THE IMPORTANCE OF THE FACIAL PIT OF THE NORTHERN PACIFIC RATTLESNAKE (Crotalus viridis oreganus) UNDER NATURAL CONDITIONS IN SOUTHERN BRITISH COLUMBIA

by

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ABSTRACT

The facial pits characterizing the snake subfamily Crotalinae have been demonstrated to be important as thermoreceptors in detecting the presence of prey animals and in directing the strike towards them. So specialized a receptor as the pit organ, if it is to survive, must be functionally effective. If this organ is important in locating prey under natural conditions it would be expected that if these pits were destroyed this importance would be reflected in growth rates, weight changes, or survival. In twenty of forty snakes collected in the spring of 1963 the pits were destroyed by electric cautery. After weighing, measuring, and marking, the snakes were released at the point of capture. The growth of the recaptured cauterized and non-cauterized snakes was compared. In addition, controlled tests were made with the recaptured snakes, using live mice and light-proof boxes to determine the effectiveness of cautery. A significant statistical difference was found in the growth rates of the females, the cauterized snakes growing more slowly. No difference was found in the growth rates of the males. However, the controlled tests indicated the pits to be important to the males as well as to the females. Weight changes were too variable to reveal differences between normal and cauterized snakes and no difference in survival was evident between the two treatments. To overcome the effect of individual variation in growth rate further study is required of larger samples over a longer time period.

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INTRODUCTION

The Facial Pit

Animals, to maintain contact with their environment, depend upon various sensory receptors adapted for the reception of particular stimuli from environment. One such type of receptor is the facial pit occuring in snakes of the subfamily Crotalinae. The pit is located somewhat below a line from the nostril to the eye and slightly nearer the nostril (Klauber, 1956). According to Dowling (1959), the pit is the only distinguishing feature between the true vipers (Viperinae) and the pit-vipers (Crotalinae). Since it occupies the position of the loreal scale in the pitless snakes, although the exact location varies among the species, the pit is often called the loreal pit (Klauber, 1956), another name commonly applied being "facial pit". The locality of the pit in *Crotalus viridis oreganus* may be seen in Figures 1 and 2.

Anatomy of the Pit

Early studies of the facial pit have been discussed by Lynn (1931) who was the first to use fresh material in his detailed anatomical studies of it. Lynn's work was done mainly on the copperhead, *Agkistrodon contortrix*.

The pit consists of two chambers separated by the pit membrane. Allowance is made for the pit in the maxillary bone by a deep fossa. Figures 3 and 4 will illustrate more clearly the gross anatomy of the facial pit. The outer opening is generally oval or pear-shaped, having a groove from the posterior extremity to the eye. The inner chamber connects to the outside by means of an opening located in this groove. The opening is surrounded by a sphincter and is usually tightly closed (Lynn, 1931).

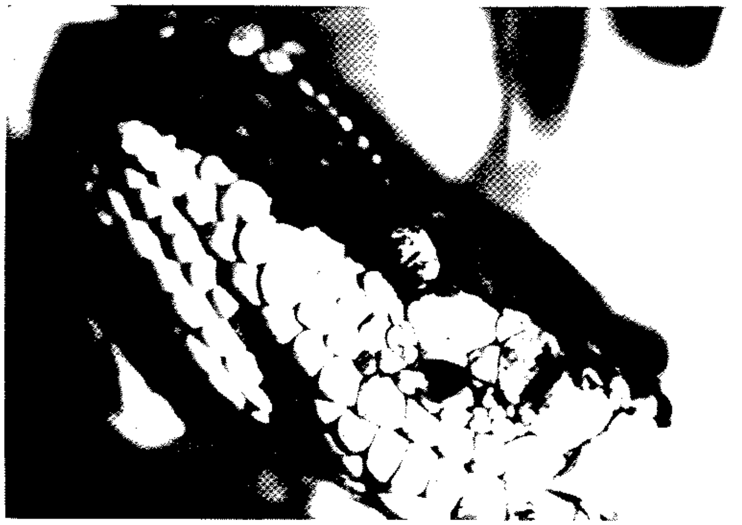

Figure 1. Side view of rattlesnake head showing facial pit. The pit membrane is visible.

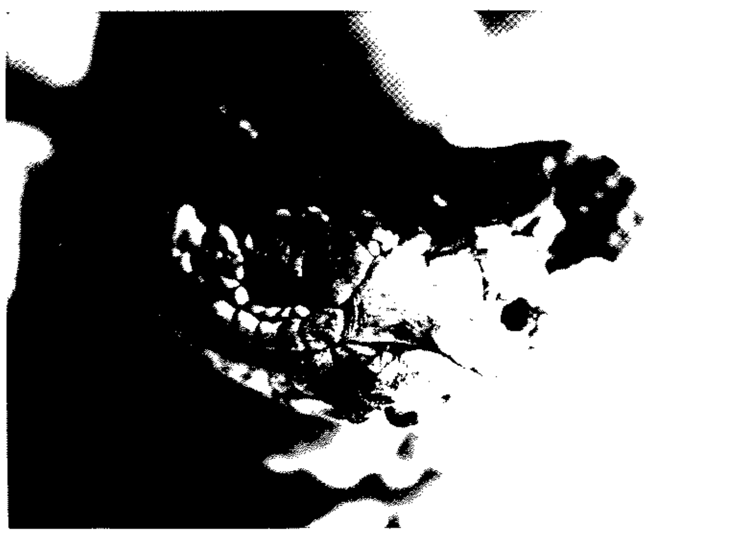

Figure 2. Front view of rattlesnake head showing the two facial pits.

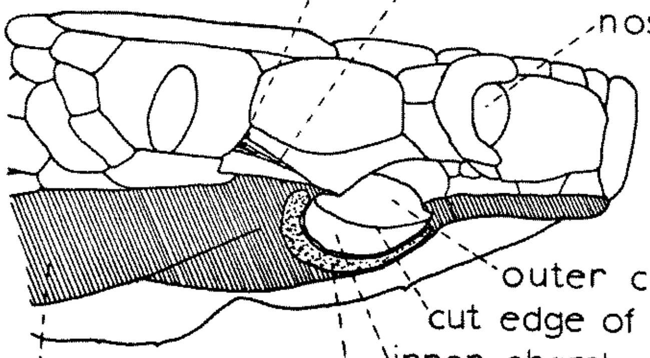

Figure 3. Drawing of right side of rattlesnake head dissected to show the facial pit. X7.

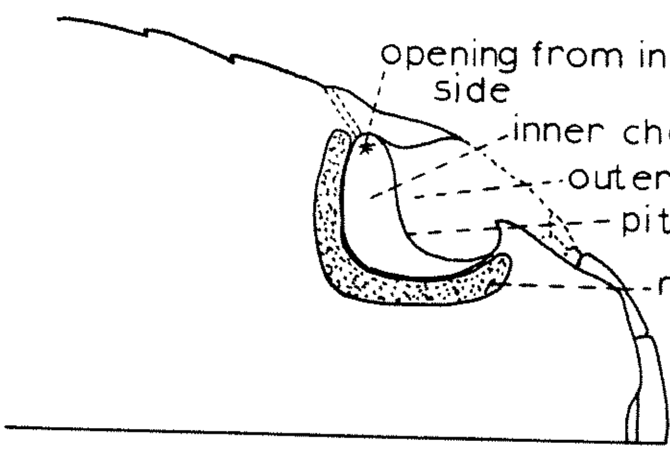

Figure 4. Diagram of underside of rattlesnake head dissected to show the facial pit.

The membrane between these two chambers, the pit membrane, was found by Bullock and Fox (1957) to be 10 microns thick in recently moulted adults.

The facial pits are innervated by branches of the trigeminal nerve. "In snakes having no pits, the trigeminus supplies the skin of the face and the roof of the mouth together with certain of the muscles. Its fibres, which supply nerve endings in the skin, are believed to be chiefly sensory in nature, probably functioning mainly in the perception of the tactile stimuli. In the pit vipers, on the other hand, by far the major portion of both the ophthalmic and the supramaxillary branches of the trigeminal goes to supply the pit, furnishing this organ with a nerve supply which is comparable in amount to that of any sense organs of the head" (Lynn, 1931).

Bullock and Fox (1957), in their study, found the innervation of the pit to be very rich - 500 to 1500 axon endings per square millimeter. They compare this with the 800 optic nerve fibres per square millimeter in the retina of man. These nerve endings are palmate in structure and are not connected with any type of sensory cell.

Purpose and Physiology of the Pit

Numerous authors have suggested special functions of the pit. These suggestions reviewed by Klauber (1956) are ears, extra nostrils, analogous to certain "tear sacs" of ruminants, olfactory, bringing air in contact with venom thus affecting the chemical properties, secretory follicles, an unspecified sixth sense similar to the lateral line system of fishes and tactile.

Not until the experiments of Noble and Schmidt (1937) was the facial pit known to be a thermoreceptor. Noble earlier (1934) had considered the pit to detect air vibrations, a purpose not believed to be important in nature. Noble and Schmidt found that pit vipers deprived of sight and olfaction, the nostrils plugged and tongue ablated, could distinguish between warm and cold light bulbs and also between a warm freshly killed rat and a chilled rat.

In more recent studies (Bullock and Cowles, 1952; Bullock and Faulstick, 1953; Bullock and Diecke, 1956) nerve impulses were recorded mainly from the superficial branch of the superior maxillary division of the trigeminal nerve, which is one of the three nerves supplying the pit membrane. It was shown that the nerve fibres supplying the pit are spontaneously active. The rate of neuronal discharge increased with increase in temperature of the organ, which would accompany an increase in body temperature, or with radiation from objects warmer than the ambient temperature impinging upon the pit membrane. The spontaneous discharge was inhibited by a decrease in body temperature or the presence in the receptive field of an object cooler than the ambient temperature. Bullock and Cowles, by recording from the forementioned nerve, have shown no response to sound, odours, vibration of substratum, touching the head and pit, or to well heat-filtered light of moderate intensity. Changes in rate of discharge were induced by mechanical deformation of the membrane, brushing the upper lip, the effect of which is weak, abrupt air movement, temperature changes of the body, and common objects, the temperature of which is above or below a neutral point, brought into the receptive field. Bullock and Faulstick (1953) pointed out that neutral objects are those emitting the same radiation as the surroundings and not those at the snake's body temperature. For example, if a snake's body temperature is above room temperature objects at a temperature intermediate to that of the snake and its surroundings will increase the level of neuronal discharge.

