flow relationships through one group of organisms on the shortgrass prairie ecosystem.

LITERATURE REVIEW

Bioproductivity

Basically the energy flow through a trophic level equals the total assimilation (biomass plus respiration) at that level (Odum, 1959). Complex natural communities can be divided into different trophic levels, where each level contains organisms which obtain food from plants by the same number of steps (Elton, 1927). In a study of bioproductivity, the amount of energy flow through specific organisms, and consequently through trophic levels, would be determined. This study was concerned with various aspects of energy flow through four species of shortgrass prairie snakes in order to determine the ecological efficiency of this group. No studies were found which concern bioproductivity of these species. However, numerous studies were found which concerned one or more of the "components" necessary for determining bioproductivity. Data concerning the prairie garter snake (*Thamnophis radix* Kennicott), the gopher snake (*Pituophis catenifer affinis* Hallowell), the prairie rattlesnake (*Crotalus viridis viridis* Rafinesque), and the western hognosed snake (*Heterodon nasicus nasicus* Baird and Girard) were therefore reviewed under the appropriate major "component" headings: growth, movement, reproduction, population density, food preference, respiration, natural predators, longevity, and trapping and marking techniques.

Growth

C. viridis adults were found to lose approximately 4% of their body weight during the dormant period. It was further found that young snakes of the same species lost over 20% of their body weight (Klauber, 1937).

Fitch and Glading (1947) found that adult female *C. viridis* usually weigh from 300 to 400 g, and seldom exceeded 500 g. Males were found to be considerably larger, occasionally more than 1200 g.

It was suggested that a rodent or lizard population of small sized individuals must have been available to provide food for young snakes during their first year if they were to survive (Fitch, 1947).

Fitch (1949) estimated that *P. catenifer* and *C. viridis* must consume twice their own weight in prey species annually to survive. Fitch found growth in *C. viridis* highly variable. He found that young were about 280 mm; after 18 months they had reached approximately 500 mm, and at the age of 3 years they had reached the small adult size of about 700 mm. Growth rates for gopher snakes were found to be more rapid than for rattlesnakes. Weight change for individuals of either species were unpredictable. Fitch estimated that a 2-year-old *P. catenifer* would have a head and body length of more than 800 mm.

In a study of *P. catenifer* in Nebraska, Imler (1945) concluded that young grow about 15 inches the first year and 7 or 8 inches in the second year.

The overwintering mortality for *C. viridis lutosus* was found to be 34%. It was further found that the average body weight lost by an adult was 7.6%. Hatchling *C. viridis lutosus* had high mortality rates and lost an average of one-fourth of their body weight overwintering (Hirth, 1966*b*).

Movement

Fitch found a complete lack of any homing tendency by *C. viridis* when released at some distance from the point of original capture. He found that these rattlesnakes remained in small areas and seemed to lack long wandering tendencies. *P. catenifer* were also found to be attached to limited areas of a few hundred feet in diameter, at most, and remain in such areas over periods of years. Fitch also studied the garter snake, *Thamnophis elegans*, in the vicinity. He found them limited to the intermittant streams and found evidence that they wandered far more extensively than other species, evidently following the watercourses. He found that although different in other respects, all nine species of snakes in the area studied were similar in their seasonal activity. They were dormant from mid-October through mid-March and appeared in greatest numbers shortly after emergence. Snakes were found to taper off abruptly during the dry months of June, July, and August. This was thought to be due to the change to nocturnal activity periods. Adults kept in simulated natural surroundings were rarely seen at all during the summer days, but young were prowling early in the morning and evening (Fitch, 1949).

Horn and Fitch (1942) originally felt that snakes wandered at random. Stickel and Cope (1947) suggested that the long trips of some individuals and the tendency for juveniles to wander may make it appear that the populations wander randomly. Later, Fitch (1947) independently arrived at the same conclusion as Stickel and Cope. However, no evidence has been found showing that the rattlesnakes have one home base, according to Fitch. He felt that the snakes selected temporary shelters during their movements.

The movement of the prairie garter snake, *T. radix*, was studied in Illinois. Of 298 marked on a 3.2-acre strip, 41 were recaptured. Most snakes had moved less than 50 ft from the original point of capture. The investigators collected snakes by hand and did not report weights. They attempted to correlate the number of *T. radix* collected per week with weather conditions, but found no definite relationship. A growth rate of .45 inches per week was found, with a total length of 18 inches at the end of the first year. Two-year-olds grew at the rate of .37 inches per week, and at the end of the season they were 22 to 24 inches in length. Third-year snakes were estimated at 26 inches. Most of the largest snakes of *T. radix* were females (Seibert and Hagen, 1947).

Hirth et al. (1969) tracked the movement of the great basin rattlesnake, *Crotalus viridis lutosus*, tagged with radioactive Ta^{182} by using a gamma scintillometer. They found that these rattlesnakes exhibited radial dispersion patterns from the hibernaculum, and that the snakes did not remain or concentrate in any particular areas on the summer range. The rattlesnakes did not generally disperse farther than 1000 m from the den, although in some instances they were found 1.02 km away. Snakes showed a mass wandering tendency and the authors suggested that a foraging range would apply better than a traditional mammalian home-range concept. The rattlesnake population was found to have a foraging range of about 2.5 km^2. The investigators found that gopher snakes, *Pituophis catenifer deserticola*, emerged in late April, while the rattlesnakes emerged from the dens in early to middle May. In the fall the snakes began to return to the den before the onset of cooler weather. Rattlesnakes came back first, usually starting in early September.

The authors indicate that a biological clock mechanism may trigger the return. During the summer rattlesnakes moved randomly in both direction and distance. Rattlesnakes shedding their skins could be located in almost the same spot daily until the molting was complete. After the molting they would rapidly leave the area. No rattlesnakes were ever found below ground in this study, and a high percentage of them did not rattle when approached. The authors imply that this may be due to human selection against the rattle, where snakes that make noise are killed and the quiet ones survive and produce offspring. Sixteen rattlesnakes were recaptured out of 51 marked in this study.

In 1.5 hr a *C. viridis* moved 100 m to return to a den. If a rattlesnake could continue at this rate, it could travel a kilometer in 15 hr. Hirth (1966*a*) also proposed that snakes follow scent trails to return to the den site.

Spacial relationships have been studied in some common snakes by using radiotelemetric methods. Snakes were force-fed radio transmitters and were followed. *P. catenifer*, the gopher snake, was found to move an average of 142 m/day (Fitch and Shirer, 1971).

Reproduction

Rahn (1942) presents evidence for a 2-year reproductive cycle for *C. viridis* in Wyoming. He showed that sperm can survive the winter in the vagina and ovulation may occur in the spring.

Other indications were found that *C. viridis* breeds on alternate years. Fitch found that some ova are usually much larger than others, and that the smallest ones may not be destined to develop into snakes during that season. He expected litters averaging less than 9.9, which was the average number of large eggs per female (Fitch, 1949).

About 171 days elapse between the dates of spring mating and the fall appearance of newborn young in the subspecies, *C. viridis oreganus* (Fitch and Glading, 1947).

Imler (1945) records an average of 12.8 eggs per female *P. catenifer sayi* in Nebraska. Schmit and Davis (1941) report clutches of 10 and 19 in *P. catenifer*.

A sex ratio of 1.38 males to 1 female was found for 243 *P. catenifer*. There were more male than female *C. viridis*, but it was noted that the difference may have been due to the fact that males were more active and had larger ranges and, therefore, were caught more frequently (Fitch, 1949).

Stebbins (1954) reports that captive gopher snakes, *P. catenifer*, have an egg incubation period requiring from 64 to 71 days, and that the average clutch size was 6.8. He further reports that western hognosed snakes, *H. nasicus*, average 11 eggs per female in Kansas. The eggs are laid in June or July and hatch in late August or September. Stebbins lists *T. radix* as mating in April and May. Young are born from late July through September and broods range from 13 to 40. At birth, Stebbins estimated the total length at 6 or 7 inches (152 to 179 mm).

Population Density

Such factors as secretiveness, inactive periods, erratic nature of movements, and unknown rates of population turnover cause population densities to be difficult to measure. Fitch wrote that home ranges were larger for male *C. viridis* than for females. From recapture data, he estimated the density of rattlesnakes at 1.2/acre, and gopher snakes occurred in a density of about .3/acre, both having an average weight of nearly .5 lb. per snake. It was found that both *P. catenifer* and *C. viridis* were attached to areas a few hundred feet in diameter, at most, and remain in such areas over periods of years (Fitch, 1949).

Literature reviewed by the United States Department of the Interior showed that pesticides affect population changes in many groups of animals (Stickel, 1968). Bauerle and Spencer (1971) studied organochlorine pesticides in *P. catenifer* and *C. viridis* on the Pawnee National Grassland. They found that *P. catenifer* contained a mean of .20 ppm of p,p'-DDE, .04 ppm of dieldrin, .013 ppm beta benzene hexachloride, and .01 ppm heptachlor epoxide. *C. viridis* contained .62 ppm p,p'-DDE and .03 ppm dieldrin.

Food Preference

Food preferences of *C. viridis* and *P. catenifer* were similar, but methods of hunting were shown to differ. The rattlesnake lies at a strategic point, strikes, and then attempts to track down its poisoned prey. The gopher snake tends to actively search out its prey and, therefore, commonly feeds on prey in the nests. Snake predation pressure was distributed over many species, and it eliminated a substantial annual increase of ground squirrels, cottontails, and kangaroo rats--three of the species which are important destroyers of range forage. It was found that 69.5% of the food items found in *P. catenifer* were eggs or young rodents which must have been found in the nest by the prowling snake. Of 164 rattlesnakes containing food, however, only two had eaten animals (rabbits) too young to have left their nests. The percentage, by weight, was estimated for the diet of *C. viridis* for 285 items and found as follows: ground squirrel, 68.8%; cottontail, 17.3%; kangaroo rat, 5.5%; pocket gopher, 2.5%; woodrat, 1.7%; six species of mice; four species of lizards; and one species of chipmunk, quail, towhee, and spadefoot toad, each less than 1% (Fitch, 1949). Table 1 contains a summary of reported food items from species present on the Pawnee Site.

Respiration and Temperature

Brody (1945) reported that:

> "In poikilotherms the speed of the life processes, such as feeding, growth, metabolism, aging, etc., increases with temperature up to a certain limit (depending on species) in accordance with the Van't Hoff law, just as the speed of inanimate reactions does. Since temperature probably affects the anabolic (productive) and catabolic (destructive, maintenance, aging) processes to an equal degree, the gross or overall energetic efficiency of the transformations is likely to remain unchanged. By the same reasoning, if all other conditions are equal, the gross energetic efficiency is likely to be the *same* in poikilotherms and homeotherms in spite of enormous body temperature and energy-metabolism differences."

The effect of body temperature on 0_2 consumption in the gopher snake, *P. catenifer affinis*, was studied by taping snakes to a rubber rod and fitting them with a mask. It was found that resting oxygen consumption (T_B) increases with body temperature according to the equation

$$\text{ml } 0_2 \text{ g}^{-1}\text{hr}^{-1} = 0.324/(37.4-T_B)$$

where T_B = 10 to 35°C (Greenwald, 1971).

The effect of temperature on carbon dioxide production in *T. radix* was studied by Kerns (1971). It was found that the mean values for adults of both sexes were as follows: .00158 mg CO_2/g/min at 22°C, .00194 mg CO_2/g/min at 28.5°C, and .00369 mg CO_2/g/min at 35°C.

Table 1. Reported food items of four species of snakes from the Pawnee Site.

Species	Birds	Bird Eggs	Carrion	Earthworms	Fish	Frogs	Insects	Lizards	Reptile Eggs	Small Mammals	Mollusks	Salamanders	Snakes	Tadpoles	Toads	Leeches
Crotalus viridis	K	K				K		K		K						
	F							F		F					F	
															D	
										S						
	G							G		G					G	
Heterodon nasicus								P	P	P			P			
	G					G		G	G	G		G			G	
	E					E		E		E					E	
						H		H				H			H	
	A									A					A	
Pituophis catenifer	S	S								S						
	G	G						G		G						
	C	C								C						
	A	A								A						
	F	F						F		F						
Thamnophis radix			H	H	H	H	H								H	H
			S	S	S	S	S								S	

Key to the authority cited: A--Anderson, 1965; C--Conant, 1958; E--Edgren, 1955; F--Fitch, 1949; K--Klauber, 1956; P--Platt, 1966; S--Schmidt and Davis, 1941; D--Stabler, 1948; G--Stebbins, 1954; H--Stebbins, 1966.

Hirth et al. (1969) found that rattlesnakes, *C. viridis*, possessed locomotor and defensive ability at 9.6°C body temperature. They feel that the ecological minimum for rattlesnakes is below 9°C.

The optimum activity air temperature for *C. viridis* was between 80° and 90°F (Fitch and Glading, 1947).

Klauber (1956) found that a specimen of *C. viridis lutosus*, acclimated at 3.5°C, could crawl around without urging and could flicker its tongue. He places the ecological minimum at 8°C and the normal activity range between 26.5° and 32°C. Klauber also noted that partially frozen rattlesnakes are often able to recover.

Hirth et al. (1969) studied the thermal responses and behavior of the gopher snake, *P. catenifer deserticola*, using a hygrothermograph and telethermometer. Cloacal temperatures were recorded and compared to air temperature, ground temperature, and relative humidity in the field. They found that the maximum voluntary thermal tolerance was about 32°C. Body temperatures dropped rapidly at night (as much as 12°C for 3 hr). The gopher snake showed no behavioral changes from 20° to 15°C, indicating that its voluntary minimum may not have been reached.

The critical maximum temperature of the gopher snake, *P. catenifer deserticola*, was 40.5°C, and the threshold for normal locomotion of juvenile snakes was about 18°C. Brattstrom (1965) feels that this is near the voluntary minimum.

Seasonal changes in the body composition of *Thamnophis sirtalis* were studied at northern latitudes. Evidence was found to support the suggestion that a reduction in the water content percentage in the autumn represented a resistance to freezing (Aleksiuk and Stewart, 1971).

Lueth (1941) studied the effects of temperature on prairie garter snakes, *T. radix*. He found that between 50°F and 86°F, snakes had a rectal temperature nearly equal to the external temperature. However, at temperatures below 50°F the snakes had temperatures higher than ambient, and above 80°F the snakes had temperatures below ambient.

Natural Predators

Fitch (1949) shows that hawks, owls, and coyotes are major predators of *P. catenifer* and *C. viridis*. He further notes that man is responsible for killing large numbers of the breeding populations of both species.

Evidence of rattlesnake scales and several radioactive tags in the fecal pellets of badgers were found (Hirth et al., 1969).

Longevity

C. viridis is likely to be as old as 20 years in the wild. Life expectancy was found to increase as larger size was attained. This conferred increasing immunity to the dangers that beset small young (Fitch, 1949).

Trapping Techniques

In an attempt to control bullsnakes on a Nebraska wildlife refuge, Imler (1945) developed an effective wire trap for catching snakes. Further modifications of this trap (Dargan and Stickel, 1949) led to the development of wire mesh funnel traps, which were used in conjunction with 25-ft drift fences to divert snakes to the traps. By using this method, Dargan and Stickel caught 67 snakes, with 13 recaptures, in a 2-year period.

Stebbins (1954) recommends the use of pit traps and funnel traps for collecting snakes.

A 3-ft tall bronze fence was used to divert snakes emerging from a hibernaculum into funnel and can traps (Hirth et al., 1969).

Marking Techniques

In 1933, Blanchard and Finster (1933) developed the scale clip method for marking live snakes for future recognition. Use of this quick, simple, and essentially painless technique of clipping specific belly scutes was important for snake population studies. Most other marking methods required pain or extensive handling which served to alter normal behavior patterns.

Hirth et al. (1969) tagged snakes with radioactive Ta^{182} using gamma scintillometers for tracking. Radiotelemetric methods have been used to study snake movements (Fitch and Shirer, 1971).

METHODS AND MATERIALS

On January 20, 1970, field work began at the IBP Pawnee Intensive Site with the initial selection of study areas and the construction of traps. Regular observations began on April 4, 1970, to determine the time of emergence of wintering snakes from their dens. Beginning on May 3, 1970, each study plot was surveyed three times per week, until October 12, 1970 at which time most snakes were back in their dens.

During 1971 sampling began on April 15. Snakes were surveyed approximately 15 times per month on alternate days from April 29 through October 13, 1971. Most snakes had returned to their dens by October 13, 1971.

STUDY AREA ON THE PAWNEE INTENSIVE SITE

Snakes were collected on three selected plots on the intensive study area (Fig. 1). The first study plot (the ridge section) was purposely

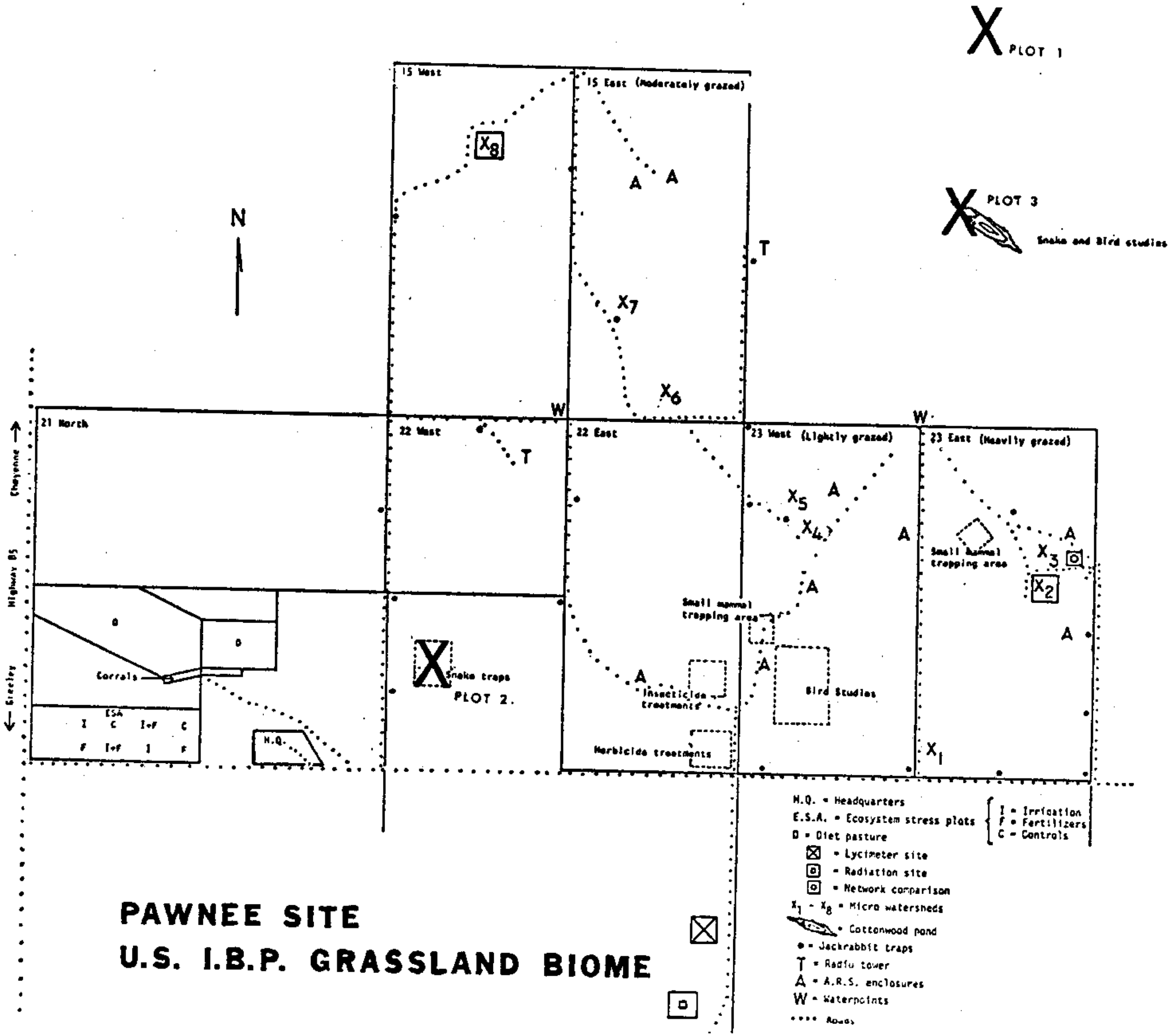


Fig. 1. Intensive study area on the Pawnee Site.

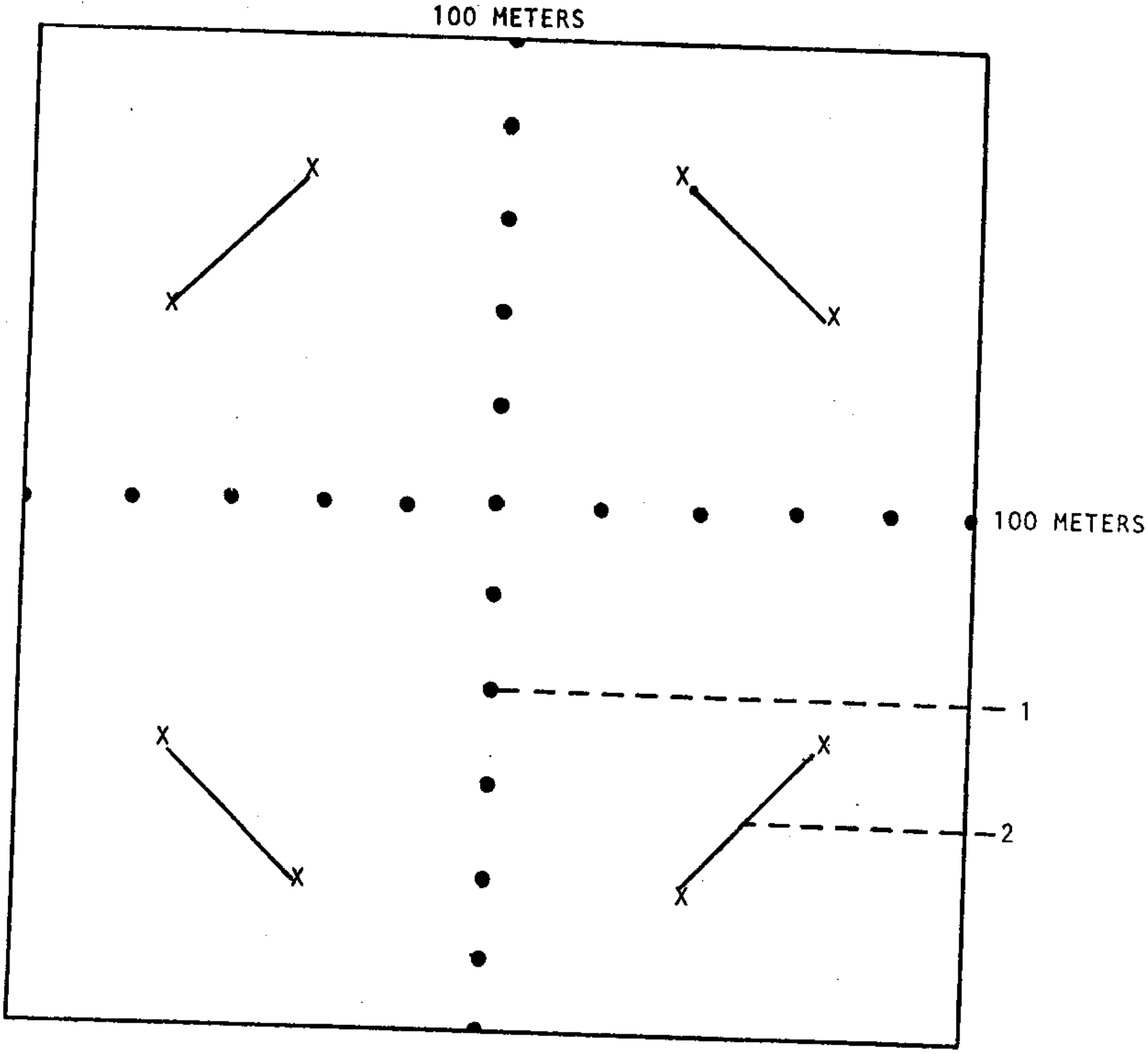
selected to minimize human influence on snake activities. This plot was located approximately 700 m north of Cottonwood Pond in section 11. Small animal burrows provided potential denning and residence sites for snakes in nearby ravines. Major plants in this plot were *Aristida longiseta*, *Atriplex canescens*, and *Opuntia polyacantha*.

The second study plot (the prairie dog town section) was located on the edge of an active black-tailed prairie dog town. It was about 900 m northeast of the Pawnee Site headquarters in section 22, and it was about 200 m east of a frequently traveled road.

The third study plot (Cottonwood Pond section) was located on the edge of the only permanent water on the Pawnee Site. Vegetation on this plot mainly consisted of cattails, *Typha angustifolia*, and reed grasses. During moist years much of this study plot was subjected to commercial haying operations, and cattle were frequently present on this area during the summer months.

Each of the study plots were square, having an area of 2.5 ha. The sides of each plot were further subdivided into 10-m intervals which were designated by white markers placed at ground level. The markers served as a grid to accurately locate captures (Fig. 2).

Study areas for destructive sampling were located on the Pawnee Grassland within 10 miles of the Intensive Site. Snakes were collected from these known denning locations at intervals for fat body studies, egg counts, dry weights, and other measurements.



1. Pit traps spaced 10 m apart.

2. Drift fences with funnel traps at the ends (X).

Fig. 2. Diagram of drift fence and pit trap locations on study plot no. one and no. two.

SNAKE COLLECTING PROCEDURES

Method 1

Snakes were collected on each of the study plots 3 days per week from May 3 until October 12, 1970, and on alternative days from April 15 through October 13, 1971. Each study area was surveyed by slowly walking back and forth between 10-m markers. This put the observer at a maximum distance of 5 m from any snake, a close visible or audible distance in the shortgrass prairie. Providing no tagging had to be done, 40 min was required to survey each plot. The time of day for observations varied with the season. During June, July, and August most observations took place in the morning or in late afternoon and into the crepuscular period.

Method 2

One method of snake capture was by continuous trapping using drift fences and funnel traps. Drift fences were constructed of rustproof metal strips that were 15 m long and 20 mm high. This barrier was supported by metal stakes every 2 m and were positioned flush with the ground. Funnel traps were placed at the ends of each drift fence (Fig. 3). Each trap employed a cone-shaped wire mesh to funnel animals moving around the barrier from either side into a cylindrical hardware cloth trap. The funnel cone was held flush to the ground by galvanized nails.

The opening of the funnel trap was constructed so that fine wires extended into the trap at the narrow opening. The wires did not interfere with the entrance of small animals into the trap, but prevented their escape. A door was placed at the rear of the trap for quick removal of specimens, and a sun shade was constructed for each trap. Snakes, lizards,

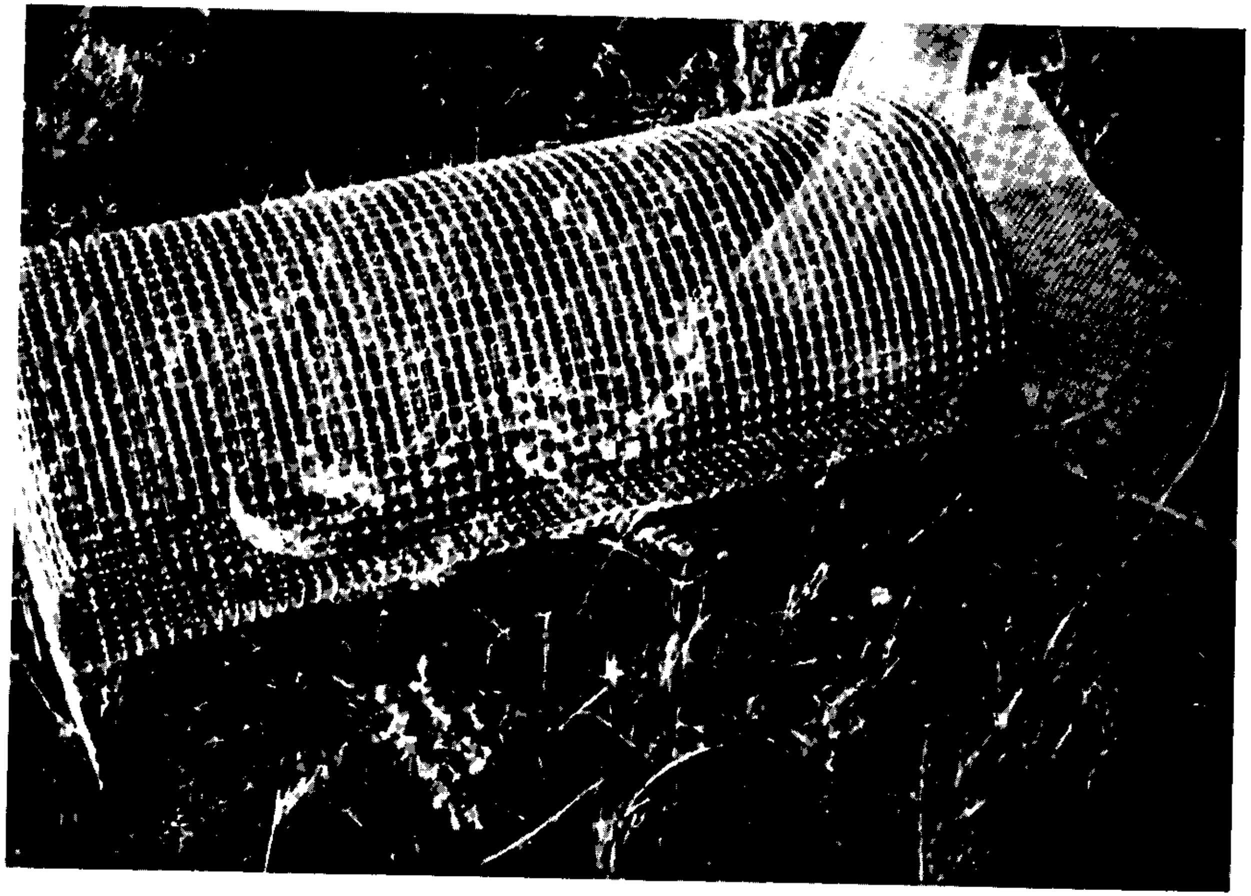


Fig. 3. Funnel trap (drift fence removed) containing *P. catenifer* at study plot number one.

insects, and small mammals confronted with the drift fence barrier were diverted into the traps.

Each study plot had four drift fences with traps. Two drift fences were placed at the Cottonwood Pond plot in 1970. They became ineffective in early June 1970, because vegetation became so tall and dense that fences would no longer divert animals to the traps. During 1971 a lawn mower was periodically used to cut the vegetation along the drift fence, and this made the traps effective. Four drift fences with funnel traps were used during 1971 and were placed along the north and the west end of Cottonwood Pond.

Method 3

Night lighting for nocturnal species was done on June 17, June 19, July 26, and August 4, 1970. On each occasion, a group of observers walked the study areas and the surrounding hills after dark using headlamps, flashlights, and Coleman lanterns. Red filters were placed over the same number of lights on July 26 and August 4. At least 4 hr were spent on each of these occasions.

Method 4

Nearly 3 hr per week were spent driving the Intensive Site roads and the surrounding gravel and asphalt roads observing snakes at dusk. Snakes have been shown to move onto such roads in spring and fall to control body temperature. The 2-mile stretch of seldom used asphalt highway, southeast of the Intensive Site, was regularly checked for snakes throughout the study.

Method 5

Pits 60 cm deep and 25 cm wide were drilled into the ridge and prairie dog town study plots on September 16, 1970, by the use of a power fence-post digger. Twenty pit traps, placed 10 cm apart and arranged in an equal cross, were placed on each study plot. A rustproof metal sleeve, 20 cm deep, was placed in each hole at ground level to prevent animals from escaping. The outside holes of the cross-shaped series of pit traps had short drift fences, 2 m by 15 cm.