With regard to the function of the pit organ, which as mentioned earlier has no sensory cells other than nerve endings, Bullock and Diecke (1956) have hypothesized that the receptors are responding to temperature changes in the tissues resulting from radiant energy, these temperature changes being enhanced by the thin membrane.

It can be argued that if so specialized a receptor is to survive it must be functionally effective. As suggested by their vertical elliptical pupils, crotalines are mainly nocturnal or crepuscular in habit. This is true also of boids and viperines. It has been shown by Noble and Schmidt (1937) that some boid species, having thermoreceptors in the form of labial pits, can distinguish between warm and cold objects as well as can the crotalines. They have further suggested, although it has not yet been substantiated, that certain supranasal cavities occuring in some viperine genera might function as thermoreceptors. In the case of a nocturnal snake, hunting in the dark, such a thermoreceptor would aid in locating endothermic prey animals and in directing the strike. The very position of the crotaline facial pit suggests such a function.

Regarding the importance of the facial pit, according to Noble and Schmidt, "it appears then that although crotalid snakes are highly specialized in the extreme elaboration of the tongue-Jacobson's organ mechanism for trail finding and the facial pits for warm blooded prey detection, the primitive olfactory and visual mechanisms still have important functions. Further they may suffice alone under ideal conditions of food capture such as maintains in a large laboratory cage. Crotalids deprived of pit and tongue would doubtlessly have a difficult time under natural conditions for both structures have important sensory functions." They conclude that "in the absence of vision the labial pits of Boidae and the facial pits of Crotalidae are the most important sensory mechanisms for directing the strike towards warm blooded prey". From their study Bullock and Diecke presume that "crotalids should have an advantage hunting warm blooded or cool (moist) prey at night or underground and in locating warm or cool regions of the substratum".

Purpose and Scope of this Study

If the facial pits have an important function under natural conditions in locating and directing the strike towards the prey it would be expected that snakes deprived of pits would be less successful in securing food than those with normal facial pits. Further, it would be expected that this reduction in effeciency of feeding would be reflected either in impaired survival or in reduced growth rates of those snakes deprived of the thermoreceptive sense as compared to those of normal snakes, or if not possibly in weight changes. To the writer's knowledge no research on this aspect of the facial pit has yet been carried out. It is the purpose of the present study to attempt to fill the gap - to determine, in the case of the Northern Pacific Rattlesnake (Crotalus viridis oreganus), the importance of the facial pits under natural conditions as reflected by growth rates, changes in body weight or differential survival.

Since a field study of this species had not been undertaken as yet in the northern limits of its range, it is the writer's interest to include in the scope of this study such aspects of rattlesnake ecology as population density and composition, general growth rates, records of food items and summer movements of the snakes.

METHODS

The Study Area

An area suitable for study with a sizeable rattlesnake population was required. A second requirement, perhaps related to the first was that there be a minimal amount of human interference with the snake population.

The area selected lies on the east side of the Okanagan Valley about 10 miles south of Oliver. About two-thirds of the area lies on the 69 Ranch and the remainder on the Inkaneep Indian Reservation (Figure 5). Only two wintering dens could be found on the area. These were located in the same rocky bluff at an elevation of 1500 to 1600 feet above sea level. The sandy bench below the rock bluff lies at an elevation of 1200 feet sloping gradually to the valley floor at an elevation of 1000 feet. At the narrowest point in this area the distance from the rock bluff to the valley floor is 2000 feet.

On the rock bluff, in the vicinity of the dens, the most common tree is *Pinus ponderosa*, which is rather scattered both on the rocks and on the sand flat below. Perhaps the most common shrub in the den area is *Philadelphus lewisii*, which occurs down to the sand flat but not on it. Other shrubs common on the rock bluff are *Artemisia tridentata*, *Ribes cereum*, *Rhus glabra*, *Rhus radicans* and *Amelanchier cusickii*.

On the sand flat below, perhaps the most conspicuous shrub is *Purshia tridentata*, although *Artemisia tridentata* and *Chrysothamnus nauseosus* appear to be the most common. *Amelanchier* and *Rhus glabra* occur only in localised areas here. Two common grasses occuring on the sandy bench and rock bluff are *Agropyron spicatum* and *Aristida longiseta*.

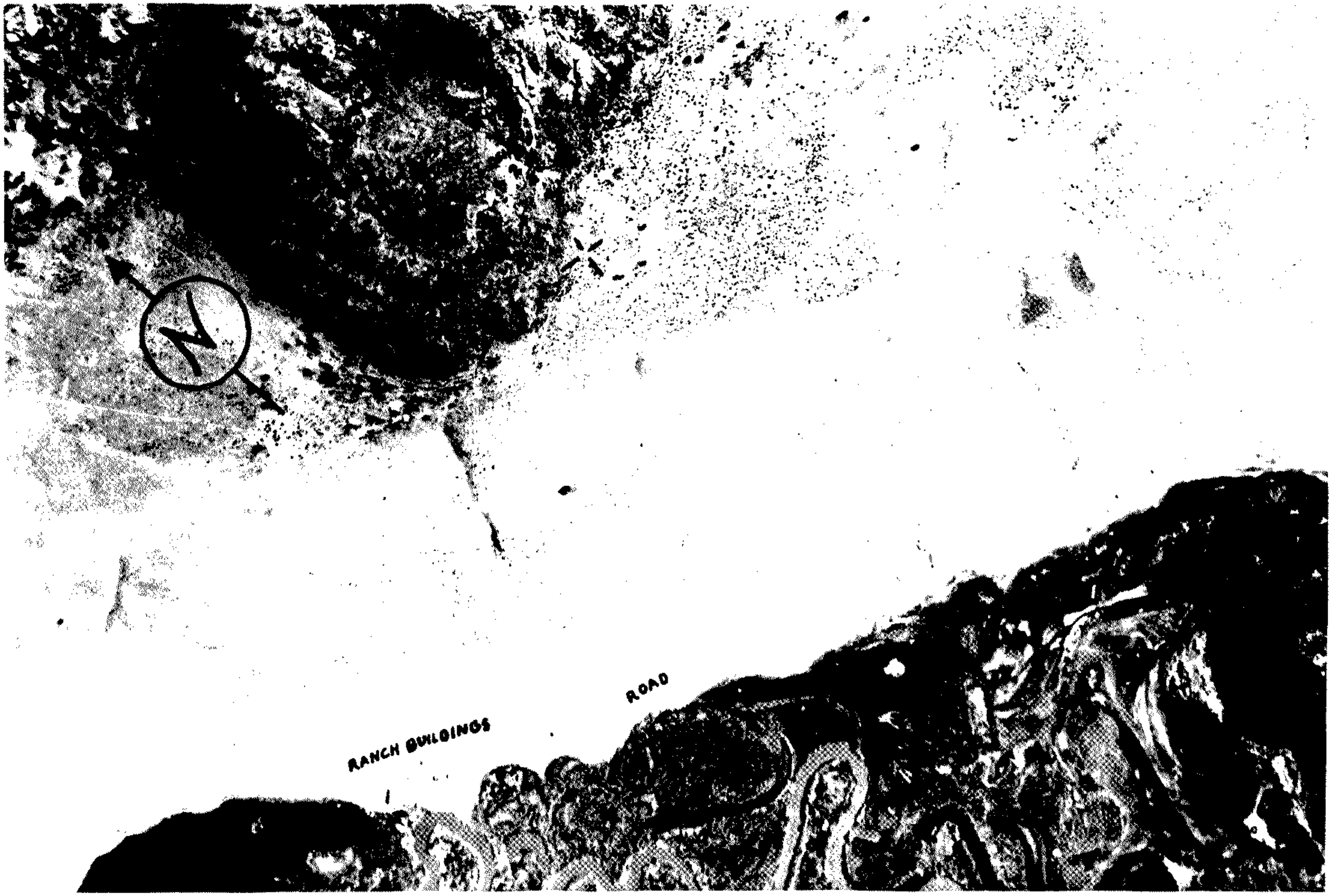

Figure 5. The study area. Scale: 1" = 800'. Air Photo by B. C. Government.

The valley bottomland is mainly meadowland, covered with various grasses, the vegetation of the wetter areas consisting mainly of Scirpus spp.? and Typha latifolia. Hay is cut and baled on this meadow usually during the first part of August. Along the old river channel (a new channel was dug in 1956) and in wetter areas generally common species are Salix spp. and Betula occidentalis. Less conspicuous is Rhus radicans which appears to invade the lower edges of the sand hill from the bottomland.

A road traverses the area, as can be seen from Figure 5 along the lower edge of the sandhill. The ranchhouse was occupied only during the winter, during which time cattle are kept on the area. The only human activity was haying in late summer and pheasant hunting in the autumn. Road traffic was light and mainly by members of the Inkaneep Indian Band. Conversation revealed that very few rattlesnakes were seen on the road. All in all the area proved ideal for rattlesnake study in that there was a minimum of human interference. Only two casualties to rattlesnakes are known to have occurred due to human activity during the entire study period. One of these, apparently run over by a car, was found on the road on June 25, 1962. Another was killed accidently by a tractor in late September, 1963, during land clearing in the bottomland area.