Method 6

Snakes were collected away from these permanent study grids on the Intensive Site. Other U.S. IBP research teams that found snakes in the course of their work on the Pawnee Site were requested to capture them when possible, place them in bags in the shade, and leave a note on the main chalkboard. The response to this request was excellent, and consequently numerous snakes were collected by other investigators.

Method 7

Once each week during the 1971 collecting period, a "prime time line transect" was made on the intensive study area. In this method, the starting point and direction of movement were randomly selected. The investigator moved in a straight line, watching for snakes, for a distance of 1 mile from the starting point. These transects were walked during selected periods of the day when snakes were assumed to be most active. They usually occurred early in the morning or at dusk when the temperature approached 25°C. Approximately 3010 m^2 of ground per week were sampled by this method.

Method 8

Respiration was determined by a Beckman Model 315A infrared gas analizer with a Moseley Model 680 autograph. Snakes were placed in a temperature-controlled continuous air flow chamber to measure CO_2 production. Data were collected at 23.5° and 30°C with a scrubbed air flow of 570 ml/min. Snakes were allowed time for acclimation, and measurements were taken only when snakes were inactive. Average sized male snakes of each species were selected to eliminate variations due to gravid conditions or physical abnormalities. This study was meant to provide only an estimate of respiration rates in the different species; therefore, only four snakes were used.

Method 9

Food utilization was measured on an individual *C. viridis* in order to determine the number of kilocalories of energy lost to the body by excretion. Six male laboratory mice (*Mus musculus*) were selected from the same litter for this study. Live weight was determined for three mice; they were sacrificed and then dried at a temperature of 200°C until the body weight remained constant. The dry weight was then recorded. For the second group of three mice, the live weight was determined and each was fed to an acclimated *C. viridis* on alternating days over a 5-day period. This snake was an 813-mm, 276.3-g male which was kept in a covered cage at 22°C. The snake had not been fed for 2 weeks previous to the experimental feedings. The floor of the cage was lined with chromatographic blotter paper which had been dried to a constant value and weighed. Two weeks after the final feeding of mice, the blotter paper was removed with the excrement, re-dried to a constant value, and weighed. Excrement was then removed (by scraping), blended, and analyzed for the number of kilocalories per gram by bomb calorimetry at the Natural Resource Ecology Laboratory at Fort Collins, Colorado.

Method 10

Gross energy determinations were made on one individual of each species in order to determine the caloric value of each snake's biomass. The following sized snakes were used: *T. radix*, 54.7 g and 632 mm in total length; *P. catenifer*, 595.2 g and 1472 mm; *H. nasicus*, 65.3 g and 478 mm; and *C. viridis*, 95.9 g and 541 mm. Each snake was frozen alive, thawed, ground in a food grinder, and blended for 5 min in a commercial blender at medium speed. The mixtures of each snake sample were then frozen and taken to the CSU Department of Biochemistry for freeze-drying. After completion of the freeze-drying, samples were blended again and three randomly selected samples from each species were measured in the bomb calorimeter by IBP technicians.

SNAKE MARKING TECHNIQUES

Sex Determination

All snakes were weighed, measured, sexed, marked, and immediately released (Appendix Table 1). Males were recognized by probing caudally with a moistened probe behind the vent, a deep pocket signifying the presence of inverted hemipenises.

Clip Methods

All snakes were marked by a standard scale clip [modified Blanchard and Finster (1933) method]. In this method the enlarged belly scute covering the vent was given the no. 0. Moving anteriorly, the next scale was no. 1

followed by no. 2, and so on. The tenth belly scute was no. 10, the eleventh was no. 20, the twentieth was no. 100, the twenty-first was no. 200, etc. By this numbering system, many snakes can be marked in one area. A small triangular section was cut into the dermal layer of each scute, leaving a scar. The scar has been shown to remain as long as 3 years if properly cut, but clips were renewed with each recapture to counteract any new growth.

The prairie rattlesnake (*C. viridis viridis*) was marked by a second method. A number was sealed onto the newest rattle nearest the head, with a heavy coating of clear enamel. This mark was readily identifiable to other investigators in the field who did not know the scale clip code. A special holding device was constructed, using a soft plastic tube and circular clamps, to enable a single investigator to mark and measure snakes.

DESTRUCTIVE SAMPLING TECHNIQUES ON VALIDATION SITES

Some 27 specimens of the prairie rattlesnake, *C. viridis*, were collected from two denning sites on the Pawnee Grasslands in 1970. These snakes were frozen on capture and later dissected. Fat bodies and eggs were weighed and counted. Snakes were dried at 100°C to a constant weight, weighed, ashed, and then ash weights were determined for each specimen. Snakes were collected and processed both in the spring and fall in order to compare fat storage, egg counts, and growth for this period of time.

MODIFIED TECHNIQUES

The prairie garter snake, *T. radix*, required different techniques early in the summer of 1970. By May 29, these were present in such numbers that after 100 snakes were marked it was considered necessary to reduce sampling to once every 3 weeks. Some 20 University of Northern Colorado students participated in collecting these snakes at Cottonwood Pond on June 25 and August 13, 1970. Groups of students spread 1 m apart walked slowly through the study area capturing snakes by hand or net. After July 1970, the dense vegetation greatly hampered all collecting efforts in the Cottonwood Pond area.

Beginning in 1971, the mowing of vegetation in front of drift fences made trapping effective. This became the major collecting method for *T. radix*, and traps were emptied on alternating days throughout 1971.

RESULTS BY SPECIES

Thamnophis radix Kennicott, The Prairie Garter Snake

During 1970 and 1971, 228 *T. radix* were marked and released in the field. Males made up 39.9% of the marked population. There were 43 recaptures during 1970 and 1971 for an 18.9% recapture rate (Table 2).

The larger snakes of this species were usually females. The mean weight of the marked population was 39 g with a standard deviation of 33 g (Fig. 4). The mean length of this population was 525 mm with a standard deviation of 142 mm. The coefficient of correlation of length to weight was +.860, and the regression equation best fitting the length to weight curve of the population in Fig. 4 was

$$\text{Weight} = -15.2 + .0018\ \text{Length}^2$$

Growth rate. From the use of two indexes (weight and length), the growth rate of *T. radix* was .002 g/snake/day, and .018 mm total length/snake/day (Table 3). The maximum growth per unit time was by female no. 200. This snake gained 48.5 g and 296 mm in 52 growing days. *T. radix* no. 300

Table 2. Numbers of snakes marked or recaptured during each month of 1970 and 1971. Note that in 1970, sampling occurred every third day, whereas in 1971 it occurred on alternate days. In 1970 there was large group collecting both early and late in June, after which collecting was greatly hampered by long grass in the Cottonwood Pond plot. This accounts for the large difference in numbers of *T. radix* between June and July, 1970. Increased captures of *C. viridis* in October 1971, were due to discovery of a denning area south of study area two.

Species	April		May		June		July		August		September		October	
	1970	1971	1970	1971	1970	1971	1970	1971	1970	1971	1970	1971	1970	1971
T. radix	0	0	29	1	99	33	4	46	10	26	1	15	0	0
P. catenifer	0	0	2	8	3	5	3	1	1	2	0	3	2	1
C. viridis	0	1	3	4	2	0	1	3	0	2	2	7	0	12
H. nasicus	0	0	3	1	0	2	3	6	0	2	0	0	0	0

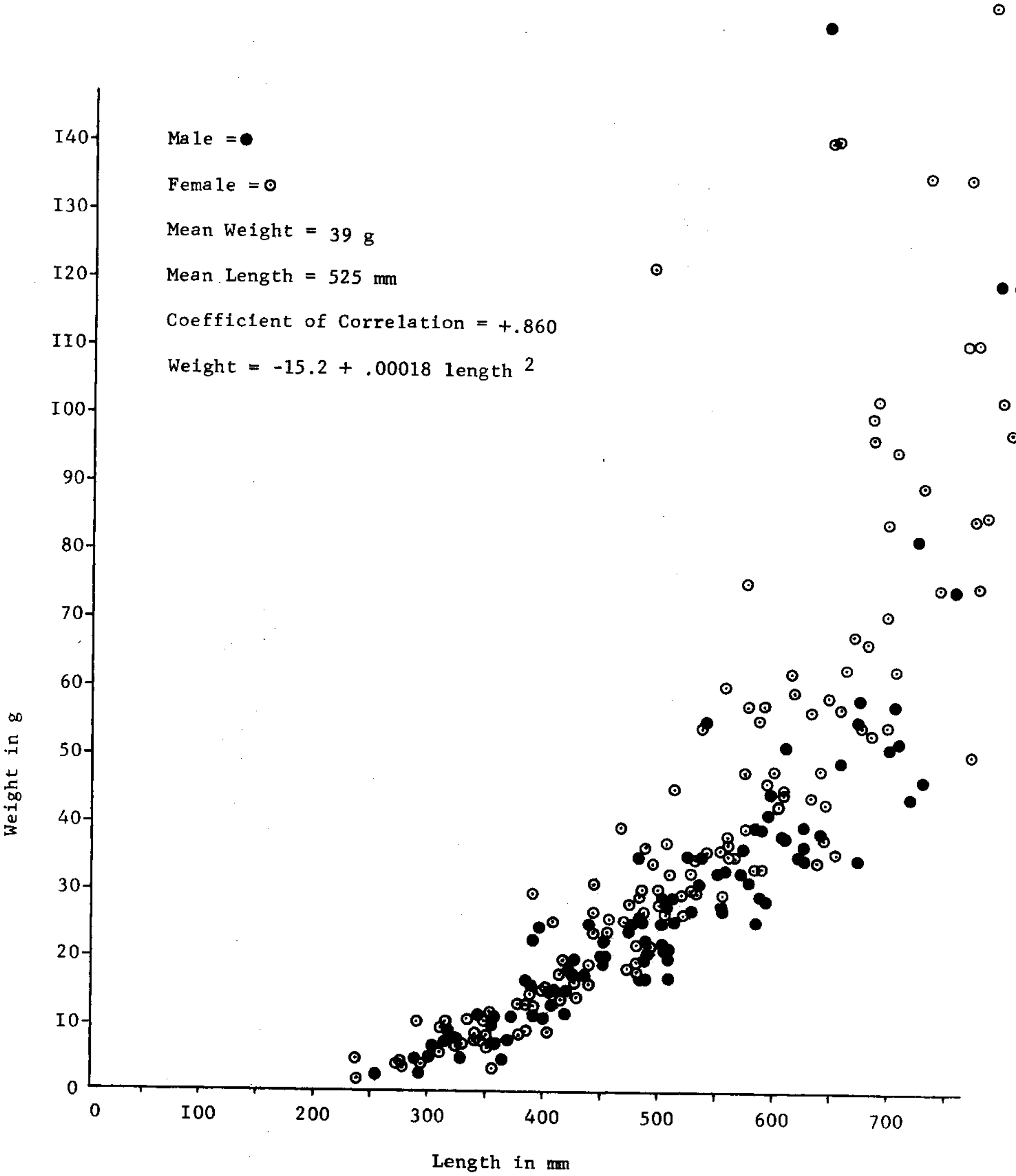


Fig. 4. Weight vs. length of prairie garter snakes (*T. radix*) marked on the Intensive Site during 1970 and 1971.

Table 3. Growth of individual *T. radix* recaptured during 1970 and 1971.

Snake Number	Sex	Growing Time (Days)	Weight Change (g)	Length Change (mm)
1	F	33	1.2	2
3	M	212	21.9	63
5	M	201	6.1	57
9	F	225	-58.0	7
14	F	31	.4	3
16	F	107	69.1	241
22	M	79	11.8	25
28	M	25	-.3	0
32	F	135	-4.3	356
34	M	120	3.2	11
36	F	173	.3	1
39	M	219	4.9	76
41	F	22	.9	0
58	M	140	24.9	121
60	M	22	.2	0
84	F	122	8.6	22
93	F	176	-16.4	0
94	F	50	21.5	89
104	M	147	7.6	95
117	F	6	-1.3	0
121	F	169	40.1	89
122	M	169	9.6	76
140	F	114	22.3	51
155	F	53	5.7	0
195	F	17	5.7	29
196	M	84	4.6	6
200	F	52	48.5	296
202	M	60	-26.4	51
208	F	27	-1.6	0
236	F	10	-1.7	6
241	F	12	.3	0
288	F	49	-58.2	50
32 Snakes Measured	20 F 12 M	3061 Growing Days[a]	155.4 g Total Population Weight Gain	1842 mm Total Population Length Gain

[a] Growing days were considered to be from May 1, 1970, through September 15, 1970, and from May 15, 1971, through September 15, 1971, for *T. radix*.

was seriously damaged by predators between recaptures and showed the maximum weight loss of 58.2 g in 49 days, although during that period this female grew 50 mm in length. There were large fluctuations in growth rates between individuals in the population.

Population dynamics. In the spring of 1970, *T. radix* emerged from dens between May 1 and May 4. In 1971, they emerged during the last week in May. The population began breeding between May 18 and May 24, 1970. Breeding continued for approximately 2 weeks. Copulation was observed on May 24, 1970. In 1971, breeding occurred from June 1 through June 14. By June 26, 1971, *T. radix* no. 290 was swollen with young.

Individual snakes do not appear to be restricted in their range around Cottonwood Pond. On June 4, 1970, one specimen was recaptured over 500 m from the point of its original capture a week earlier. Another was recaptured more than 200 m from the point of original release. Although these distances would not seem large in other circumstances, in the limited moist area around Cottonwood Pond in the summer, this represents nearly all of the available territory.

Using the Lincoln index on two successive capturing dates, the population of *T. radix* was determined to consist of approximately 800 snakes/2.5 ha on a number of separate occasions during 1970 and 1971. However, a Lincoln index of the total captures compared to total recaptures for the 2-year period indicated a population of 1200 snakes/2.5 ha.

T. radix no. 9 was recaptured four times during 1970 and 1971, after it was originally marked on May 26, 1970. Snake no. 39 was recaptured three times after marking, and snakes 3, 5, 16, and 22 were recaptured twice.

Trap mortality. Trap mortality for *T. radix* was much greater than for other species and remained at approximately 3% during the study. This was mainly due to small snakes getting their heads through the ¼-inch wire mesh traps, entangling themselves, and becoming prey for carrion beetles of the family Silphidae. Napthalene was placed under the rear of the traps during August and September of 1971 to discourage these insects. Occasionally an adult snake would become damaged by the door cut into the mesh at the rear of the trap. During June 1971, cardboard was placed in the rear of the trap to discourage escape attempts and damage through these doors.

Using a Lincoln index of 800 snakes/2.5 ha and the mean weight of 39 g for the marked population, the live weight or biomass of snakes around the Cottonwood Pond study area was found to be 1248 g/ha.

Crotalus viridis viridis Rafinesque, The Prairie Rattlesnake

During 1970 and 1971, 33 *C. viridis* were marked and released on the Pawnee Site. Males made up 57.6% of this population. There were four recaptures, resulting in a recapture rate of 12.1%. The larger snakes of this species were males, and only males were recaptured. The mean weight of the marked population was 168 g with a standard deviation of 143 g. The mean length of the population was 613 mm with a standard deviation of 212 mm. The coefficient of correlation of length to weight for *C. viridis* was +.943, and the regression equation best fitting the curve in Fig. 5 was

$$\text{Weight} = -53 + .00053\ \text{Length}^2$$

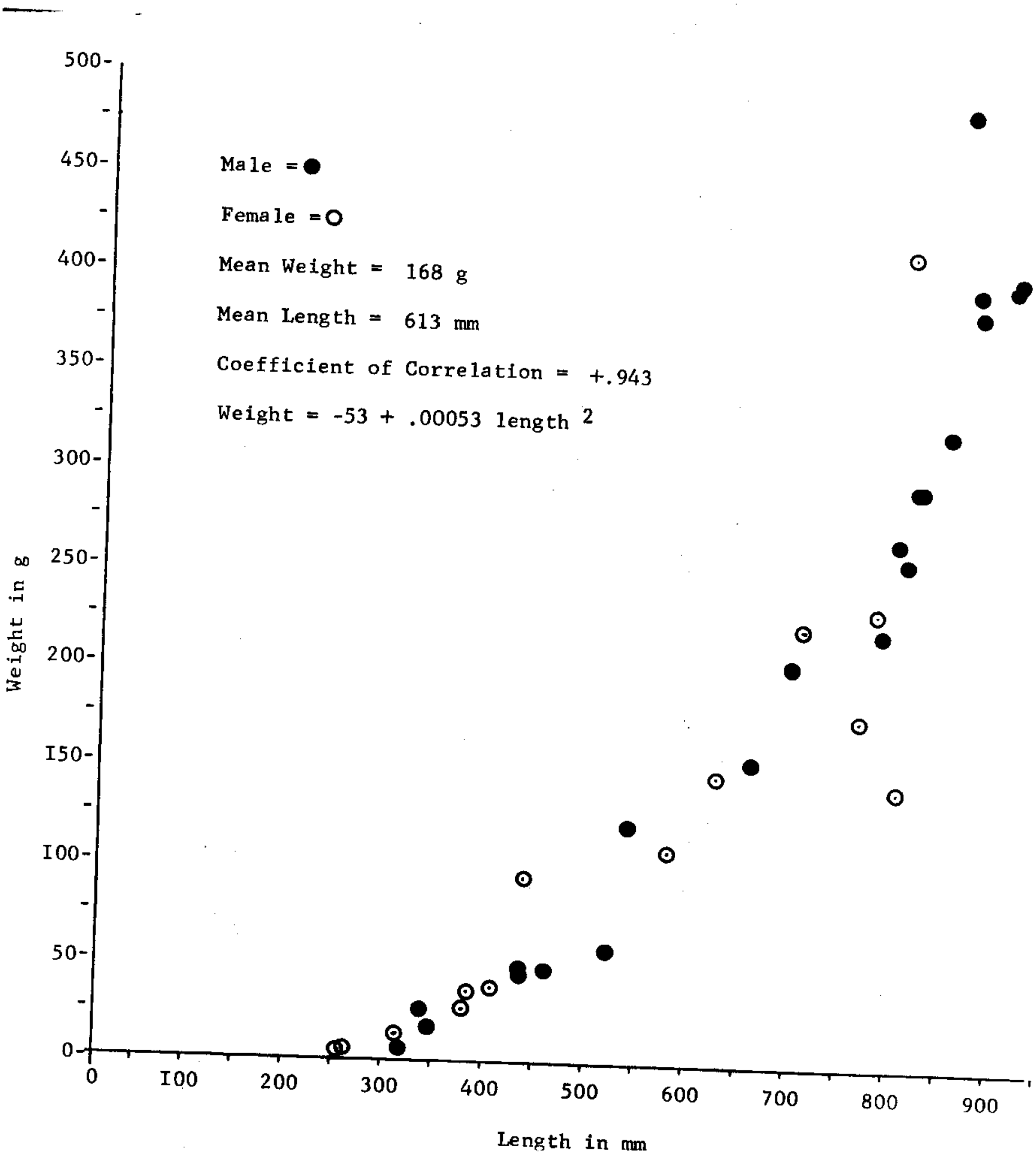


Fig. 5. Weight vs. length of prairie rattlesnakes (*C. viridis*) marked on the Intensive Site during 1970 and 1971.

Growth rate. The growth rate from four recaptures was .157 g/snake/day, and .028 mm/snake/day during the active months. The maximum weight gain measured was an increase of 86.2 g in 69 days by *C. viridis* no. 27. Maximum weight loss was in snake no. 29 which lost 14 g in 33 days and moved nearly 1 mile during that period. There were insufficient numbers recaptured to validate a growth rate on this species.

Fat storage. Fat bodies were weighed on 27 specimens of the prairie rattlesnake (*C. viridis*) collected for the egg count survey. Fat bodies from individuals collected in early May were compared with the amount of fat present in snakes collected in October 1970. There was great variation in the amount of stored fat in both emerging and denning snakes. No significant difference was found in the amount of fat per body weight in the spring-collected snakes when compared to fall-collected snakes (Fig. 6, Table 4).

Reproduction. The prairie rattlesnake (*C. viridis*) was shown to have mature eggs present in the body in both May and October of 1970 (Table 3). This tends to support Rahn (1942) who presented evidence for a 2-year reproductive cycle for prairie rattlesnakes in their northern range. This would also explain why many mature females used for egg counts did not contain eggs. Rahn (1942) indicated that spermatozoa may survive in the vaginal region over the winter. There was variation in number of specimens collected which had eggs. Egg counts varied from 9 to 37 eggs per female. Females with few eggs had large mature ones; while in cases where females had large numbers of ova, they were all small. This indicates that for a large initial number of eggs starting to develop, only a fraction eventually reach maturity. Six females with eggs were collected which were not included in Table 4 (Fig. 7). These had been killed with a shotgun by

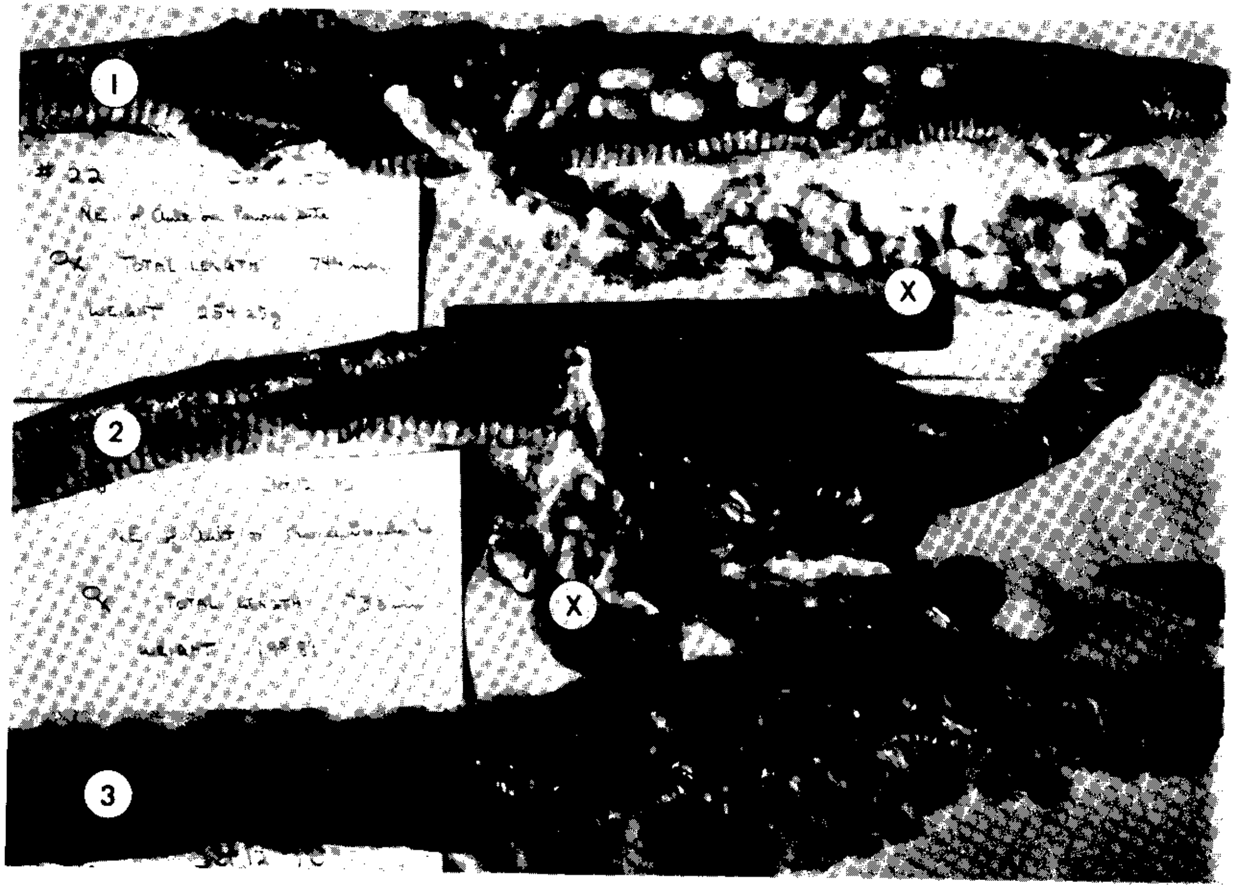


Fig. 6. Three *C. viridis* used in the laboratory phases. No. 1 contained both developed and undeveloped eggs. No. 2 and 3 had less developed eggs (just above and below key). The X indicates extensive fat body development. All snakes were collected October 12, 1970, at a denning site 9 miles northeast of Ault, Colorado, on the Pawnee Grassland.

Table 4. Data for 27 prairie rattlesnakes (*C. viridis*) collected near the intensive study area.

Specimen No.	Date Collected	Sex	Total Length (mm)	Tail Length (mm)	Live Weight (g)	Dry Weight (g)	Ash Weight (g)	Fat Body Weight (g)	Eggs No. and Weight	Locatio Collecte
1	Oct. 12, 1970	F	797	42	263.8	72.89	9.67	22.68	12-13.1g	1
2	May 10, 1970	M	767	54	159.5	65.51	10.40	10.26	--	1
3	June 6, 1970	M	631	49	88.19	24.59	4.07	2.51	--	1
4	Oct. 12, 1970	M	744	58	207.33	51.87	8.62	5.88	--	1
5	May 2, 1970	M	884	67	356.64	102.03	18.36	15.55	--	2
6	May 17, 1970	M	645	47	119.51	58.32	4.56	3.73	--	1
7	May 17, 1970	F	711	43	157.36	47.65	6.05	15.95	--	2
8	May 17, 1970	M	809	57	220.74	50.20	3.29	2.85	--	2
9	May 17, 1970	M	828	62	280.60	73.58	10.82	19.33	--	2
10	May 17, 1970	M	931	73	349.30	94.84	20.60	8.00	--	2
11	May 5, 1970	M	714	51	152.01	38.15	6.78	4.83	--	1
12	Oct. 12, 1970	F	763	45	163.45	37.91	7.37	3.17	--	1
13	May 5, 1970	F	482	26	45.24	10.12	1.70	1.63	--	2
14	Oct. 12, 1970	F	707	23	131.35	7.36	2.68	1.26	--	1
15	June 6, 1970	M	278	21	9.49	2.05	.39	.27	--	1
16	May 10, 1970	M	275	16	6.88	1.55	.24	.10	--	1
17	Oct. 12, 1970	F	263	11	7.78	1.64	.22	.02	--	1
18	Oct. 12, 1970	F	738	42	199.89	55.64	6.98	17.23	37-0.1g	1
19	Oct. 12, 1970	M	644	45	106.29	26.03	4.08	4.68	--	1
20	Oct. 12, 1970	M	681	54	124.64	30.21	4.70	2.28	--	1
21	Oct. 12, 1970	F	312	16	14.39	3.30	.46	.06	--	1
22	Oct. 12, 1970	F	744	35	254.25	76.26	8.79	19.49	--	1
23	Oct. 12, 1970	F	588	31	69.81	14.41	1.08	1.01	9-0.2g	1
24	Oct. 12, 1970	M	598	42	82.96	18.67	10.05	1.70	--	1
25	Oct. 12, 1970	M	690	49	147.49	36.02	5.59	2.43	--	1
26	Oct. 12, 1970	F	729	42	150.11	31.60	5.85	.92	--	1
27	Oct. 12, 1970	F	291	17	11.40	2.60	.38	.32	--	1

[a/] Location: 1--12 miles northeast of Ault, Colorado on the Pawnee Grassland.
2-- 6 miles northeast of the Intensive Site Headquarters for the Pawnee Site.

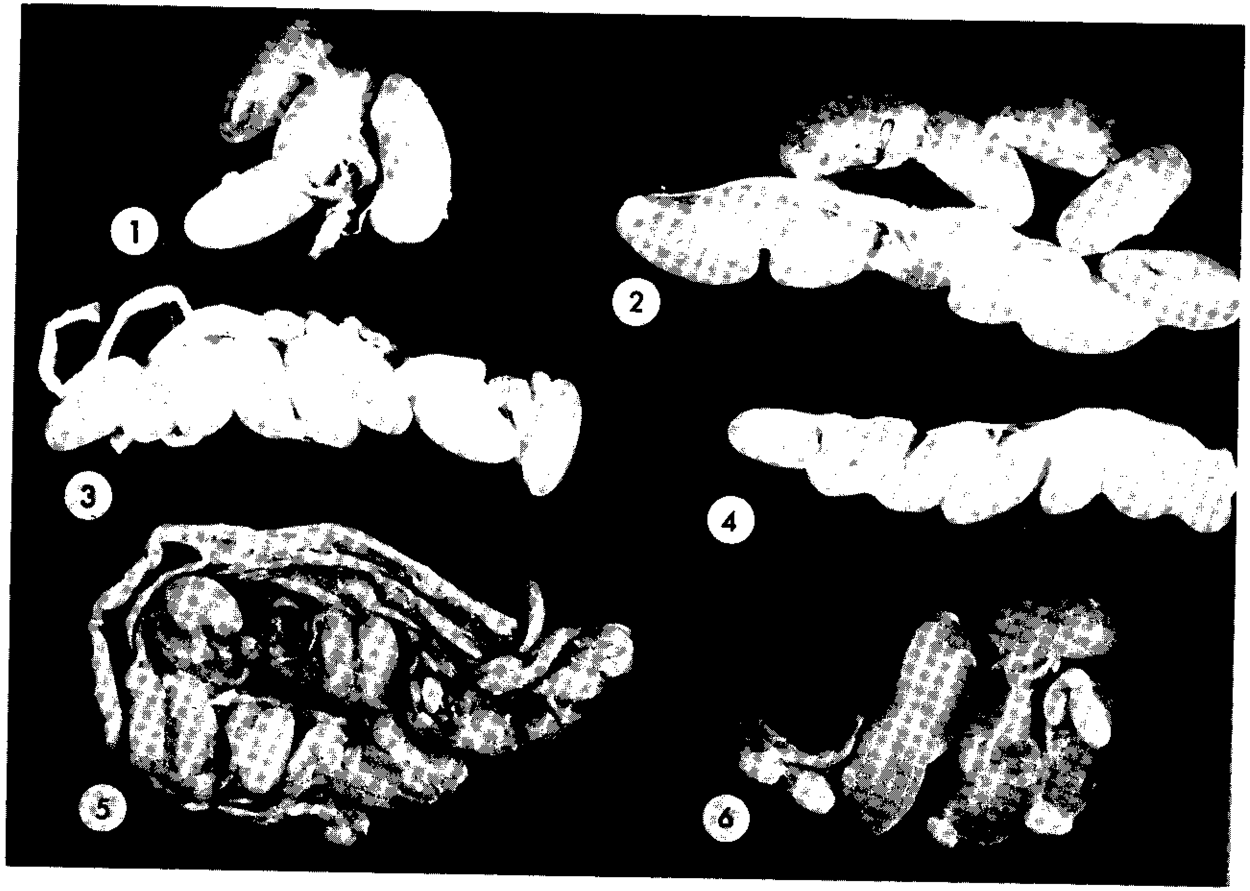


Fig. 7. Representative egg masses from six prairie rattlesnakes (*C. viridis*). Note undeveloped smaller eggs in each mass.

residents near the Intensive Site and could not be used for any other purpose but egg counts. Table 5 shows the size relationship of eggs with the total egg count.

Activity. In 1970, *C. viridis* emerged between May 7 and May 13, and none were observed after September 24 on the study area. However, a number of snakes were taken from a known denning site within 6 miles of the study area during the second week in October by local residents. In 1971, *C. viridis* were emerging between April 28 and May 2. Snakes were denning until as late as October 20.

Pituophis catenifer affinis Hallowell, The Gopher Snake

During 1970 and 1971, 31 *P. catenifer* were marked and released. Males made up 29% of this population. There was one recapture, resulting in a recapture rate of 3.2%. The larger snakes of this species were males. The mean weight of the marked population was 326 g with a standard deviation of 232 g. The mean length of the marked population was 967 mm with a standard deviation of 344 mm. The coefficient of correlation of length to weight for *P. catenifer* was +.948, and the regression equation which best fits the curve in Fig. 8 was

$$\text{Weight} = -66.3 + .00037\ \text{Length}^2$$

Growth rate. No growth took place in the one recapture of *P. catenifer*. A juvenile (340 mm) *P. catenifer* marked on June 2, 1970, may indicate recent hatching. On June 18, 1971, a juvenile *P. catenifer* was collected which weighed 11.6 g and was 356 mm long. In 1970, the *P. catenifer* population emerged between May 25 and May 27. None were collected after October 6. In 1971, *P. catenifer* were found emerging between May 13 and May 17. On

Table 5. Egg counts from six prairie rattlesnakes (*C. viridis*) collected 2 miles east of the Intensive Site in September 1970.