The Hibernating Dens

The two hibernating dens were originally discovered by the writer several years ago. Den No. 1 (Figure 6) consists of a horizontal crevice in a sloping rock face, the opening of which is about 2 inches in height. Inside, the crevice appears to slope slightly upward. On emergence, the snakes are first seen in this crevice. Later, as the weather warms, they may be found scattered about in other crevices and in talus in the immediate vicinity of the den opening. The exposure of the den slope is toward the west and

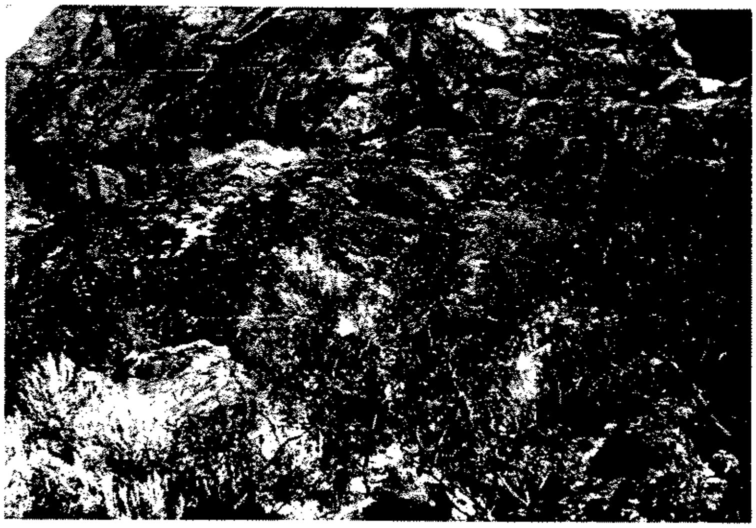

Figure 6. Den No. 1. The arrow indicates the main entrance.

Figure No. 7. Den No. 2. The grab-stick (about four feet in length) indicates the main entrance.

slightly south.

Den No. 2 appears to be more indefinite in location than the other in that the snakes are found scattered over a wider area. The entire area consists of talus. One of the most important openings appears to be a small pile of broken rocks (Figure 7). The exposure of this area is more to the south than that of Den No. 1. The distance between the two dens is about 700 feet.

Methods of Capture

In the spring and autumn while the snakes were in the vicinity of the dens they were captured by means of a grab-stick and a canvas bag attached to a heavy wire loop on a handle. This method enables rapid capture of snakes thus lessening the number of losses due to escape. Care was taken to avoid excessive pressure on each snake by the grab-stick to prevent injury.

Funnel traps after the design of Fitch (1960) were set along the base of the rock bluff and along the lower edge of the sand bench. During 1962, 16 trap stations were set out, two of these consisting of one trap each, with a funnel at each end, and the remainder consisting of two funnel traps facing one another, one on either end of a drift fence. Figures 8 and 9 illustrate the funnel traps. The traps were made from ¼ inch mesh wire and the drift fence from fly screen. In the summer of 1963, the number of trap stations was increased to 27, each one containing two traps and a drift fence. The traps were checked almost every day and were checked in the morning in order to prevent exposing the snakes to the heat of the day. Even with this precaution two rattlesnakes, four blue racers and one bull-

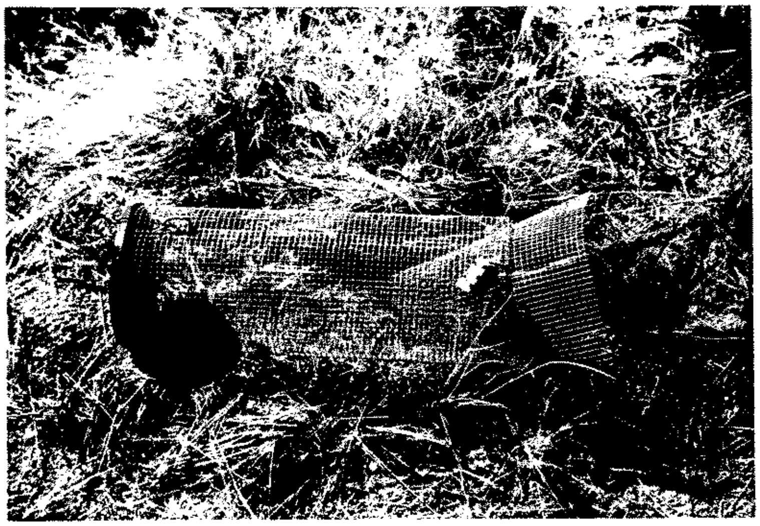

Figure 8. Funnel trap showing one end and part of drift fence.

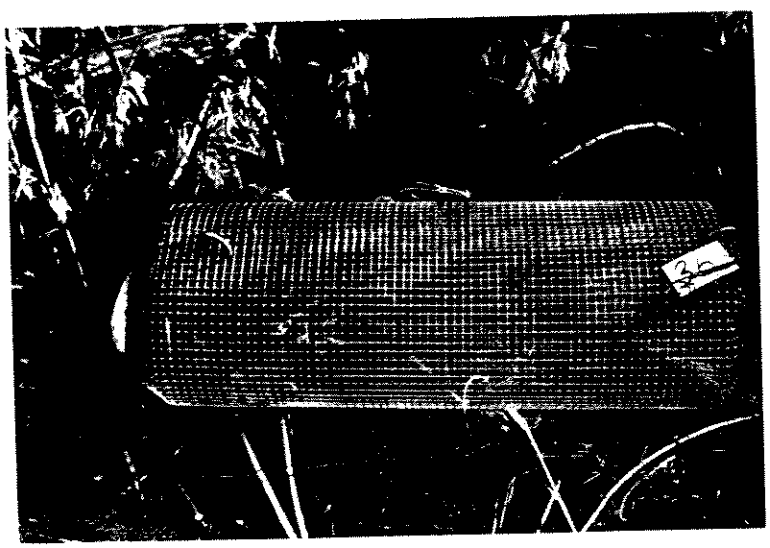

Figure 9. Rattlesnake in funnel trap.

snake died of overexposure. The traps were covered with dry grass and whatever other material was handy but the noon-day heat was still severe. Snakes were taken from the traps by removing the funnel and emptying them into a cloth bag for transportation to headquarters for processing.

Several snakes were captured while the writer was wandering through the study area searching for them, or checking the traps. However this did not prove very fruitful and neither did searching at night with a flashlight, although one rattlesnake was captured by this latter method.

Procedures

For examination the snakes were brought to headquarters. Weighing was done by placing the snake in a pre-weighed cloth bag and placing it on the pan of a triple-beam balance. For measuring (Figure 10), a measuring board was constructed to which a steel tape could be attached in the same position every time. The snake to be measured was grasped behing the head with the left hand and the snout held against a block at the zero mark on the tape. The tail was grasped in the right hand and the snake held until it completely relaxed at which time the measurement was read. All snakes were measured in the same manner except the extremely small snakes of about 30 cm. in length which proved difficult to pick up safely in this manner. These were noosed behind the head with a noose-clamp designed for this purpose and held by substituting the clamp for the left hand and measured in this manner. To determine the amount of variation in measuring, 11 captive individuals were measured daily over a period of 7 days.

Sexing was done by inserting a blunt probe into the cloaca and probing for hemipenes. Marking was done after the method of Blanchard and Finster (1933) by clipping the subcaudal scutes. An example would be a snake marked as $R_{2,5}L_8$ in which the right corners of the second and fifth scutes caudad from the vent and the left side of the eighth were clipped (Figure 11). In all cases, in order to avoid confusion in identification, the first scute clipped caudad from the vent was evenly numbered. In addition the rattles were painted different colours according to the area in which the snakes were captured using model enamel (pactra'namel or Humbrol Plastic Enamel). Painting the rattles served several functions: (1) it was hoped that the snakes with painted rattles would perhaps be immune from human depredation in that they might be recognised as part of a research project; (2) addition of new rattle segments could easily be noted in the case of snakes with incomplete rattle-strings; (3) identification was augmented.

During processing the snakes were palpated in order to determine if they contained food items.

During the first stage of the study (spring 1962) an attempt was made to block the thermoreceptive sense by injecting liquid latex into the outer cavity of the facial pit, white vinegar having been injected first to act as a coagulant for the latex. A total of 22 snakes were treated in this way. Seven of these, obtained outside the study area, were retained as captives in order to determine the permanence of the latex. Since it was found that the latex block was lost during the shedding of the skin a more permanent method of deleting the thermoreceptive sense was desired.

During the following spring (1963) electric cautery was used after first having tried this on captive individuals to determine the effect on the snake. The entire pit membrane was destroyed using a hyfrecator with a fine needle point. Twenty of the forty snakes captured at the dens were treated in this way.

Figure 10. Measuring a rattlesnake, using the measuring board.

Figure 11. View of subcaudal surface of rattlesnake Number 75, marked as $R_{2,5}L_{3}$. The anal plate can be seen at the extreme right of the picture (arrow).

Observations on the Reactions and Feeding of Cauterized and Non-cauterized Snakes

Casual observations were made from time to time concerning the reactions of cauterized and non-cauterized snakes to the writer's hand when waved or held immediately in front of a wire screen or the snake's cage. These observations will be discussed more fully in a later section.

For more formal observation of the effect of cauterization on their behaviour the snakes were presented one at a time with live white mice in a test cage measuring 12 inches by 20 inches by 12 inches deep. As very few of the captive snakes showed any interest in food it was necessary to select reliable feeders as determined by frequent testing and to operate on these for use as experimental animals. Two were selected. In one of these the pits were destroyed by electric cautery. The other, in order to determine if the operative treatment had any effect on behaviour, was subjected to a sham operation. This was done by cauterising an area of skin on the snout between the pit and the nostril. These two snakes were given a week's rest to allow healing and then presented, one at a time, with a mouse. Further tests were carried out using a light-proof box of the same dimensions as the test cage. In addition to these two snakes, two recaptured cauterized snakes and two normal snakes were found to be reliable feeders and were tested in the same way. Each test was conducted by placing the snake in the light-proof box. Five minutes later a live white mouse was placed in the box with the snake. The box was opened briefly at 2 minute intervals for the first 20 minutes, at 5 minute intervals for the next 20 minutes and then at 10 minute intervals for the total period of one hour. In some cases sounds of a scuffle inside the box indicated that the mouse had been struck and the box was opened immediately to determine if this was so.

If while in the dark box the snake did not strike the mouse, it was placed in the light cage. One minute later a mouse was placed in the cage and the time required for the snake to catch the mouse was recorded. A snake, after eating a mouse, was not tested again for a week.