Number	Egg Size		Total Count
	Large = 15 mm (+)	Small = 15 mm (-)	
1	4	11	15
2	11	22	33
3	9	13	22
4	7	15	22
5	16	16	32
6	6	19	25

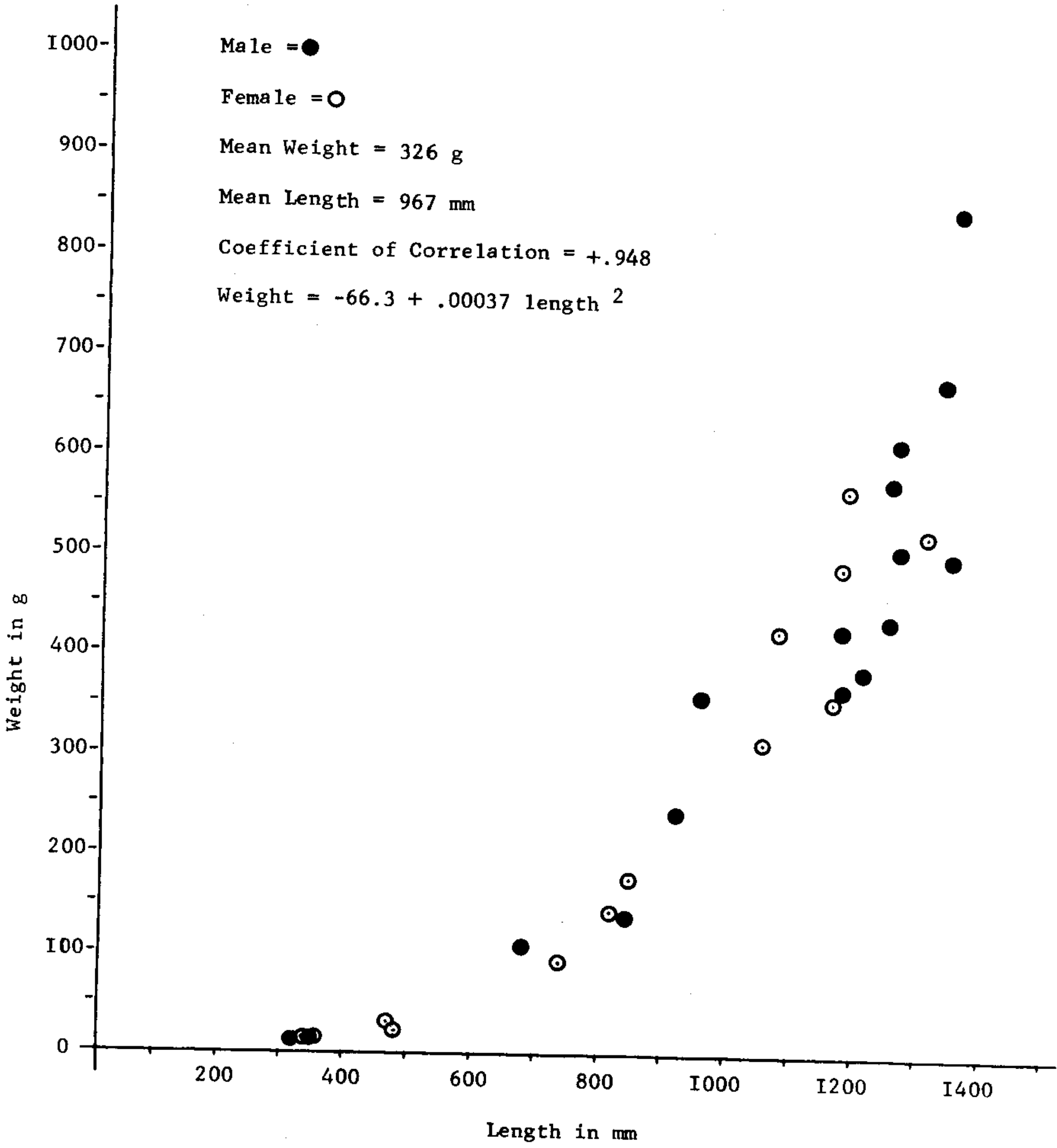


Fig. 8. Weight vs. length of gopher (bull) snakes (*P. catenifer*) marked on the Intensive Site during 1970 and 1971.

May 27, 1971, *P. catenifer* no. 23 and 24 were observed copulating. No snakes of this species were collected after October 4, 1971.

Heterodon nasicus nasicus Baird and Girard, The Western Hognosed Snake

During 1970 and 1971, 17 *H. nasicus* were marked and released on the Pawnee Site. Of this population, 70.6% were males. Larger individuals of the marked population were males. There were no recaptures. The mean weight of the marked population was 67 g with a standard deviation of 45 g. The mean length of the marked population was 462 mm with a standard deviation of 95 mm. The coefficient of correlation of length to weight for *H. nasicus* was +.943, and the regression equation which best fits the curve in Fig. 9 was

$$\text{Weight} = -44.7 + .0051\ \text{Length}^2$$

Growth rate. *H. nasicus* had emerged by May 21, 1970. None were marked after July 24, 1970. In 1971, emergence occurred between May 27 and May 31, and no specimens were marked after August 27. A 7-g and 203-mm *H. nasicus* was marked on June 1, 1971, and may indicate the approximate size of a specimen born the previous fall.

Thamnophis elegans terrestris, The Western Garter Snake

One specimen of *T. elegans* was collected in a funnel trap at Cottonwood Pond on September 6, 1971. This was the day after a heavy rainfall and flash flooding in the vicinity, which may account for the appearance of this species. *T. elegans* is commonly found in the foothills 20 miles west of the Pawnee Site.

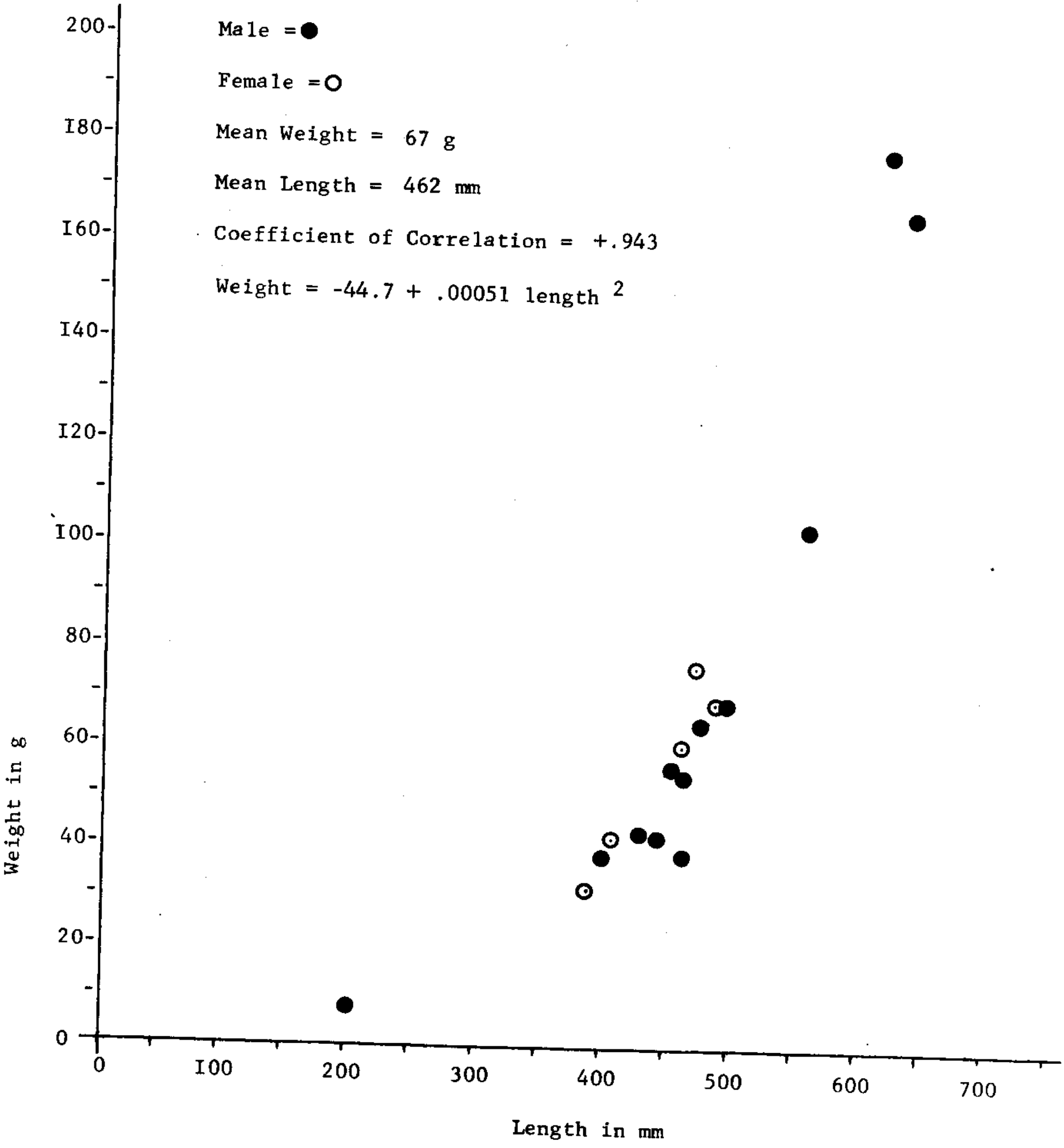


Fig. 9. Weight vs. length of western hognosed snakes (*H. nasicus*) marked on the Intensive Site during 1970 and 1971.

OVERALL RESULTS

Continuous trapping by using drift fence-funnel traps was the most effective collecting method for snakes. Walking grid lines and spotting from roads were both effective methods of finding snakes on the shortgrass prairie. No snakes were collected from pit traps, although they proved effective for small mammals, birds, and insects. No snakes were collected by night lighting techniques, and none were ever seen crossing the roads late at night from vehicles.

Between May 1 and September 30, 1971, two specimens of *P. catenifer* (no. 27 and 28) were collected by using the prime time line transect technique. A total of 16 ha were sampled by this method during 1970 and 1971 and yielded 740.9 g of snake for a standing crop of 46.3 g/ha. This appears to be a low estimate when compared to trapping data.

Active Periods

During June, July, and August, all species of snakes were most active during the crepuscular period of the day. *T. radix* and *P. catenifer* appeared to be active during all parts of the day. In the early spring and late fall, all species were active at midday when the temperature was above 16°C. *H. nasicus* and *T. radix* disappeared nearly 1 month earlier than *P. catenifer* and *C. viridis* in the fall. This may be attributed to the former two species not returning to the surface to bask and hunt during the warm days of late fall.

Energy Utilization

Three live laboratory mice of the same litter were fed to a male *C. viridis* at room temperature. The snake consumed a total of 72.88 g live weight of mice in a 1-week period at 22°C in a secluded cage. From animals 1, 2, and 3 (Table 6), it was found that 32% of the live weight of these mice was dry weight. Therefore, the snake had consumed 23.32 g dry weight. Odum (1971) lists small vertebrates as having an average of 5.6 kcal/g dry weight. Using that figure, the snake consumed about 130.59 kcal.

After a 3-week period, 3.63 g of wastes from snakes were collected from a blotter on the floor of the cage. Two samples of the feces were measured by bomb calorimetry at the Natural Resource Ecology Laboratory and were found to contain 3.610 kcal/g. Therefore, of the original 130.59 kcal consumed, 13.10 kcal was lost to feces. This shows that about 90% of the energy available was assimilated by the rattlesnake, *C. viridis*.

Infrared Gas Analyzer Respiration

Respiration of snakes was determined by continuous measurement of the increase in CO_2 production per unit time and by fitting the amount produced into the following equations:

$$K = \frac{\text{mg } CO_2/\text{mole} \cdot \Delta\text{ppm/min} \cdot \text{standard temp} \cdot \text{atmospheric pressure} \cdot \text{vol system with snake}}{\text{standard M vol} \cdot \text{standard pressure in mm Hg} \cdot \text{temp of the system}}$$

$$\text{mg } CO_2/\text{min} = K\left(\frac{\Delta\text{ppm}}{\text{min} \cdot 273 + \text{temp}}\right)$$

$$\text{mg } CO_2/(\text{g} \cdot \text{min}) = \frac{\text{mg } CO_2/\text{min}}{\text{weight of snake in g}}$$

Table 6. Energy conversion in *C. viridis*.

Animal Number	Live Weight (g)	Dry Weight (g)	% Live to Dry Weight
1	30.36	9.91	32.6%
2	18.94	5.95	31.4%
3	18.63	5.89	31.6%
4	36.37	Fed to Snake	
5	17.21	Fed to Snake	
6	19.30	Fed to Snake	

where K is a correction factor to convert the observed measurements to standard temperature and pressure.

In these calculations the respiratory quotient value (RQ = the ratio of moles or volumes of CO_2 produced to moles, or volumes of O_2 consumed) was assumed to be 1.00. Whittow (1970) reports some RQ values for reptiles at the 0.85 level under certain conditions. Most of the work on RQ values found in the literature was done on lizards. Oxygen utilization studies on snake species from the Pawnee Site are currently being undertaken at the Natural Resource Ecology Laboratory.

Smaller animals have relatively larger surface areas than larger animals and, therefore, generally have higher respiration rates. This would give them greater CO_2 production per gram. In this case, four different species were being compared. Each individual selected was larger than the mean of its population (Fig. 4, 5, 8, and 9) on the Pawnee Site, with the exception of *H. nasicus*. Smaller snakes showed a greater percent CO_2 increase (Table 7) with the exception of *T. radix*. The prairie garter snake, *T. radix*, was restricted to a permanent water habitat, and the differences found could be related to physiological differences between the species. The purpose for this respiration analysis was to provide gross parameters of CO_2 production by each species, and therefore, only one specimen of each species was used in this phase of the study.

Gross Energy

Gross energy results of snakes measured by bomb calorimetry are as follows. The mean value determined from three samples of each species is *C. viridis*, 5.073 kcal/g; *H. nasicus*, 3.957 kcal/g; *P. catenifer*, 4.626 kcal/g; and *T. radix*, 3.986 kcal/g.

Table 7. CO_2 production by selected specimens of snakes from the Pawnee Site.

Species	Weight (g)	Length (mm)	Sex	mg/(g · min) CO_2 Produced at 23.5°C	mg/(g · min) CO_2 Produced at 30.0°C	Percent Increase
P. catenifer	535.0	1312	M	.00169	.00218	129
C. viridis	348.3	828	M	.00127	.00442	348
T. radix	45.4	658	M	.00611	.01687	276
H. nasicus	23.7	339	M	.00505	.02496	494

Den Locations

No permanent denning site was located on the U.S. IBP Grassland Biome Intensive Site for future use, although a great deal of time was spent searching for dens during the warm days of late September and October of 1970 and 1971. One area of heavy *C. viridis* concentration was located several hundred meters south of the prairie dog town section (study plot no. two). The snakes appear to be scattered into individual or small group dens. This may be due to human hunting pressure on the population during recent years. During 1970 and 1971 few *C. viridis* rattled when approached until the investigator was within 1 m of them, or was reaching with a snake stick.