Microscopic Examination of the Cauterized Pit

The pit regions of four cauterized snakes and two normal snakes were sectioned and stained with hematoxylin and eosin by Miss Hiliary Short. These sections were examined to determine the extent of tissue damage caused by cauterization.

RESULTS AND DISCUSSION

The Population

Over the two summers, 1962 and 1963 and in the spring of 1964, a total of 99 rattlesnakes were captured and marked in the study area. Fifty-two of these were captured in Den No. 1, 27 in Den No. 2 and the remainder in the traps or by searching for them. Many of the snakes captured at the dens were captured elsewhere in the study area as well. The total number of recaptures for the 99 marked snakes was 123. Including the initial captures the number of instances of capture was 222. At the dens a total of 137 captures was made while 34 were made in traps, 42 were made by searching and 9 snakes were born in captivity. It is quite evident that the most reliable method of capturing large numbers of rattlesnakes in visiting the den areas.

From Table I the number of trap-days per rattlesnake in 1962, with 16 trap stations, was 52.5. In 1963, with 27 trap stations, the number of trap-days per rattler was 145.4. Perhaps an explanation for the discrepency might be in that the traps were set over a longer period in 1963 and the greater activity period, with regard to success in trapping, occurred late in the summer, from mid-July on. It is interesting to compare these figures with those of the other two most common snakes in the area. Coluber constrictor averaged 49.2 trap-days per snake in 1962 and 52.9 in 1963. Pituophis catenifer averaged 112.4 days per snake in 1962 and 100.2 in 1963. It would seem from this that an increase in the number of trap-days would result in an increase in catches for C. constrictor and P. catenifer but not necessarily so for C. v. oreganus. The nocturnal habits of rattlers compared to the diurnal habits of the other two species may in some way be responsible for this.

Sex Ratio

Forty-eight of the ninety-nine snakes captured in the study area were males and fifty-one were female, the male/female ratio being .94. In one brood of 5 born in captivity in 1962 the male/female ratio was 3/2 and in the other brood of 4 the ratio was 3/1. A brood born in 1963 in which 5 out of 6 were captured revealed a male/female ratio of 2/3. The sex ratio data for the dens is presented in Table II. The variation in these ratios is undoubtedly not representative of the true ratios but is due to sampling error. In all cases more snakes were seen than were captured.

Table III shows the total number of captures of each sex at the dens, in traps and by searching. More females than males were captured at the dens. This may be due to a greater wandering tendency in males, in that they may leave the dens earlier than the females and not return as soon. The fact that many more males than females were captured in the traps would tend to support this.

TABLE I. Species Captured in Funnel Traps

	Species	No. captured	No. trap-days per individual
1962	Coluber constrictor	16	49.2
	Pituophis catenifer	7	112.4
	Crotalus viridis	15	52.5
	Hylo regilla	2	393.5
	Perognathus parvus	12	65.6
	Neotoma cinerea	2	
	Microtus montanus	1	
	Sorex cinereus	1	
1963	Coluber constrictor	55	52.9
	Pituophis catenifer	29	100.2
	Crotalus viridis	20	145.4
	Thamnophis sirtalis	5	581.4
	Hyla regilla	9	323.0
	California Quail (chick)	2	
	Perognathus parvus	21	138.4
	Reithrodontomys megalotis	5	581.4
	Peromyscus maniculatus	1	
	Sorex spp.	1	
	Sorex cinereus	1	
	Sorex vagrans	1	

Composition of Population

Figure 12 illustrates the composition of the population as revealed by the spring samples. The sizes of the samples are rather inadequate but perhaps the 1963 spring sample is the most indicative in that it is the largest. It must be remembered that 14 individuals, 8 males and 6 females, were removed in the fall of 1963.

TABLE II. Actual Number of Individuals Captured at the Den Areas.

Time of Year	Den	Male New Young	Male Older	Female New Young	Female Older	Male/Female Ratio Total	Male/Female Ratio Excl. young
Spring 1962	1	3	4	-	3	2.33	1.33
	2	-	3	1	3	.75	1.0
	Total	3	7	1	6	1.43	1.17
Fall 1962	1	4	1	2	5	.71	.20
	2	3	2	1	2	1.67	1.0
	Total	7	3	3	7	1.00	.43
Spring 1963	1	1	7	5	10	.53	.70
	2	-	8	-	8	1.0	1.0
	Total	1	15	5	18	.70	.83
Fall 1963	1	2	5	3	4	1.0	1.25
	2	-	2	1	2	.67	1.0
	Total	2	7	4	6	.90	1.17
Fall 1963 removed		2	6	2	4		
Spring 1964	1	-	7	2	11	.54	.64
	2	1	1	-	2	1.0	.50
	Total	1	8	2	13	.60	.62

TABLE III. Total Instances of Capture by the Three Methods Used.

Time of Year	Method of Capture	Male	Female	Total	Male/Female
Spring 1962	Den visits	11	7	18	.64
Fall 1962	Den visits	9	21	30	.43
Spring 1963	Den visits	17	24	41	.71
Fall 1963	Den visits	8	11	19	.73
Spring 1964	Den visits	9	15	24	.60
Total		54	78	132	.69
Summer 1962	Funnel traps	8	7	15	1.14
Summer 1963	Funnel traps	14	6	20	2.33
Total		22	13	35	1.69
Summer 1962	Searching	4	19	23	.21
Summer 1963	Searching	7	10	17	.70
Total		11	29	40	.38

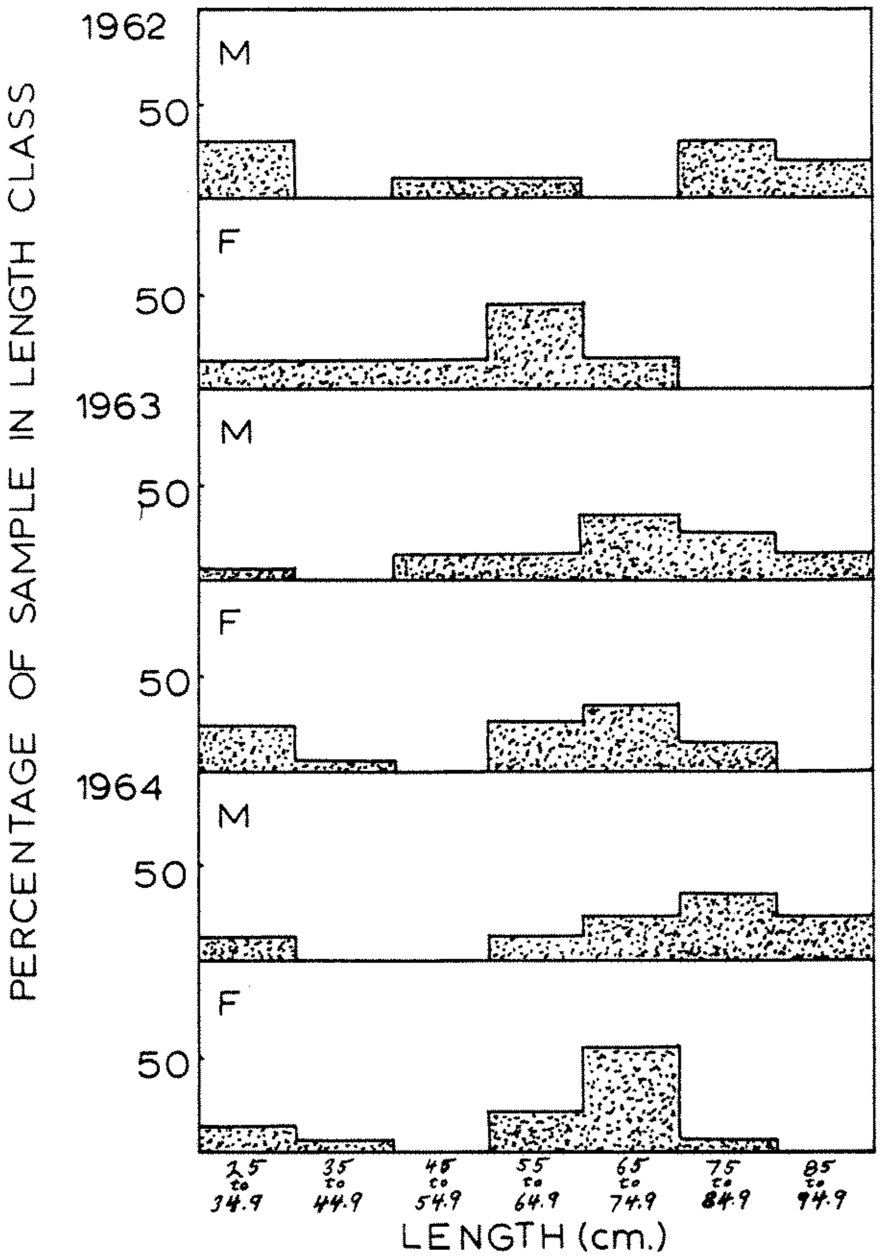

Figure 12. Histogram showing the composition of the spring samples by length.

Population Estimates

In 1962 a total of 51 rattlers was marked. Two of these were known to be dead by the spring of 1963. One had died of heat prostration in a trap and the other, a newborn young, appeared to have been killed by a predator. Based on a total of 49 marked snakes and a total of 36 captured in the spring of 1963, excluding the unmarked young-of-the-year, of which 20 were recaptures, the population estimate at 95 percent confidence limits was 88±26.

By the time the snakes had entered hibernation in the fall of 1963 a total of 87 had been marked. Six of these were known to be dead by the spring of 1964, 2 of these from the previous summer. Two of the remaining four had been killed by predators, one had become entangled in the cloth carrying bag and the fourth had been killed accidently by the blade of a bulldozer. Fourteen rattlers had been taken into captivity in the fall of 1963, leaving a total of 69 marked snakes in the field. Exclusive of newborn unmarked young, 21 were captured in the spring of 1964, 14 of these recaptures. At 95 percent confidence limits the population estimate was now 104±32.

If the figures from spring 1963 and 1964 are combined to obtain a larger sample size as was done by Fitch (1949) the estimate is 99 snakes. By the Schnabel method, using data accumulated during the entire study period the estimate is 124 snakes. In view of the fact that obviously not all of the snakes were captured, the figure may more closely approximate the actual population size.

The snakes were all captured within an area measuring 4100 feet by 2000 feet, or 188 acres in area. Using the spring 1964 estimate of 104 rattlesnakes, the density is estimated at .55 rattlesnakes per acre. Using the estimate of 124 snakes, the density estimate is .66 snakes per acre. However it is quite probable that some of the snakes may wander well out of the area, although this may be balanced by those wandering into the area from outside.

Birth Rate

In the present study, data is available from only 4 broods of snakes. The average number per brood was 5.3, ranging from 4 to 6 young. Three of the broods were born in captivity when the female had been held overnight for examination. One of the captive-born broods was born prematurely, the six young having yolk sacs attached and being very small. One of these young lived in captivity for some time but the others were either stillborn or died soon after. The remaining 2 captive-born broods appeared normal. The 3 females were captured at the dens, which would indicate that the young are born within the den area.

During the summer of 1963, a gravid female was captured 4 times in the Den No. 1 area, from April 14 to August 20. She was generally captured in the vicinity of the same rock. On August 27, 6 young, 5 of which were captured, were seen together near this same rock. These were probably the brood of this female, as no other had been seen in that vicinity previously. Table IV presents the brood data.

Food

In addition to the mammals listed previously in Table III, *Microtus pennsylvanicus*, occurring in the meadow land, might be added as a food species. Another species possibly used would be *Sylvilagus nuttali*, which

TABLE IV. Brood composition, Size, and Date of Birth

Date of birth	Place of birth	Males	Females	Total
August 19, 1962	captivity	3	2	5
August 21, 1962	captivity	premature		6
August 27, 1962	captivity	3	1	4
Between Aug. 20 & Aug. 27, 1963	Den No. 1	2	3	6*

*one not captured

is common in this area. Several years ago the writer found the remains of a small rabbit in a scat from a snake collected a few miles north of the area. The most common and perhaps the most important food species in the area is Perognathus parvus. Stuart Iverson (pers. comm.) in 1964 placed a conservative estimate at 13 to 17 mice per acre as the population density of this species.

Only four food records were obtained. Such a small number might be expected in that most of the captures of snakes occurred at the dens and those snakes captured in traps were probably in search of food. A scat from a female collected at Den No. 2, August 17, 1962, contained hair from Perognathus parvus. Another scat found in the carrying bag with 2 snakes collected together on July 23, 1963, at the base of the rock bluff also contained hair from Perognathus parvus. On July 28, 1963, a young snake, measuring 40.9 cm. in total length, was found in a trap with a freshly regurgitated adult *Perognathus parvus*. On September 6, 1963, a rattler was collected on the sand hill below the rock bluff. A scat obtained from this snake contained *Microtus* hair similar to that of *M. pennsylvanicus*. It is likely that this snake had been hunting in the bottomland.

Wanderings and Home Ranges

Using the greatest distance between points of capture for each individual, it was found that 26 recaptured male rattlers had moved a total of 21,170 feet or an average of 814 feet per snake. Actually, the distances moved were recorded for 17 of the 26 snakes. Twenty-eight females moved a total of 10,882 feet, averaging 389 feet per snake. The distances recorded were for 14 of the 28 females. In both the males and females, the snakes for which no distances were recorded had been recaptured in the same spot, in most cases at the den area. Obviously these snakes have moved for they were not captured at the dens during the summer except in the case of one gravid female which was recaptured four times at Den No. 1 throughout the summer of 1963. Snakes captured below the dens, of course, also had moved since they had come from dens and must return to them for hibernation. Since the number of recaptured males approximates that of recaptured females, it is evident that the males wander farther than the females. Five males were recorded to have moved more than 2000 feet as compared to two females moving this same distance (Table V). Records of 2000 foot movements included, in each case, captures in the bottomland, (Figures 13 to 15). Of seven snakes recorded from the bottomland, five were subsequently recaptured at the dens. Fitch (1949) in studying this same subspecies, thought that movements beyond 1500 feet probably represented shifts away from the home

TABLE V. Comparing Sex, Length of Snake and Distance Moved.

Length (cm.)	25-34.9		35-44.9		45-54.9		55-64.9		65-74.9		75-84.9		85-94.9		Total	
Distance moved	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
0-300	5	2	1	1	1	2	1	5	2	5		1	1		11	16
301-600				1			1	4		2	2		2		5	7
601-900							2	1			1				3	1
901-1200			1					1				1	1		2	2
1201-1500																
1501-1800																
1801-2100																
2101-2400								1			1				1	1
2401-2700										1	2		1		3	1
more than 2700													1		1	
															26	28

range. Disregarding distances beyond 1500 feet he found the average distances moved for males to be 630 feet and for females 467 feet. However, in the present study, since the snakes returned to the dens after moving 2000 feet this cannot be regarded as a shift away from the home range. Home range shall be discussed further presently.

The greatest distance moved was by a male whose discarded skin was found in the bottomland 4095 feet away from the point of release at Den No. 2. The time interval here was 3 months. The greatest distance moved during the shortest interval was by another male which moved 2069 feet in less than 15 hours (Figure 15, No. 16).

Figures 13 to 15 illustrate the wanderings of 6 snakes. That snakes may use the same range from year to year is suggested by the movements of No. 46 (Figure 13). The fact that most of the snakes did return to the dens from distances up to 2000 feet would indicate that they must be quite familiar with the range over which they prowl and must depend on learning to find their way back to the dens. The home ranges seem to be somewhat linear in shape if the data presented are adequate. However it is quite probable that the snakes wandered considerably farther than indicated by recapture.

That young snakes born at the dens may find their way back in the fall is shown by a young female released August 19, 1962 at Den No. 1. She was captured at the den the following spring (1963) and 3 months later was captured 800 feet away from the den in a trap on the sand flat below. She was recaptured a week later in another trap also 800 feet away from the den. The following spring (April 6, 1964) she was recaptured at Den No. 1. That young may travel a considerable distance from the dens is indicated by a female measuring 32.3 cm. in length captured on the road, at least 2000 feet

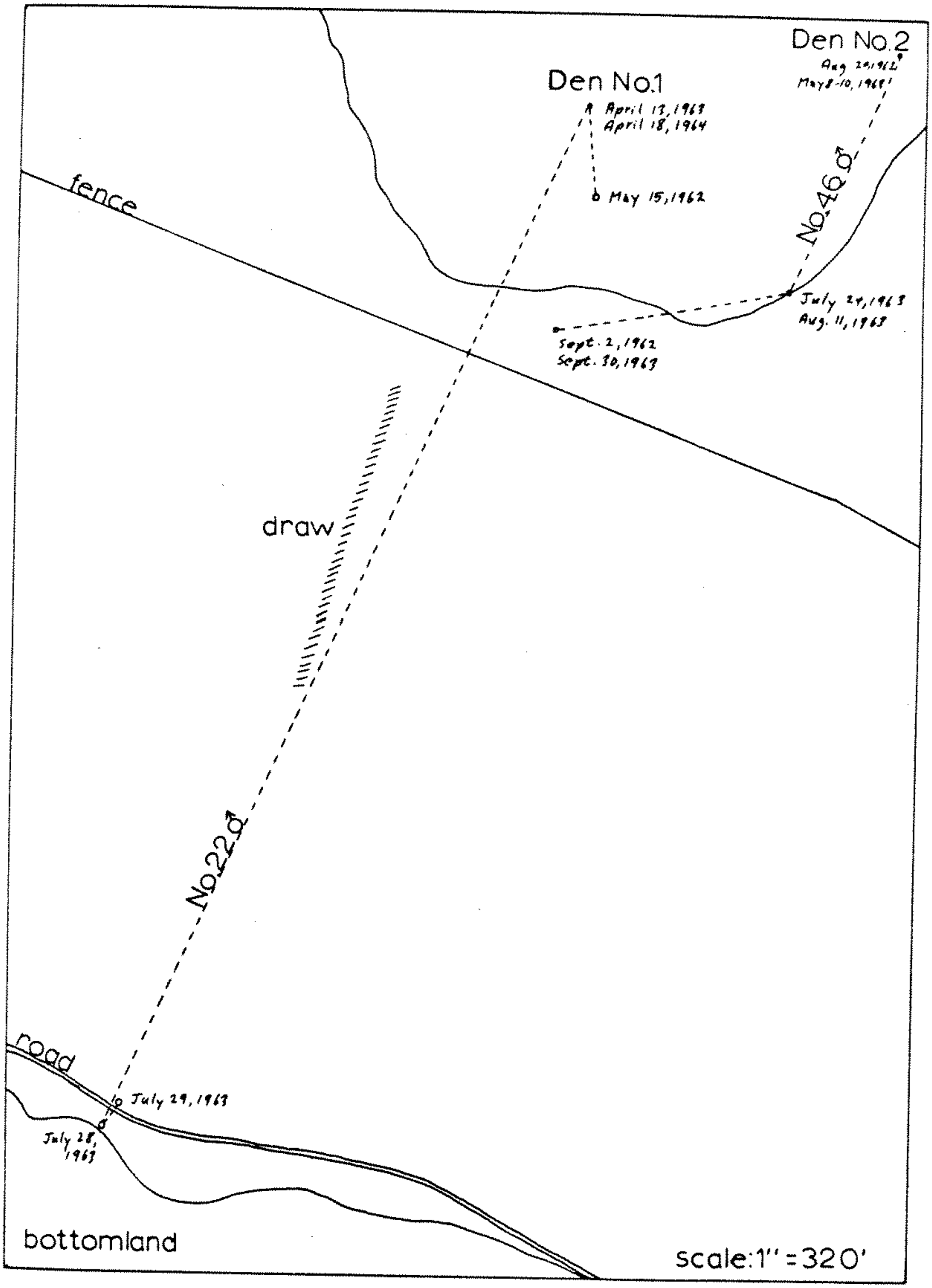

Figure 13. Movements of rattlesnakes 22 and 46.