Biomass Determination

During the time period from June 1 through August 31, 1970 and 1971, snakes collected on the study grids were considered to be "resident snakes." Each year, before June 1 and after August 31, snakes could have been moving through the grids to a denning site and thus were not considered residents. On study plot no. one (the ridge section), three specimens of *H. nasicus* and five of *P. catenifer* were collected during the time period in 1970 and 1971 in which they would be considered resident snakes. The total live weight of these individuals was 841.3 g (*H. nasicus* 126 g and *P. catenifer* 715.3 g), giving a combined yearly residence of 168.3 g/ha snakes/year. In addition, eight *C. viridis* were marked and released from study plot no. one during May, September, and October of 1970 and 1971, for a nonresident live weight of 179.7 g/ha of *C. viridis* per year. It was quite possible that some of the nonresident snakes were actually residents on the study plot; but because of their sedentary nature during the hotter months, they were not moving enough to be collected by drift fence-funnel trap techniques. However, the lower value representing resident snakes was used for model construction.

Study plot no. two, the prairie dog town plot, had no resident snakes on it during 1970 and 1971, according to the arbitrary dates for residence already mentioned. However, six specimens of *C. viridis* were collected during May, September, and October (1970 and 1971) for a total of 812.6 g of snake (live weight), or 162.5 g/ha nonresident snakes/year. Numerous other snakes, including *C. viridis*, *P. catenifer*, and *H. nasicus*, were collected and marked within several hundred meters of study plot no. two, but these were not to be used for density determinations.

In summary, it was determined that the density for all species of snakes in the vicinity of study plot no. one was approximately 168.3 g/ha/year of resident snakes. That figure could have been increased by 35.9 g/ha/year if as few as one-fifth of the nonresidents had actually been sedentary residents during the summer months. At study plot no. two there were 0 g/ha/year of resident snakes. If one-fifth of the nonresidents had been sedentary residents, that figure would increase to 32.5 g/ha/year. Study plot no. one had a low frequency of disturbance by man, and study plot no. two had a high frequency of disturbance. If these two areas are considered together, then the mean live weight of resident snakes on the Intensive Site would approximate 84.3 g/ha/year. If one-fifth of the snakes collected as nonresidents were actually residents, a maximal value of 118.5 g/ha/year of snake would be possible. A minimal value would be 0 g/ha/year of snake.

DISCUSSION

The ecological impact of snakes on the shortgrass prairie was to be determined in such a way that a computerized energy flow model could be constructed from data presented. The resultant model would be one component of a complex series representing the major energy relationships within the shortgrass prairie. If such energy relationships are determined, mathematical manipulation of selected factors in the ecosystem, and the resultant effect upon the various life forms, would be feasible.

This study provides a reasonable estimate of energy flow by employing information from the literature, by performing specific pilot studies in the laboratory, and by determining population dynamics in the field. Organization and integration of data was inherent in the determination of bioproductivity of snakes on the shortgrass prairie. Energy flow relationships were linked with prey density and seasonal variations in order to provide for the effects of ecosystem manipulation. The following discussion concerns the construction of a generalized energy flow model and the rationale supporting the inclusion of each specific factor in the model.

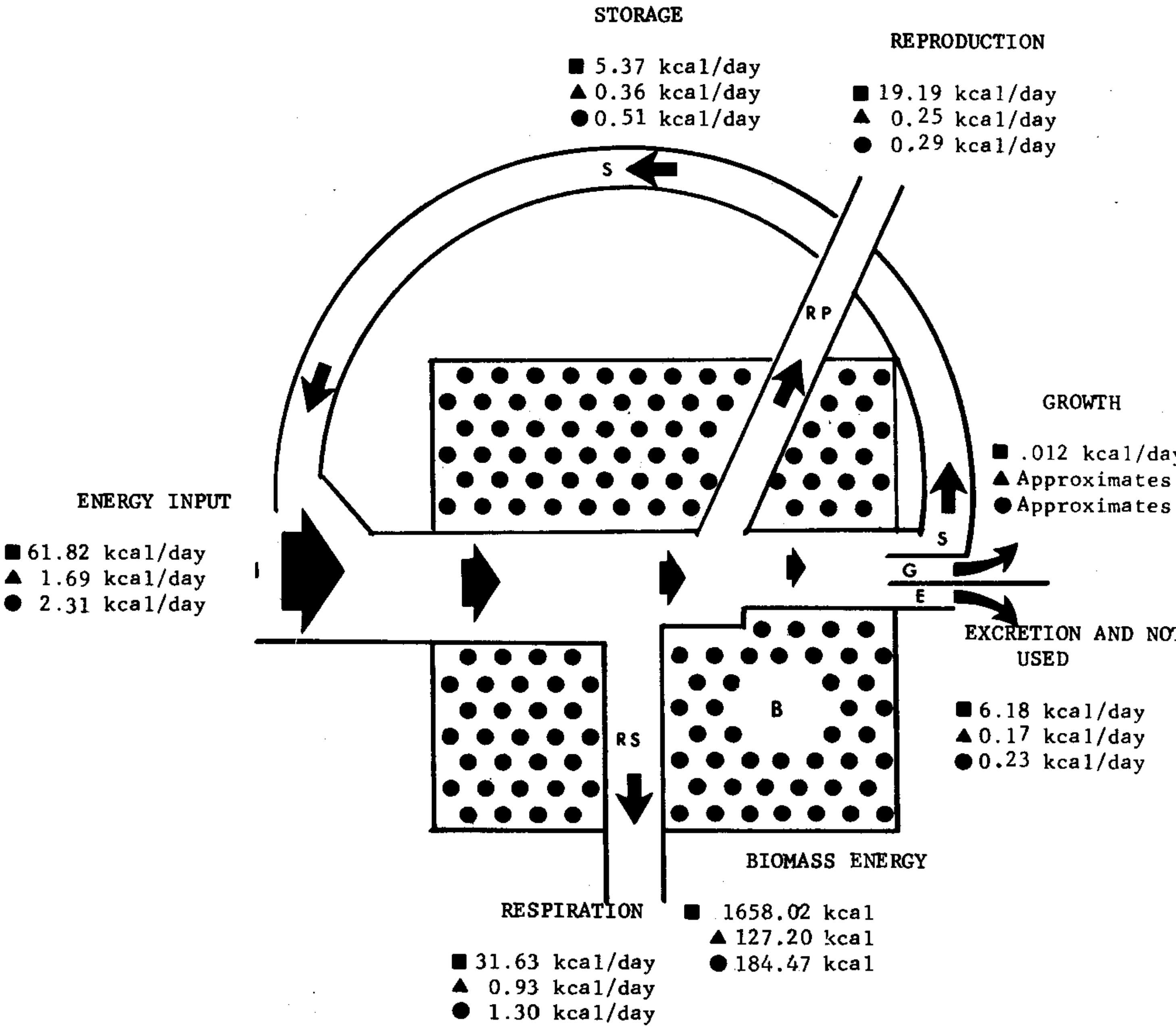
ENERGY FLOW MODEL

Caloric Value Determination of Biomass per Hectare of the *T. radix* Population and of the Combined *P. catenifer*, *H. nasicus*, and *C. viridis* Populations

Using a Lincoln index of 800 snakes per 2.5 ha and a mean weight of 39 g for the marked population, the live weight of *T. radix* on the Cottonwood Pond study area was found to be 1248 g/ha. Odum (1971) lists two-thirds of the live weight value of most animals as being water and minerals, leaving a dry weight population biomass of 415.96 g/ha. Gross energy results from freeze drying and bomb calorimetry showed that *T. radix* contained 3.986 kcal/g dry weight. Therefore, the biomass energy value from the *T. radix* population would be 1658.02 kcal (Fig. 10).

The mean live weight of resident snakes on the Intensive Site at study plots no. one and two was determined to be 84.3 g/ha (15% *H. nasicus* and 85% *P. catenifer* by weight). Dry weight in grams per hectare for each species was determined in the same way as in the *T. radix* population. Gross energy determinations showed that *P. catenifer* contained 4.626 kcal/g dry weight, and *H. nasicus* contained 3.957 kcal/g dry weight. Therefore, the total energy equivalent of biomass available from these two populations would be 127.20 kcal.

A second caloric value was calculated for the populations found on study plots no. one and two, which may indicate a reasonable "maximum" biomass energy (in kilocalories per hectare). In these calculations the live weight biomass (in grams per hectare) was increased to 118.5 g/ha/year by the addition of one-fifth of the snakes collected during early spring and late fall. Those snakes (mainly *C. viridis*) were placed in the nonresident group because at the time of year they were collected, they "may" have been moving through the study plots to a denning site. It was reasonable to conclude that some of these nonresident *C. viridis* may have been sedentary residents during the summer months, but were not captured due to their nocturnal, nonwandering, hunting behavior. If one-fifth (arrived at arbitrarily) of this group were actually present on the plots during the summer, the biomass (in grams per hectare) would be increased by 34.2 g live weight. When this figure was converted to dry weight, multiplied by the gross energy determination of 5.073 kcal/g of *C. viridis*, and added to the *P. catenifer*-*H. nasicus* figure, a maximum biomass energy (in kilocalories per hectare) of 184.47 kcal was determined for the dry study plots.



■ = T. radix population
▲ = Combined P. catenifer, H. nasicus, and C. viridis populations
● = Combined P. catenifer, H. nasicus, and C. viridis populations, including one-fifth of the early spring and late fall snakes which were not considered residents

Fig. 10. Components for a universal model of ecological energy flow. I = input or ingested energy; RP = reproduction; RS = respiration; B = biomass; G = growth; S = stored energy; E = excreted or not used energy. (Modified from Odum, 1971.)

Energy Storage Determination for Dormant Periods by Snake Populations

Klauber (1937) found that *C. viridis* adults lost approximately 4% of their body weight during the winter. Hirth (1966*b*) found the average weight loss for *C. viridis* to be 7.6% in adults. In the following calculations of stored energy, the figure of 6% weight loss per dormant period was used.

T. radix was assumed to lose 6% of its live weight during the winter months for the purpose of this model construction. No studies were found in the literature concerning weight loss in this species. Since the biomass of the *T. radix* population at Cottonwood Pond was determined as a constant value of 1248 g/ha, 6% of that biomass (74.88 g of mixed fats) would need to be stored by the population for the winter period. Brody (1945) states that there are 6.6 kcal/g of mixed fat. Therefore, 494.2 kcal were stored per year, or 5.37 kcal were stored per day of the 92-day growing season by the *T. radix* population.

The biomass of snakes per hectare present on study plots no. one and two was found to be 84.3 g. If 6% of this figure was stored for the winter period in mixed fats [(6.6 kcal/g), (Brody, 1945)], then .36 kcal/day would be stored each day of the 92-day growing season by the combined *C. viridis*, *P. catenifer*, and *H. nasicus* populations.

By adding one-fifth of the nonresident *C. viridis* to the biomass (increasing it to 118.5 g/ha) and calculating the 6% mixed fat storage at 6.6 kcal/g, a maximal storage value of .51 kcal/day was determined for the combined dry-land populations.

Caloric Energy Devoted to Population Growth

The population of *T. radix* was found to be growing at .002 g/day of the growing seasons. Since *T. radix* was measured to have 3.986 kcal/g, this would mean that .008 kcal/day were shunted to population per hectare growth. At the two significant figure levels used in the calculation of caloric values, this would be rounded to .01 kcal/day.

Insufficient data were collected on *C. viridis*, *H. nasicus*, and *P. catenifer* to establish the growth rates of the populations. From the data collected on these species and that taken on *T. radix*, an estimation of the population growth rate would approximate zero. Zero growth rate, or 0 kcal/day, was the figure used in the bioproductivity model.

Growth rate was not affected by the addition of one-fifth of the nonresident *C. viridis*. Zero growth rate, or 0 kcal/day, was used in the model.

Caloric Energy Excreted or Not Used by Snake Populations

It was found by feeding and bomb calorimetry methods that 10% (rounded to the nearest .10%) of the dry weight input was eventually produced as "excreted" (uric acid) or "not used" (hair, bone) material by *C. viridis*.

No studies were found on the excretion rates of *T. radix*. For modeling purposes, the assumption was made that the rate would be similar for that of *C. viridis* in quality per gram of snake though greater in water content, since *T. radix* is found in a moist environment. The minimum input of energy per day into the population on one hectare was 61.82 kcal, so the "excretion--not used" portion would be 10% of that figure, or 6.18 kcal.

No studies were found concerning excretion rates of *P. catenifer*, *C. viridis*, or *H. nasicus*. Laboratory studies showed that 10% of the input is excreted or not used in *C. viridis*. It was assumed that *P. catenifer* and

H. nasicus would have similar excretory rates to *C. viridis*. With an energy input minimum of 1.55 kcal/day into the populations per hectare, the "excretory--not used" energy (10% of input) would equal 0.16 kcal.

The addition of one-fifth of the nonresident *C. viridis* biomass increased the input energy to 2.07 kcal/day. The "excretory--not used" energy (10% of input) would therefore be 0.19 kcal.

Calories Lost to Respiration by Snake Populations

During the 92-day growing seasons between June 1 and August 31, 1970 and 1971, it was assumed that snakes moved to cooler microhabitats in the heat of the day and to warmer ones during cooler periods to regulate body temperature. Utilization of shade produced from small bushes, vertical movements in rodent burrows, and early morning-late afternoon sunning are examples of such temperature regulation. Fitch and Glading (1947) listed the optimum activity air temperature for *C. viridis* as being between 80° and 90°F (27° to 32°C). However, Hirth et al. (1969) found that the maximum voluntary thermal tolerance was about 32°C in *P. catenifer*. They further noted that body temperatures dropped rapidly at night. Brattstrom (1965) lists the threshold for normal locomotion of 18°C (64.4°F) for *P. catenifer*. Ground temperature at depths accessible to snakes on the shortgrass prairie seldom drops below 5°C during the year. The energy flow model presented is based upon mean values during the 92-day growing season. An average day-night respiration temperature of 23.5°C was estimated for the season, from both nightly low temperatures and the daily behavioral temperature modifications made by snakes. Respiration during winter dormancy was included on the energy flow model under the category of caloric value of mixed fat storage of energy.

At 23.5°C, *T. radix* was found to produce .00611 mg of CO_2/g of snake/min (1 mg of CO_2 = .00569 liters of CO_2 at 23.5°C; 1 liter CO_2 = 5.047 kcal). Therefore, using the resident biomass of *T. radix* at 1248 g/ha for a 24-hr day, the *T. radix* population used 31.63 kcal in respiration.

The mean respiration rate of .00267 mg CO_2/g of snake/min for the combined biomass of *H. nasicus*, *P. catenifer*, and *C. viridis* was used to calculate the respiration on study plots no. one and two. Using the conversion factors above for respiration for a 24-hr period, the resident biomass of 84.3 g/ha used .93 kcal/day in respiration.

If the resident biomass was increased to 118.3 g/ha by nonresident *C. viridis*, 1.30 kcal/day would be used in respiration.

Energy Used for Reproduction

In *T. radix* the resident biomass of 1248 g/ha would be equal to 32 snakes of the mean population size of 39 g. Using the sex ratio of 60.1% females found in the field study, it was calculated that 19 would be females. Stebbins (1954) reported that brood sizes of *T. radix* range from 13 to 40. For the purpose of this model, an average brood size of 14 snakes per female at a weight of 5 g per young snake was assumed. With the dry weight of each young containing 3.986 kcal/g, a total of 1765.36 kcal/ha would need to be stored by the *T. radix* population for reproduction. This would amount to 19.19 kcal/day of the 92-day growing season, assuming the figure of two-thirds of the body weight as H_2O or minerals (Odum, 1971). With such a high reproductive potential, a great deal of energy in the *T. radix* model would be drawn for reproduction.

The 84.3 g/ha biomass of resident snakes from study plots one and two was made up of 15% *H. nasicus* and 85% *P. catenifer*. In the *H. nasicus* population sampled, 29.4% were females and 71% of the *P. catenifer* population were females. Imler (1945), Schmit and Davis (1941), and Stebbins (1954) all report different average clutch sizes for *P. catenifer*. Since Stebbins (1954) reported on captive snakes, the studies of Imler (1945) and Schmit and Davis (1941) were given some priority, and a figure of 10 young per female weighing 7 g each was used for this model. Stebbins (1954) reported that *H. nasicus* average 11 eggs per female. The field data showed the smallest size of *H. nasicus* to be 7 g. Gross energy determinations resulted in 4.626 kcal/g dry weight for *P. catenifer* and 3.957 kcal/g dry weight of *H. nasicus*. Using two-thirds of the body weight as water or minerals (Odum, 1971), .18 kcal/day was calculated for *P. catenifer* and .06 kcal/day for *H. nasicus*. Therefore, the combined populations use .25 kcal/day for reproduction during the 92-day season.