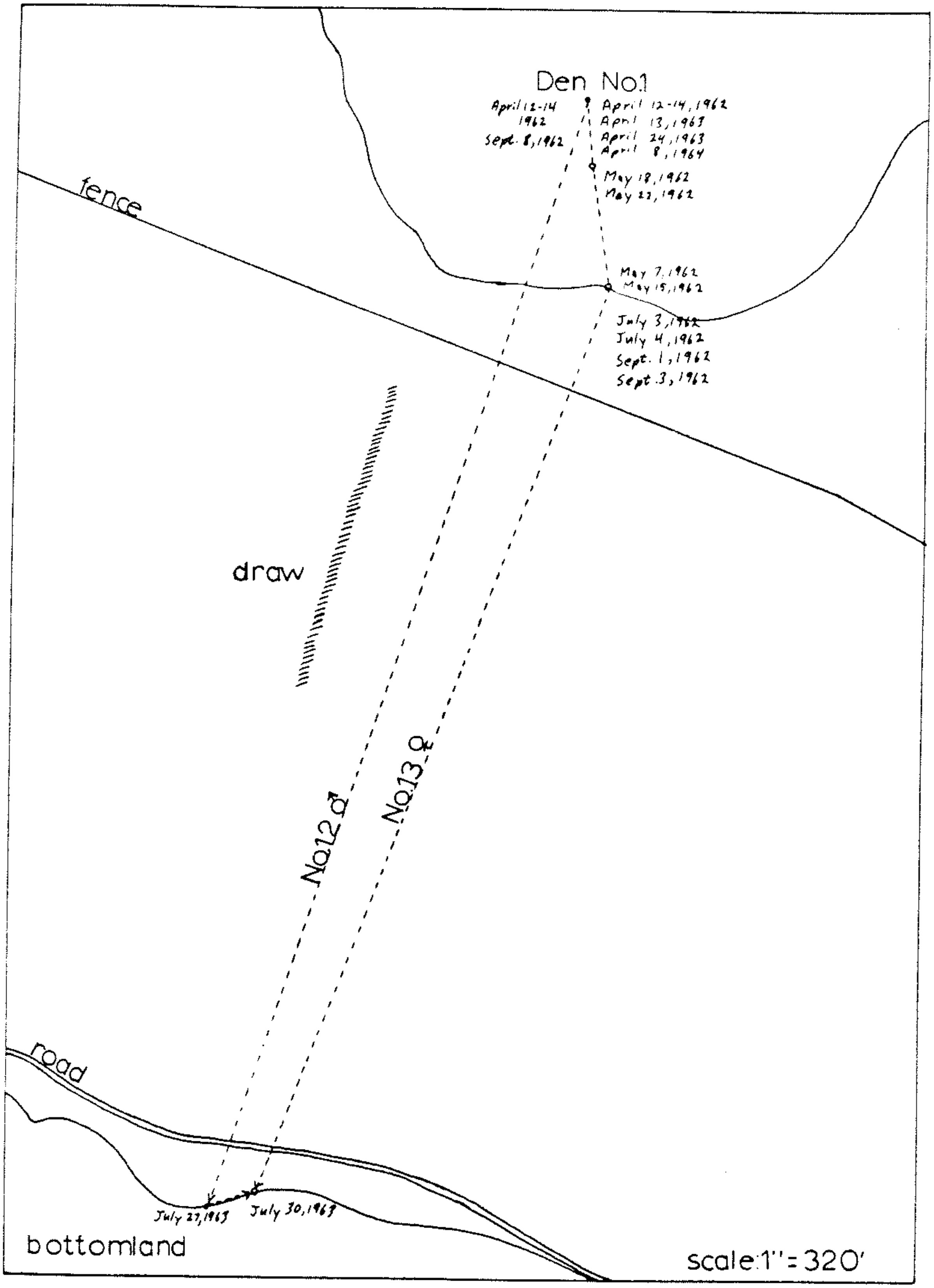

Figure 14. Movements of rattlesnakes 12 and 13.

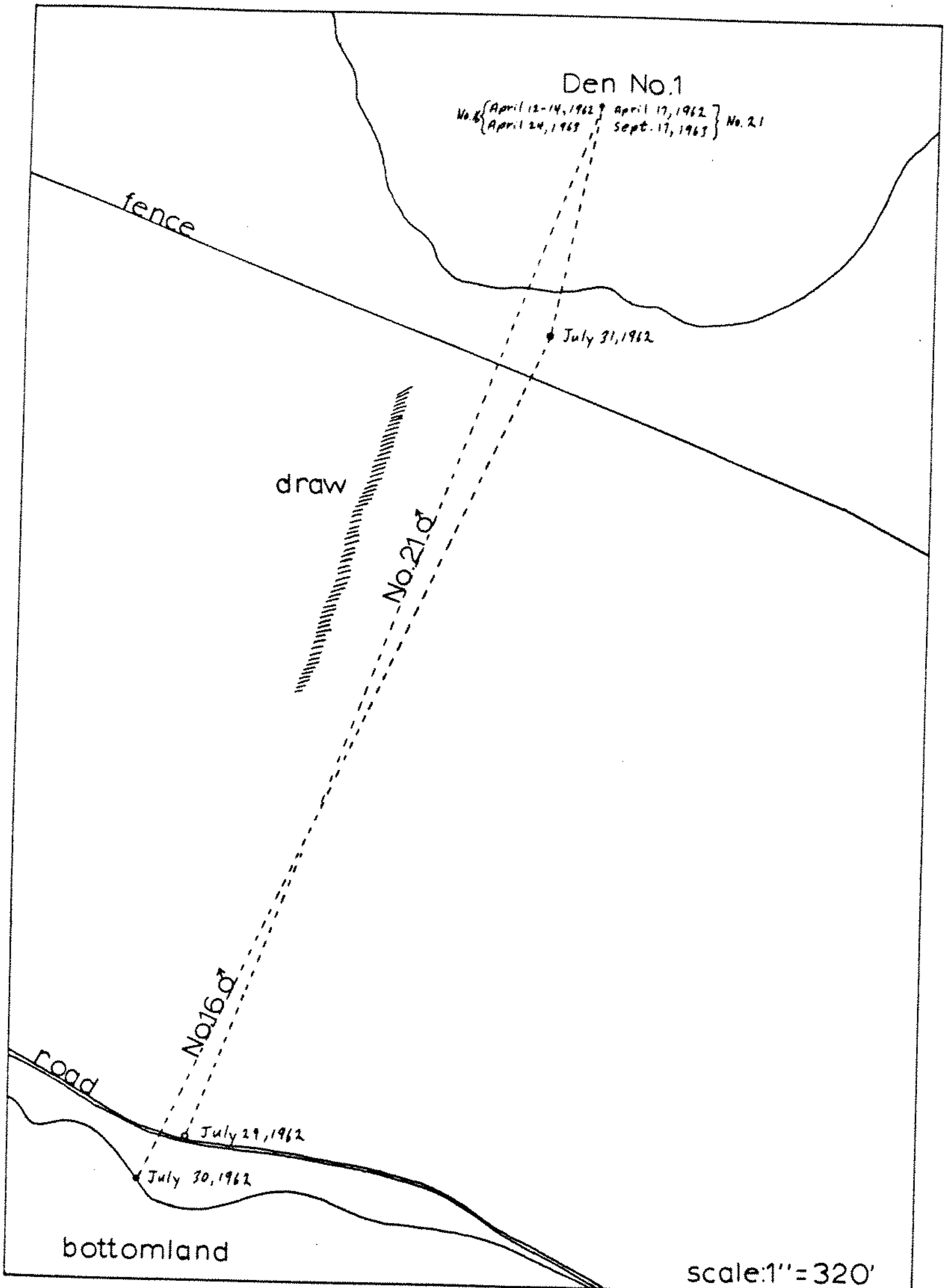

Figure 15. Movements of rattlesnakes 21 and 16

from the nearest den. However this snake was not subsequently recaptured. Generally the snakes wandering the greatest distance were the largest (Table V) and therefore probably were the oldest and most familiar with the range.

In spite of the fact that the two dens were so close in proximity and the possibility that snakes from the two dens may have crossed paths, for example No. 46 and No. 16 (Figures 13 and 15), no mixing between the dens was observed. However, in cases where the initial capture of a snake was made away from a den there is no way of knowing from which den it came. Rattlesnake No. 33 was first captured in a rocky draw about 200 feet below Den No. 1. It was recaptured 9 months later at Den No. 2. This is the only case known of a possible movement from one den to the other. It is possible that such movements may occur more often in young that do not yet have a definite home range.

Growth

Perhaps one of the first considerations to arise regarding growth in snakes, especially when recapture data are used, involves the validity of the measurements. Living snakes are particularly difficult to measure accurately. In order to test the repeatability of my measurements of length eleven captive rattlesnakes were measured daily over a period of seven days or less. It was assumed that no significant growth would occur through this period. Measured length showed a variation ranging from .7 to 4.5 percent of the total length in different individuals. The mean variation expressed as a percentage of the body length was 2.25 percent. The standard error ranged from .08 to .45 (Table VI). In no case did this variation in measurement reveal a consistant increase in length during the seven day period.

The method used to obtain an overall picture of the growth of Crotalus viridis oreganus in British Columbia was that used by Klauber (1937) supplemented by recapture data (Figure 16). Up to and including the age of two years the pattern appears distinct. Beyond this age the pattern is not at all well defined; perhaps this due to individual variation in growth rate overshadowing the generally slower growth rate in length. The average total length at birth of seven males was 29.7 cm. (27.3-31.4) and of six females 29.4 cm. (28.2-30.4). Two one year old males averaged 37.4 cm. (33.8-40.9) and three females of the same age averaged 37.5 cm. (35.1-39.2). The rattle strings consisted generally of two segments. At two years of age most of the snakes had five segments in the rattle string. The males at this point averaged 60.6 cm. and the females, 55.2 cm. in total length. Recapture data (Figure 17) seems to indicate that by three years the males may reach about 75 cm. in total length and have a rattle string of 8 segments. Figure 16, based on fifty records, although the data may be inadequate, appears to indicate the general trend.

Instantaneous growth rates, expressed as percentage of head-body length per growing-season-month, for males and females are given in Table VII. It must be realized, of course, that the rate of growth over a particular growing season is not likely to be uniform. A decline in growth rate with increase in age is indicated in Table .

It is interesting to compare the growth of this subspecies in the northern limits of its range with that of some of its more southern relatives. Fitch (1949), studying the same subspecies in the San Joaquin Valley about 800 miles farther south, found that at two years of age the snakes averaged 3 cm. in head-body length and had six rattle segments. This is 7 cm.

TABLE VI. Variation in Measurement of Eleven Captive Rattlesnakes

Snake no.	Sex	No. measurements	Range	Mean	Standard Deviation	Standard Error	Percent variation of total length
31	M	7	91.7-92.3	92.0	.2000	.0756	.65
38	F	5	74.0-74.9	74.4	.3000	.1342	1.21
29	M	7	80.0-82.9	81.3	1.1800	.4460	3.57
23	F	7	84.5-85.9	85.3	.4796	.1813	1.64
8	F	7	62.6-65.5	64.4	.8888	.3359	4.50
64	M	7	73.4-75.1	74.3	.4899	.1851	2.29
67	F	7	65.2-67.2	66.3	.7071	.2672	3.02
20	M	7	75.9-76.9	76.4	.3162	.1195	1.31
[illegible]1	M	7	79.4-80.9	80.1	.5099	.1927	1.87
85	M	5	31.8-32.6	32.1	.2828	.1265	2.49
8	F	4	31.7-32.4	31.9	.2828	.1414	2.19

longer than the average male head-body length of 56 cm. at two years indicated by the present study in which most of the snakes at that age had five rattle segments. The growing season in the San Joaquin is somewhat longer, being seven to eight months in duration. Fitch found a growth rate of 2.4 cm. per month in first year young and 2.2 cm. per month in well grown young, between 36.5 and 66.3 cm. in head-body length. Table VII, if the first two

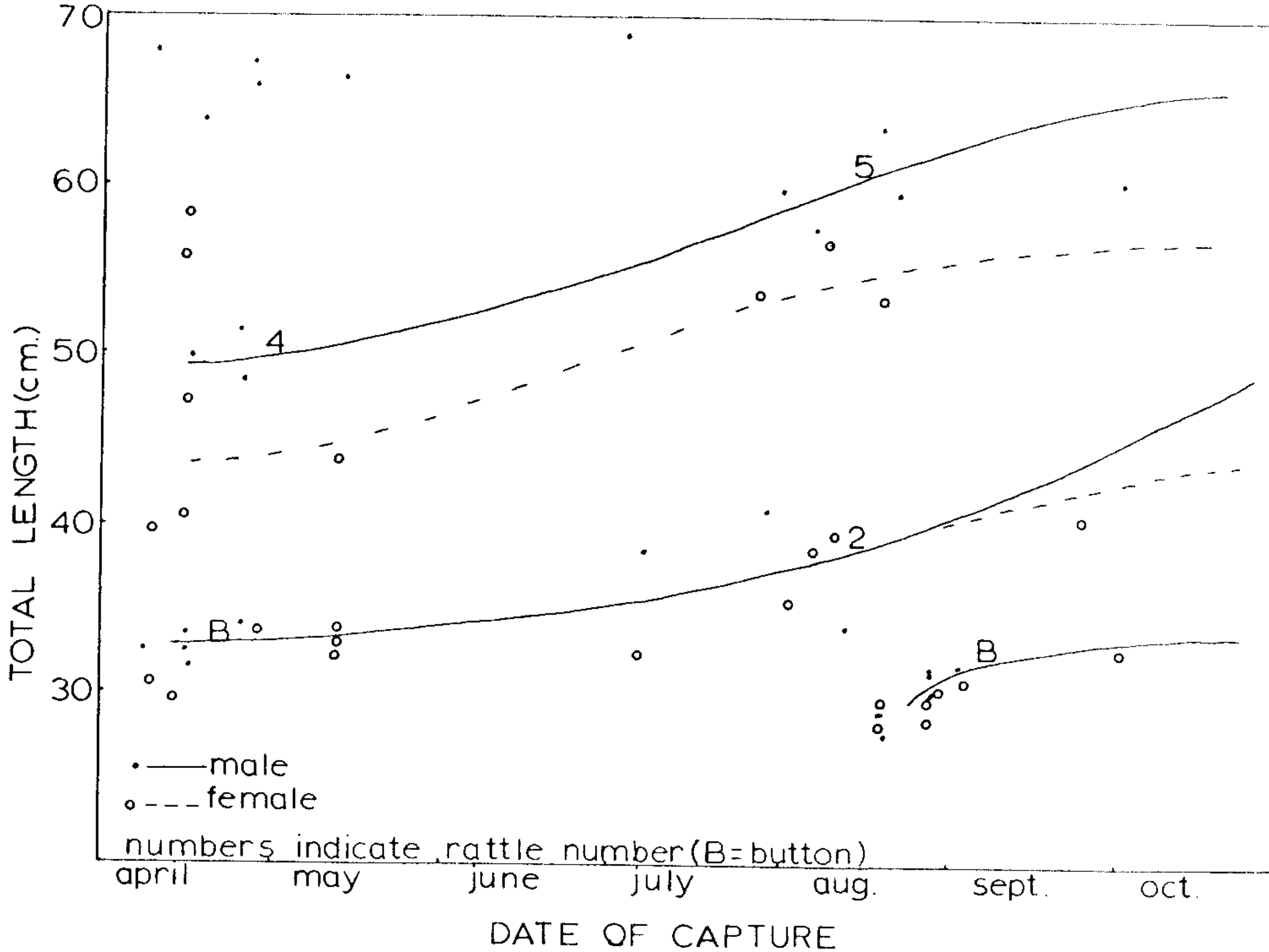

Figure 16. Growth in length of *Crotalus viridis oreganus* up to 2 years of age in British Columbia.

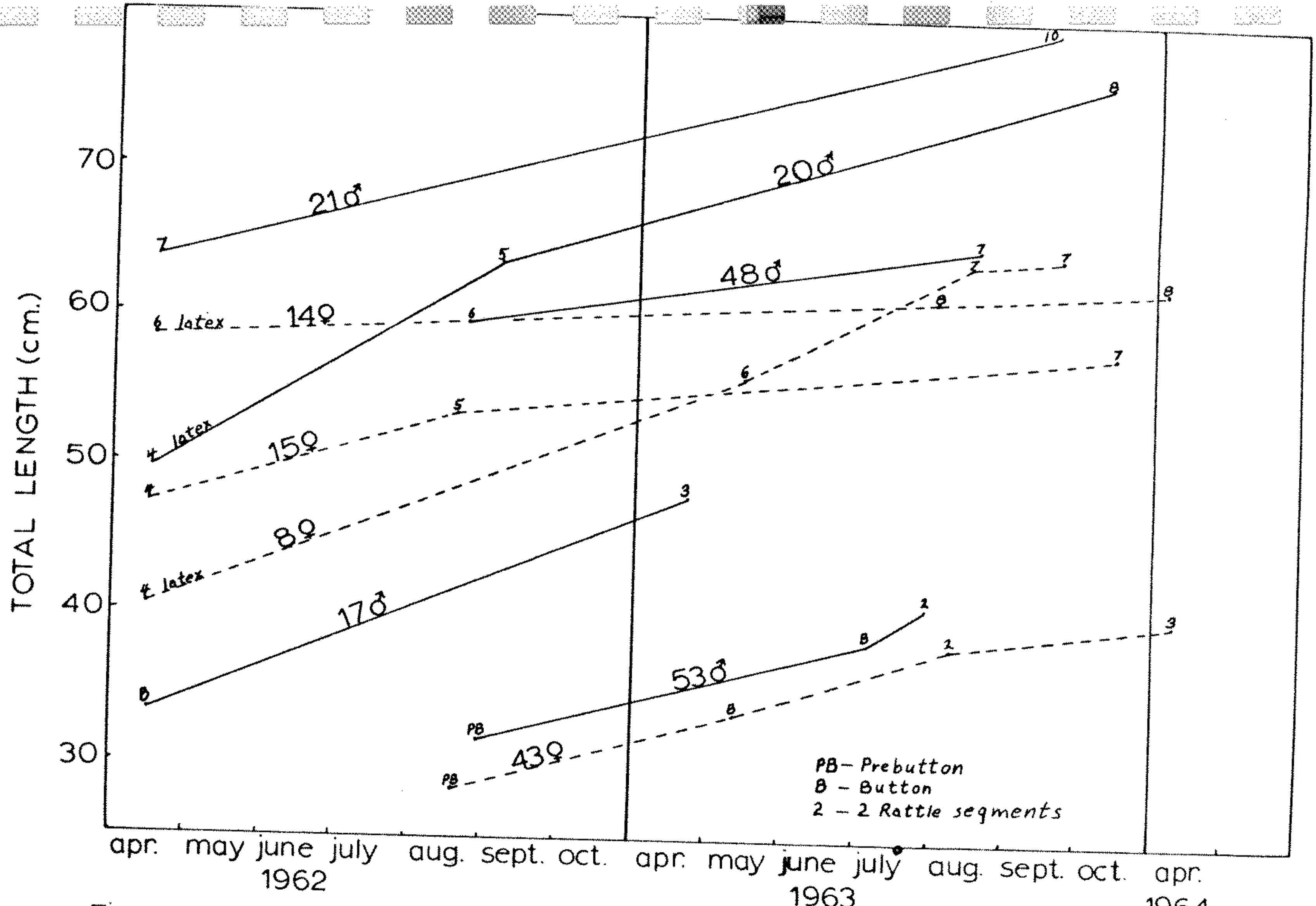

Figure 17. Growth in length of rattlesnakes, based on recapture data.

columns are averaged, indicates a rate of 1.8 cm. per month for first year young and 1.5 cm. per month for well grown young. Klauber (1937) in studies on C. v. helleri from San Diego Counto found this species to reach a length of less than 80 cm. at two years and to have eight or nine rattle segments. In 1956 based on a larger sample, he increased this figure to 80 cm. for males but decreased the rattle number to seven or eight. The growing season there is about eight months. Perhaps the growth rate of C. v. lutosus studied by Heyrend and Call (1951) near Grantsville, Utah, more closely approximates that of the subspecies in the locality of the present study. They found the head-body length of the males at two years of age to be 55.6 cm. and the number of rattle segments to be four or five.