When the resident biomass was increased by 34.2 g/ha of *C. viridis* nonresidents, an increase in reproductive potential occurred. Fitch (1949) expected a litter size of 10 young on alternate years in the northern range. Five young per year at 5 g each, converted to dry weight and multiplied by 5.073 kcal/g gross energy, would give the energy for reproduction from one adult female. Since the *C. viridis* population consisted of 42.4% female, with a mean size of 168 g each, 34.2 g of snake would represent 9% of one female. When the energy from one female, multiplied by 9% of one female, was divided by the 92-day growing season, the resulting energy value was .04 kcal/day. This value was then added to the resident reproductive energy/day for a total of .29 kcal/day.

Caloric Input of Prey Species into the Model

Fitch (1949) estimated that *P. catenifer* and *C. viridis* must consume twice their own weight in prey species annually to survive. Since field work demonstrated that total population growth per year was negligible, it was assumed that snake populations had a food intake which was of a marginal nature for survival and reproduction. This would justify using a prey intake value which was near the minimum for the survival of snake populations in the following calculations.

The caloric "inputs" used in Fig. 10 are minimal values since daily foraging energies of snakes of each species were not measured in the study. In *T. radix*, *P. catenifer*, and *H. nasicus* this foraging energy load would increase the caloric intake value, whereas in *C. viridis* which ambushes its prey it would be minimal. Determination of daily average foraging energy values was beyond the scope of this study and was unavailable in the literature. Caloric input values would also be higher during years when prey species were more abundant, or when meteorological factors provided temperatures conducive to more prime hunting time per season.

Minimal caloric input per day for the *T. radix* population was calculated by totaling the caloric values per day for respiration, growth, reproduction, and storage. This total was then increased by 10% to account for the "excretion--not used" category. Therefore, the daily caloric input value for the *T. radix* population was 61.82 kcal/day.

Minimal caloric input for the combined *H. nasicus*, *P. catenifer*, and *C. viridis* populations was also calculated by totaling the respiration, growth, reproduction, and storage values per day. This total was also increased by 10% to account for the "excretion--not used" category. The daily minimal caloric input for these combined populations was 1.69 kcal/day.

The caloric input for the combined populations, including the 34.2 g/ha biomass increase from nonresident *C. viridis*, was calculated in the same manner as the other two input values. The daily caloric input for this group was 2.31 kcal/day.

Prey species taken, which provide this caloric input on the Pawnee Site, include most small mammals and lesser quantities of birds and lizards. *T. radix* fed upon insects as well as vertebrates (mainly *Rana pipens*) at Cottonwood Pond. Harris (1972) reported that the mean summer biomass of rodents in light graze areas on the Pawnee Site was 134.6 g/ha and that the dominant rodent was *Spermophilus tridecemlineatus*. Dr. J. Ellis (personal communication) reported that live weight biomass of rodents on the IBP site was 320.70 g/ha in light graze pastures and 326.64 g/ha in heavy graze pastures. Comparison of summer biomass (in grams per hectare) of snake predator (84.30 g/ha) to a major prey (320.70 g/ha rodents on light graze pastures) was calculated, and for each gram of snake there were 3.8 g of prey.

Odum (1971) lists the general caloric value for vertebrates at 5.6 kcal/g dry weight. When the light grazed treatment area biomass of 320.70 g/ha of rodents was converted to dry weight and multiplied by 5.6 kcal/g of vertebrate, the prey energy, which was "available" for snake consumption, was 598.02 kcal/day. The combined *H. nasicus*, *P. catenifer*, and *C. viridis* populations were shown to use a minimum input of 1.69 kcal/day. This indicates that snakes were taking in only a small amount of the "energy" available from rodents.

It appeared that although snake populations were present in fairly large amounts when considering biomass (in grams per hectare), their energy requirements to maintain this biomass were quite low. It was assumed that this was due to a combination of the "behavioral" and "physiological" adaptations of this class of vertebrates to survival on the shortgrass prairie.

SUMMARY

The energy flow model presented (Fig. 10) summarizes the most reasonable estimate of energy flow through snake populations in a specific ecosystem to date. It further synthesizes and organizes much of the literature on these species for biological productivity interpretation. It directs attention toward a number of areas where additional information would be valuable in the determination of snake bioproductivity. However, continued research on each separate component, on other components, and on population dynamics of each species of snake would further increase the accuracy and reliability of this model.

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APPENDIX I

DATA

Appendix Table 1. Snake field data, 1970 and 1971.

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Crotalus viridis	1	264	9.3	F	Dog town section	May 10, 1970
	2	257	9.0	F	Ridge section	May 18, 1970
	3	464	47.0	M	2 miles E of Headquarters	May 27, 1970
	4	921	398.8	M	½ mile W of Headquarters	June 2, 1970
	5	807	144.4	F	Buffalo pen road	June 19, 1970
	6	349	20.1	M	Hill ½ mile N of Headquarters	July 7, 1970
	7	660	160.2	M	450 m SW of trailer in section 26	Sept. 24, 1970
	8	444	92.0	F	Ridge, W trap of E-W center fence	Sept. 24, 1970
	9-19	(not used)				
	20	768	177.4	F	Ridge NW fence N trap	April 29, 1970
	21	876	397.7	M	Dog town	May 1, 1971
	22	711	224.3	F	Dog town 100 m E	May 1, 1971
	23	330	9.9	M	Ridge	May 3, 1971
	24	787	224.3	M	Dog town	May 15, 1971
	25	914	393.3	M	Irrigated, NE corner & 5 yd N	July 19, 1971
	26	333	17.5	F	100 yd S of stress	July 26, 1971
	27	826	296.7	M	150 yd W of 2 cattle guard E of Hq.	July 28, 1971
	27	826	382.9	M	Dog town S	Oct. 4, 1971
	28	699	202.1	M	Dog town fence at road	Aug. 4, 1971
	29	800	267.0	M	15 E at SE cattle guard	Aug. 24, 1971
	29	813	253.0	M	Cottonwood Pond	Sept. 25, 1971
	30	387	33.5	F	Ridge NW fence S trap	Sept. 22, 1971
	31	419	34.3	F	Dog town 50 yd E	Sept. 24, 1971
	32	343	26.6	M	Ridge NW fence S trap	Sept. 25, 1971
	33	445	47.1	M	Ridge SE fence S trap	Sept. 25, 1971
	34	445	45.9	M	Dog town SW fence S trap	Sept. 28, 1971
	34	445	46.2	M	Dog town NE fence S trap	Oct. 4, 1971
	35	864	482.6	M	Dog town S 200 yd	Sept. 28, 1971
	36	819	410.3	F	Dog town SW 200 yd	Oct. 4, 1971
	37	851	323.7	M	Dog town S 50 yd	Oct. 4, 1971
	38	787	230.6	F	Dog town S 200 yd	Oct. 4, 1971
	39	381	30.2	F	Dog town SE fence S trap	Oct. 4, 1971
	40	546	119.3	M	Dog town S 200 yd	Oct. 9, 1971
	41	826	296.7	M	Dog town S 200 yd	Oct. 11, 1971
	42	635	146.8	F	Dog town SE 150 yd	Oct. 11, 1971
	43	521	53.6	M	Ridge NE fence S trap	Oct. 13, 1971
	43	521	53.8	M	Ridge SE fence S trap	Oct. 20, 1971
	44	584	104.9	F	Dog town SE fence S trap	Oct. 13, 1971

Appendix Table 1 (continued).

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Heterodon nasicus	1	445	41.4	M	100 yd W in irrigated	May 21, 1970
	2	637	164.6	M	Lynn Lake	May 27, 1970
	3	489	69.7	F	¼ mile W of dog town	May 27, 1970
	4	495	70.2	M	½ mile N on dog town road	July 8, 1970
	5	470	75.5	F	N fence W trap ridge	July 21, 1970
	6	406	43.3	F	500 yd SW of trailer in section 26	July 24, 1970
	7-19 (not used)					
	20	464	39.0	M	15 E 75 yd N of fence	May 29, 1971
	22	610	179.1	M	Cottonwood E	June 8, 1971
	23	464	61.0	F	First cattle E of Headquarters	June 8, 1971
	24	203	7.0	M	Ridge SE fence N trap	July 1, 1971
	25	432	43.5	M	Ridge NE fence S trap	July 1, 1971
	26	470	66.2	M	E middle irrigated plot	July 14, 1971
	27	464	54.9	M	Dog town 100 yd W	July 19, 1971
	28	400	38.1	M	Dog town NW of road	July 18, 1971
	29	559	104.0	M	½ mile to Cottonwood on N side of road	July 21, 1971
	30	457	57.0	M	Dog town road at cattle guard	Aug. 27, 1971
	31	394	32.4	F	First hill, base toward dog town	Aug. 26, 1971
Pituophis catenifer	1	1276	501.9	M	Post near dog town	May 27, 1970
	2	1324	682.4	M	2 miles E of Headquarters	May 27, 1970
	3	337	6.9	M	E of Headquarter's house	June 2, 1970
	4	343	10.5	F	Headquarter's garage	June 17, 1970
	5	838	143.0	M	SE trap ridge	June 25, 1970
	6	1346	--	M	¼ mile E of Headquarters	July 20, 1970
	7	470	30.0	F	Ridge N fence W trap	July 27, 1970
	8	1245	442.0	M	SE corner irrigated	Aug. 4, 1970
	9	(not used)	--	--	Field W of Headquarters	--
	10	959	358.1	M	Ridge N fence W trap	July 31, 1970
	11	356	11.5	F	Road to ridge ¼ mile past 1st gate	Oct. 1, 1970
	12	686	106.7	M	¼ mile E of irrigation on the road	Oct. 6, 1970
	13-19 (not used)					
	20	1161	365.0	F	75 yd E of 2nd guard on E road	May 15, 1971
	21	1308	527.7	F	Twin near Lynn Lake	May 20, 1971
	22	1257	622.1	M	Line aerial and Hq. road at curve	May 20, 1971
	23	1181	369.6	M	Ridge windmill	May 27, 1971
	23	1181	369.2	M	Ridge windmill W	May 29, 1971
	24	1181	495.5	F	Ridge windmill	May 27, 1971
	25	1346	500.8	M	South of Cottonwood Pond	May 29, 1971

Appendix Table 1 (continued).

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Pituophis catenifer	26	1219	386.2	M	100 yd S of Headquarters	May 29, 1971
	27	1181	427.9	M	Ray's dirt fill spot	June 4, 1971
	28	1067	313.0	F	20 yd N of Ray's dirt fill spot	June 4, 1971
	29	851	172.6	F	Ridge SE fence N trap	June 7, 1971
	30	356	11.6	M	Ridge NE fence S trap	June 18, 1971
	31	495	27.1	F	100 yd SW of Headquarters	June 22, 1971
	32	1194	559.6	F	Irrigated stress plot	July 14, 1971
	33	927	245.2	M	1st cattle, dirt N to Cottonwood Pond	Aug. 19, 1971
	34	737	95.1	F	100 yd E of 1st cattle E of Hq.	Aug. 19, 1971
	35	1359	847.4	M	½ up main pipe to irrigated	Sept. 8, 1971
	36	826	142.5	F	50 yd E of 2nd cattle E of Hq.	Sept. 10, 1971
	37	1245	577.3	M	N of dog town ½ mile where road turns	Sept. 25, 1971
	38	1092	430.6	F	Dog town W 80 yd	Oct. 4, 1971
Thamnophis radix	1	648	140.0	F	Restricted to Cottonwood Pond	May 24, 1970
	1	650	141.2	F	Restricted to Cottonwood Pond	June 25, 1970
	2	521	--	F	Restricted to Cottonwood Pond	May 24, 1970
	2	597	46.9	F	Restricted to Cottonwood Pond	July 19, 1971
	3	705	52.5	M	Restricted to Cottonwood Pond	May 26, 1970
	3	708	53.2	M	Restricted to Cottonwood Pond	June 4, 1970
	3	768	74.4	M	Restricted to Cottonwood Pond	Aug. 24, 1971
	4	356	--	F	Restricted to Cottonwood Pond	May 26, 1970
	5	451	--	M	Restricted to Cottonwood Pond	May 26, 1970
	5	451	22.7	M	Cottonwood Pond	June 2, 1970
	5	508	28.9	M	Cottonwood Pond	Aug. 11, 1971
	6	460	--	F	Cottonwood Pond	May 26, 1970
	7	445	--	M	Cottonwood Pond	May 26, 1970
	8	384	--	F	Cottonwood Pond	May 26, 1970
	9	578	74.8	F	Cottonwood Pond	May 26, 1970
	9	768	109.5	F	Cottonwood Pond, broken tail	June 14, 1971
	9	775	109.1	F	Cottonwood Pond, broken tail	June 20, 1971
	9	775	86.3	F	Cottonwood Pond, broken tail	Aug. 11, 1971
	9	775	51.5	F	Cottonwood Pond, broken tail	Sept. 6, 1971
	10	368	--	M	Cottonwood Pond	May 26, 1970
	11	518	--	F	Cottonwood Pond	May 26, 1970
	12	343	--	F	Cottonwood Pond	May 26, 1970
	13	527	--	M	Cottonwood Pond	May 26, 1970
	14	400	14.9	F	Cottonwood Pond	May 26, 1970
	14	403	15.3	F	Cottonwood Pond	June 25, 1970

Appendix Table 1 (continued).

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Thamnophis radix	15	686	102.3	F	Cottonwood Pond	May 27, 1970
	16	445	31.9	F	Cottonwood Pond, broken tail	May 27, 1970
	16	686	95.5	F	Cottonwood Pond, broken tail	Aug. 11, 1971
	16	686	101.0	F	Cottonwood Pond, broken tail	Sept. 10, 1971
	17	813	119.0	M	Cottonwood Pond, broken tail	May 27, 1970
	18	438	17.7	M	Cottonwood Pond, broken tail	May 27, 1970
	19	502	22.5	F	Cottonwood Pond, broken tail	May 27, 1970
	20	362	11.4	F	Cottonwood Pond, broken tail	May 27, 1970
	21	618	61.8	F	Cottonwood Pond	May 27, 1970
	22	483	16.6	M	Cottonwood Pond	May 27, 1970
	22	485	17.1	M	Cottonwood Pond	June 25, 1970
	22	508	28.4	M	Cottonwood Pond	Aug. 13, 1970
	23	400	12.0	M	Cottonwood Pond	May 27, 1970
	24	435	17.5	M	Cottonwood Pond	May 27, 1970
	25	362	7.0	M	Cottonwood Pond	May 27, 1970
	26	578	31.9	M	Cottonwood Pond	May 31, 1970
	27	654	58.0	F	Cottonwood Pond	May 31, 1970
	28	610	38.3	M	Cottonwood Pond	May 31, 1970
	28	610	38.0	M	Cottonwood Pond	June 25, 1970
	29	584	39.8	M	Cottonwood Pond	May 31, 1970
	30	648	161.3	M	Cottonwood Pond	June 2, 1970
	31	559	39.0	F	Cottonwood Pond	June 2, 1970
	32	495	121.9	F	Cottonwood Pond	June 2, 1970
	32	851	117.6	F	Cottonwood Pond	July 14, 1971
	33	508	28.3	F	Cottonwood Pond	June 4, 1970
	34	559	35.0	M	Cottonwood Pond	June 4, 1970
	34	610	38.2	M	Cottonwood Pond	July 1, 1971
	35	542	35.6	F	Cottonwood Pond	June 4, 1970
	36	807	165.2	F	Cottonwood Pond	June 4, 1970
	36	808	165.5	F	Cottonwood Pond	July 25, 1971
	37	286	5.8	M	Cottonwood Pond	June 4, 1970
	38	514	25.0	M	Cottonwood Pond	June 4, 1970
	39	553	33.5	M	Cottonwood Pond	June 4, 1970
	39	572	36.4	M	Cottonwood Pond	June 22, 1970
	39	629	40.6	M	Cottonwood Pond	Aug. 24, 1971
	39	629	38.4	M	Cottonwood Pond	Sept. 10, 1971
	40	330	8.2	F	Cottonwood Pond	June 4, 1970
	41	470	23.1	F	Cottonwood Pond	June 4, 1970

Appendix Table 1 (continued).

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Thamnophis radix	41	470	24.0	F	Cottonwood Pond	June 25, 1970
	42	540	30.2	F	Cottonwood Pond	June 4, 1970
	43	324	8.1	F	Cottonwood Pond	June 4, 1970
	44	508	37.9	F	Cottonwood Pond	June 4, 1970
	45	419	19.6	F	Cottonwood Pond	June 4, 1970
	46	356	12.2	F	Cottonwood Pond	June 4, 1970
	47	324	8.5	M	Cottonwood Pond	June 4, 1970
	48	394	14.3	F	Cottonwood Pond	June 4, 1970
	49	368	10.8	M	Cottonwood Pond	June 4, 1970
	50	292	11.2	F	Cottonwood Pond	June 4, 1970
	51	413	13.0	M	Cottonwood Pond	June 4, 1970
	52	254	3.6	M	Cottonwood Pond	June 4, 1970
	53	394	23.2	M	Cottonwood Pond	June 4, 1970
	54	318	10.9	F	Cottonwood Pond	June 4, 1970
	55	457	26.4	F	Cottonwood Pond	June 4, 1970
	56	273	4.2	F	Cottonwood Pond	June 4, 1970
	57	476	27.6	F	Cottonwood Pond	June 4, 1970
	58	362	11.0	M	Cottonwood Pond	June 4, 1970
	58	483	35.9	M	Cottonwood Pond	June 22, 1971
	59	241	3.5	F	Cottonwood Pond	June 4, 1970
	60	305	7.3	M	Cottonwood Pond	June 4, 1970
	60	305	7.5	M	Cottonwood Pond	June 25, 1970
	61	349	--	F	Cottonwood Pond	June 15, 1970
	62	413	--	F	Cottonwood Pond	June 15, 1970
	63	406	--	M	Cottonwood Pond	June 15, 1970
	64	368	--	F	Cottonwood Pond	June 15, 1970
	65	330	--	F	Cottonwood Pond	June 15, 1970
	66	406	--	F	Cottonwood Pond, broken tail	June 15, 1970
	67	330	--	F	Cottonwood Pond	June 22, 1970
	68	584	--	F	Cottonwood Pond, broken tail	June 22, 1970
	69	553	27.0	M	Cottonwood Pond	June 25, 1970
	70	533	33.0	F	Cottonwood Pond	June 25, 1970
	71	495	21.1	M	Cottonwood Pond	June 25, 1970
	72	432	14.3	F	Cottonwood Pond	June 25, 1970
	73	533	30.0	F	Cottonwood Pond	June 25, 1970
	74	419	19.0	F	Cottonwood Pond	June 25, 1970
	75	318	10.0	F	Cottonwood Pond	June 25, 1970
	76	394	30.1	F	Cottonwood Pond, broken tail	June 25, 1970

Appendix Table 1 (continued).

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Thamnophis radix	77	445	18.5	F	Cottonwood Pond	June 25, 1970
	78	686	53.2	F	Cottonwood Pond, broken tail	June 25, 1970
	79	279	5.0	F	Cottonwood Pond	June 25, 1970
	80	572	42.2	F	Cottonwood Pond	June 25, 1970
	81	559	33.0	M	Cottonwood Pond	June 25, 1970
	82	381	12.0	F	Cottonwood Pond	June 25, 1970
	83	572	48.0	F	Cottonwood Pond	June 25, 1970
	84	521	46.0	F	Cottonwood Pond	June 25, 1970
	84	543	54.6	F	Cottonwood Pond	July 1, 1971
	85	356	8.5	F	Cottonwood Pond	June 25, 1970
	86	673	58.0	M	Cottonwood Pond	June 25, 1970
	87	559	36.0	F	Cottonwood Pond	June 25, 1970
	88	292	4.0	F	Cottonwood Pond	June 25, 1970
	89	457	20.0	M	Cottonwood Pond	June 25, 1970
	90	826	141.0	F	Cottonwood Pond	June 25, 1970
	91	508	26.0	M	Cottonwood Pond	June 25, 1970
	92	483	27.0	F	Cottonwood Pond	June 25, 1970
	93	699	71.0	F	Cottonwood Pond	June 25, 1970
	93	699	54.6	F	Cottonwood Pond	Aug. 24, 1971
	94	559	37.0	F	Cottonwood Pond	June 25, 1970
	94	648	58.5	F	Cottonwood Pond	Aug. 13, 1970
	95	495	22.0	M	Cottonwood Pond	June 25, 1970
	96	610	52.0	M	Cottonwood Pond	June 25, 1970
	97	495	21.0	F	Cottonwood Pond	June 25, 1970
	98	343	9.0	F	Cottonwood Pond	June 25, 1970
	99	457	20.0	M	Cottonwood Pond	June 25, 1970
	100	483	20.0	F	Cottonwood Pond	June 25, 1970
	101	432	18.0	F	Cottonwood Pond	June 25, 1970
	102	495	22.5	F	Cottonwood Pond	June 25, 1970
	103	406	13.0	F	Cottonwood Pond	June 25, 1970
	104	381	17.0	M	Cottonwood Pond	June 25, 1970
	104	476	24.6	M	Cottonwood Pond	July 26, 1971
	105	711	94.0	F	Cottonwood Pond	June 25, 1970
	106	483	22.0	F	Cottonwood Pond	June 25, 1970
	107	470	24.0	F	Cottonwood Pond	June 25, 1970
	108	559	28.0	M	Cottonwood Pond	June 25, 1970
	109	356	10.0	F	Cottonwood Pond	June 25, 1970
	110	381	9.0	F	Cottonwood Pond	June 25, 1970

Appendix Table 1 (continued).

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Thamnophis radix	111	533	31.0	F	Cottonwood Pond	June 25, 1970
	112	330	5.0	M	Cottonwood Pond	June 25, 1970
	113	356	4.0	F	Cottonwood Pond	June 25, 1970
	114	292	3.0	M	Cottonwood Pond	June 25, 1970
	115	368	7.0	M	Cottonwood Pond	June 25, 1970
	116	483	26.0	M	Cottonwood Pond	June 25, 1970
	117	559	61.0	F	Cottonwood Pond, broken tail	June 25, 1970
	117	559	59.7	F	Cottonwood Pond, broken tail	July 1, 1970
	118	533	27.0	M	Cottonwood Pond	June 25, 1970
	119	419	15.0	M	Cottonwood Pond	June 25, 1970
	120	381	9.0	F	Cottonwood Pond	June 25, 1970
	121	610	45.0	F	Cottonwood Pond	June 25, 1970
	121	699	85.1	F	Cottonwood Pond	Aug. 11, 1971
	122	445	25.0	M	Cottonwood Pond	June 25, 1970
	122	521	34.6	M	Cottonwood Pond	Aug. 11, 1971
	123	495	34.0	F	Cottonwood Pond	June 25, 1970
	124	584	40.0	M	Cottonwood Pond	June 25, 1970
	125	356	11.0	M	Cottonwood Pond	June 25, 1970
	126	305	5.0	M	Cottonwood Pond	June 25, 1970
	127	343	9.0	F	Cottonwood Pond	June 25, 1970
	128	406	10.0	F	Cottonwood Pond	June 25, 1970
	129	368	8.0	M	Cottonwood Pond	June 25, 1970
	130	356	7.0	F	Cottonwood Pond	June 25, 1970
	131	381	10.0	F	Cottonwood Pond	June 25, 1970
	132	489	19.7	M	Cottonwood Pond	Aug. 13, 1970
	133	394	12.9	F	Cottonwood Pond	Aug. 13, 1970
	134	483	24.5	M	Cottonwood Pond	Aug. 13, 1970
	135	413	25.8	F	Cottonwood Pond, broken tail	Aug. 13, 1970
	136	279	3.8	F	Cottonwood Pond	Aug. 13, 1970
	137	419	11.6	M	Cottonwood Pond	Aug. 13, 1970
	138	318	7.9	M	Cottonwood Pond	Aug. 13, 1970
	139	318	6.7	F	Cottonwood Pond	Aug. 13, 1970
	140	800	97.2	F	Cottonwood Pond	Sept. 1, 1970
	140	851	119.5	F	Cottonwood Pond	Aug. 24, 1971
	141-149 (not used)					
	150	413	16.4	M	Cottonwood Pond	May 18, 1971
	151	514	16.6	M	Cottonwood Pond	June 1, 1971
	152	724	89.7	F	Cottonwood Pond	June 1, 1971

Appendix Table 1 (continued).

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Thamnophis radix	153	390	17.1	M	Cottonwood Pond	June 1, 1971
	154	345	8.4	F	Cottonwood Pond	June 1, 1971
	155	679	67.7	F	Cottonwood Pond	June 1, 1971
	155	679	73.4	F	Cottonwood Pond	July 23, 1971
	156	318	9.1	M	Cottonwood Pond	June 1, 1971
	157	629	33.7	M	Cottonwood Pond	June 1, 1971
	158	241	4.6	F	Cottonwood Pond	June 1, 1971
	159	511	27.3	M	Cottonwood Pond	June 1, 1971
	160	584	25.9	M	Cottonwood Pond	June 1, 1971
	161	565	36.1	F	Cottonwood Pond	June 1, 1971
	162	349	10.9	F	Cottonwood Pond	June 1, 1971
	163	457	23.9	F	Cottonwood Pond	June 4, 1971
	164	711	58.2	M	Cottonwood Pond	June 14, 1971
	165	429	18.4	M	Cottonwood Pond	June 14, 1971
	166	667	68.0	F	Cottonwood Pond	June 14, 1971
	167	589	28.8	M	Cottonwood Pond	June 14, 1971
	168	488	26.1	F	Cottonwood Pond	June 14, 1971
	169	540	36.0	F	Cottonwood Pond	June 14, 1971
	170	381	13.0	F	Cottonwood Pond	June 14, 1971
	171	521	28.1	F	Cottonwood Pond	June 14, 1971
	172	438	18.3	F	Cottonwood Pond	June 14, 1971
	173	470	18.8	F	Cottonwood Pond	June 14, 1971
	174	433	17.9	M	Cottonwood Pond	June 14, 1971
	175	394	12.5	M	Cottonwood Pond	June 14, 1971
	176	673	54.7	F	Cottonwood Pond	June 22, 1971
	177	508	20.1	M	Cottonwood Pond	July 19, 1971
	178-179 (not used)					
	180	565	32.9	M	Cottonwood Pond	July 19, 1971
	181-182 (not used)					
	183	629	39.3	F	Cottonwood Pond	June 14, 1971
	184-188 (not used)					
	189	495	37.1	F	Cottonwood Pond	June 20, 1971
	190	343	11.8	M	Cottonwood Pond	July 1, 1971
	191	410	16.4	M	Cottonwood Pond	July 1, 1971
	192	466	39.4	F	Cottonwood Pond	July 1, 1971
	193	445	27.0	F	Cottonwood Pond	July 1, 1971
	194	455	20.0	M	Cottonwood Pond	July 2, 1971
	195	308	5.8	F	Cottonwood Pond	July 2, 1971

Appendix Table 1 (continued).

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Thamnophis radix	195	337	11.5	F	Cottonwood Pond	July 19, 1971
	196	718	42.7	M	Cottonwood Pond	July 4, 1971
	196	724	47.3	M	Cottonwood Pond	Sept. 25, 1971
	197	622	35.2	M	Cottonwood Pond	July 4, 1971
	198	605	42.9	F	Cottonwood Pond	July 4, 1971
	199	641	36.9	F	Cottonwood Pond	July 4, 1971
	200	415	13.6	F	Cottonwood Pond	July 4, 1971
	200	711	62.1	F	Cottonwood Pond	Aug. 24, 1971
	201	587	55.9	F	Cottonwood Pond	July 11, 1971
	202	540	56.3	M	Cottonwood Pond	July 11, 1971
	202	591	29.9	M	Cottonwood Pond, newly damaged	Sept. 10, 1971
	203	572	57.9	F	Cottonwood Pond, broken tail	July 21, 1971
	204	635	45.7	F	Cottonwood Pond	July 21, 1971
	205	502	31.2	F	Cottonwood Pond	July 21, 1971
	206	552	34.2	F	Cottonwood Pond	July 21, 1971
	207	521	30.2	F	Cottonwood Pond	July 21, 1971
	208	616	61.1	F	Cottonwood Pond, broken tail	July 21, 1971
	208	616	59.5	F	Cottonwood Pond, broken tail	Aug. 16, 1971
	209	648	44.0	F	Cottonwood Pond	July 21, 1971
	210	457	26.5	F	Cottonwood Pond	July 21, 1971
	211	511	22.5	M	Cottonwood Pond	July 23, 1971
	212	503	23.6	M	Cottonwood Pond	July 23, 1971
	213	537	32.2	M	Cottonwood Pond	July 23, 1971
	214	511	29.2	M	Cottonwood Pond	July 23, 1971
	215	503	23.2	M	Cottonwood Pond	July 23, 1971
	216	591	34.3	F	Cottonwood Pond	July 26, 1971
	217	610	45.0	F	Cottonwood Pond	July 26, 1971
	218	476	24.6	M	Cottonwood Pond	July 26, 1971
	219	540	35.5	M	Cottonwood Pond	July 26, 1971
	220	597	45.7	M	Cottonwood Pond	Aug. 11, 1971
	221	648	48.8	F	Cottonwood Pond	Aug. 11, 1971
	222-224	(not used)				
	225	673	35.3	M	Cottonwood Pond	Aug. 16, 1971
	226	667	57.0	M	Cottonwood Pond	Aug. 16, 1971
	227	641	38.9	M	Cottonwood Pond	Aug. 16, 1971
	228	654	50.4	M	Cottonwood Pond	Aug. 16, 1971
	229	451	19.9	M	Cottonwood Pond	Aug. 16, 1971
	230	394	26.2	M	Cottonwood Pond, broken tail	Aug. 24, 1971

Appendix Table 1 (continued).

Species	Number	Length (mm)	Weight (g)	Sex	Location	Date Collected
Thamnophis radix	231	724	80.6	M	Cottonwood Pond	Aug. 24, 1971
	232	483	31.4	F	Cottonwood Pond, broken tail	Aug. 24, 1971
	233	749	75.2	F	Cottonwood Pond	Aug. 31, 1971
	234	800	102.8	F	Cottonwood Pond	Aug. 31, 1971
	235	584	33.5	F	Cottonwood Pond	Aug. 31, 1971
	236	648	38.5	F	Cottonwood Pond	Aug. 28, 1971
	236	654	36.8	F	Cottonwood Pond, blind eye	Sept. 6, 1971
Thamnophis elegans	237	699	58.8	M	Cottonwood Pond	Sept. 6, 1971
Thamnophis radix	238	445	26.4	F	Cottonwood Pond	Sept. 10, 1971
	239	660	64.0	F	Cottonwood Pond	Sept. 10, 1971
	240	591	42.3	M	Cottonwood Pond, belly damaged	Sept. 10, 1971
	241	629	57.7	F	Cottonwood Pond	Sept. 13, 1971
	241	629	58.0	F	Cottonwood Pond	Sept. 25, 1971
	242	591	58.6	F	Cottonwood Pond	Sept. 13, 1971
	243	597	48.9	F	Cottonwood Pond	Sept. 28, 1971
	Odd Lot					
	288	895	143.5	F	Cottonwood Pond	June 22, 1971
	288	914	147.7	F	Cottonwood Pond	July 23, 1971
	290	800	86.2	F	Cottonwood Pond	July 26, 1971
	300	737	135.7	F	Cottonwood Pond	July 14, 1971
	300	787	77.5	F	Cottonwood Pond, badly damaged	Aug. 31, 1971
	350	438	17.2	F	Cottonwood Pond	June 7, 1971
	400	775	136.3	F	Cottonwood Pond, broken tail	Sept. 6, 1971
	450	483	30.8	F	Cottonwood Pond, broken tail	July 23, 1971
	580	508	33.0	F	Cottonwood Pond	June 20, 1971