These three subspecies are somewhat comparable in adult size. According to Klauber (1956), large adult males reach 115.0 cm. in C. v. oreganus, 115.0 cm. in C. v. lutosus and 120.0 cm. in C. v. helleri. Of the ten largest males measured during the present study, all over 80 cm. in total length, the average size was 88.5 cm. The largest measured 97.3 cm.

Rattle growth

Rattle growth of C. v. oreganus indicated by the present study appears to follow the sequence of: 8 months, button; 12 months, 2; 20 months, 4; 24 months, 5 to 6; 36 months, 7 to 8. Figures 18 and 19 compare total length with rattle numbers for males and females respectively. Only those snakes with complete rattle strings or those whose complete rattle number was known through previous capture were used. Comparing figures 20 to 25, increase in rattle number appears to depend upon increase in length.

TABLE VII. Growth Rates of Male and Female Rattlesnakes of Different Age Classes, Expressed as Percent Head-body Length per Growing-season-month.

MALES

Age (Month)	0	8	20	23-32	Adult		
Head-body length (cm.)	28.8	31.0		54.6-59.0	70.0-75.1	76.6-85.6	
Number in sample	1	1		4	4	5	
Growth (cm./mo.)	1.4	2.1		1.5	.9	.7	
Growth (% head-body length/mo.)	4.8	6.7		2.4	1.2	.8	
Average	5.7						

FEMALES

Age (Month)	0	8.6-11.2	20	23-36	Adult	
Head-body length (cm.)	26.6-28.1	32.0-35.9	44.6	50.6-52.8	57.8-60.6	65.1-78.4
Number in sample	2	2	1	4	5	10
Growth (cm./mo.)	1.3	1.1	1.4	1.1	.8	.4
Growth (& head-body length/mo.)	4.8	3.3	3.1	2.2	1.4	.6
Average	4.0					

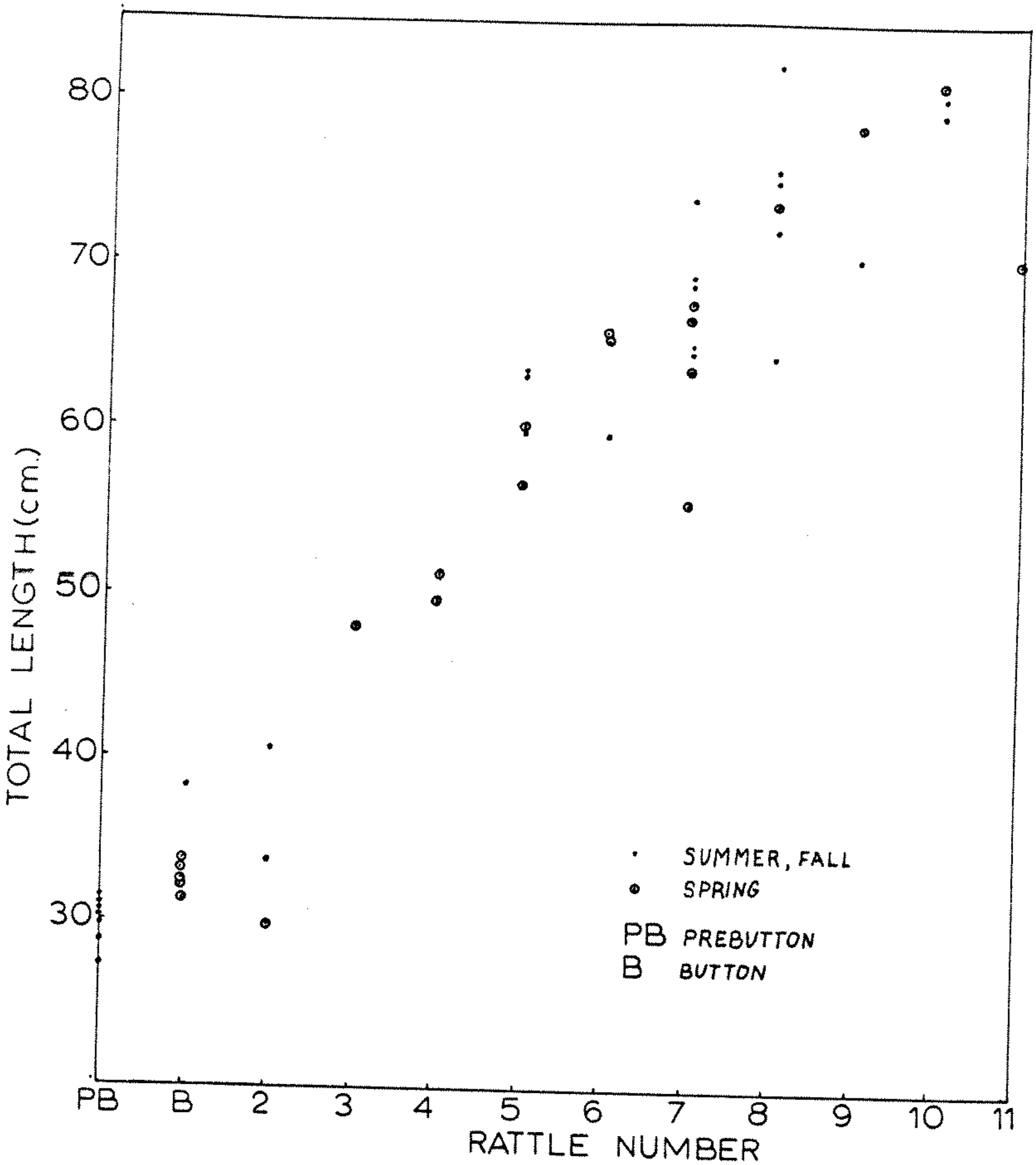

Figure 18. Comparing length and rattle number of males. Only those whose complete rattle number was known were used.

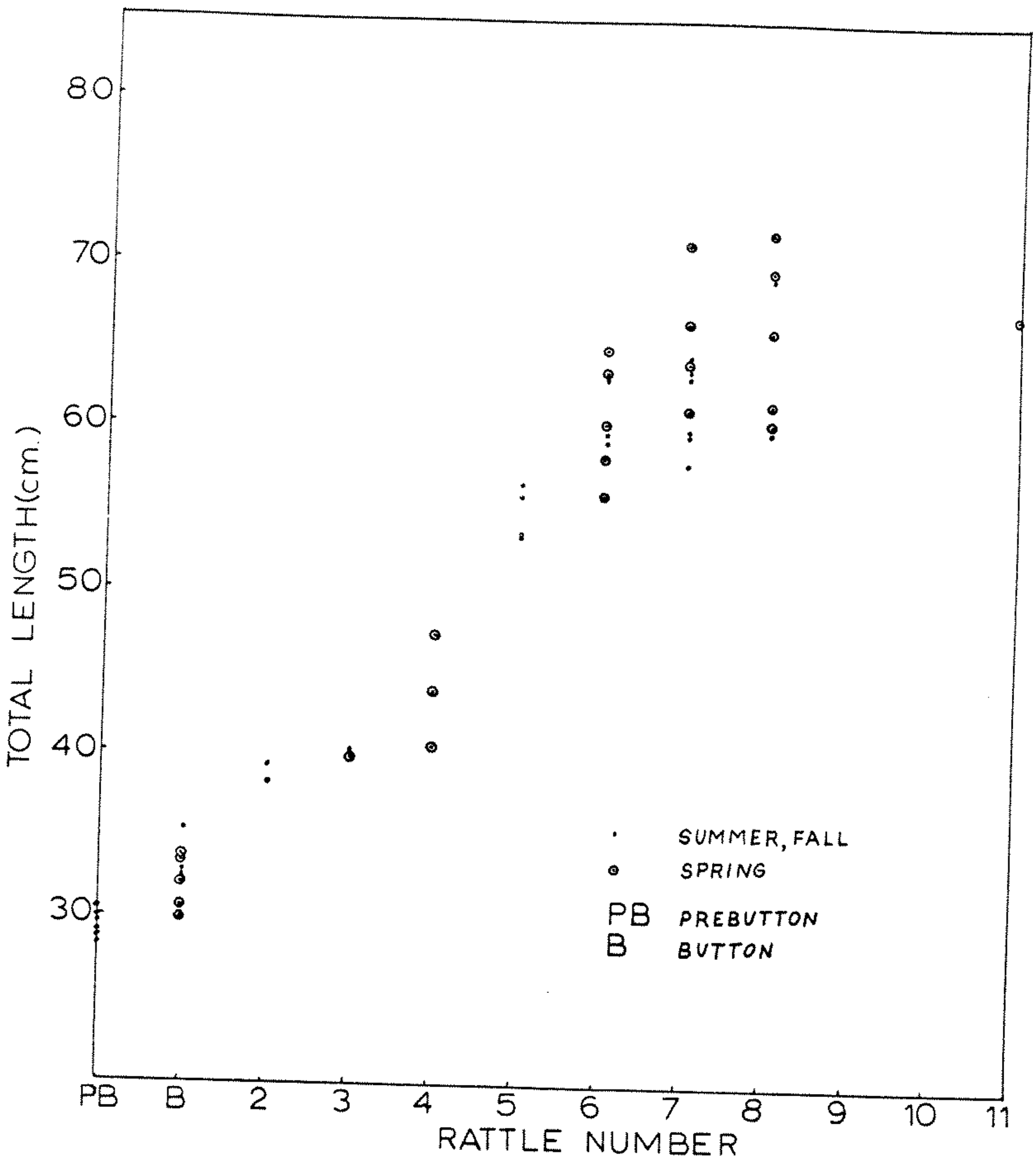

Figure 19. Comparing length and rattle number of females. Only those whose complete rattle number was known were used.

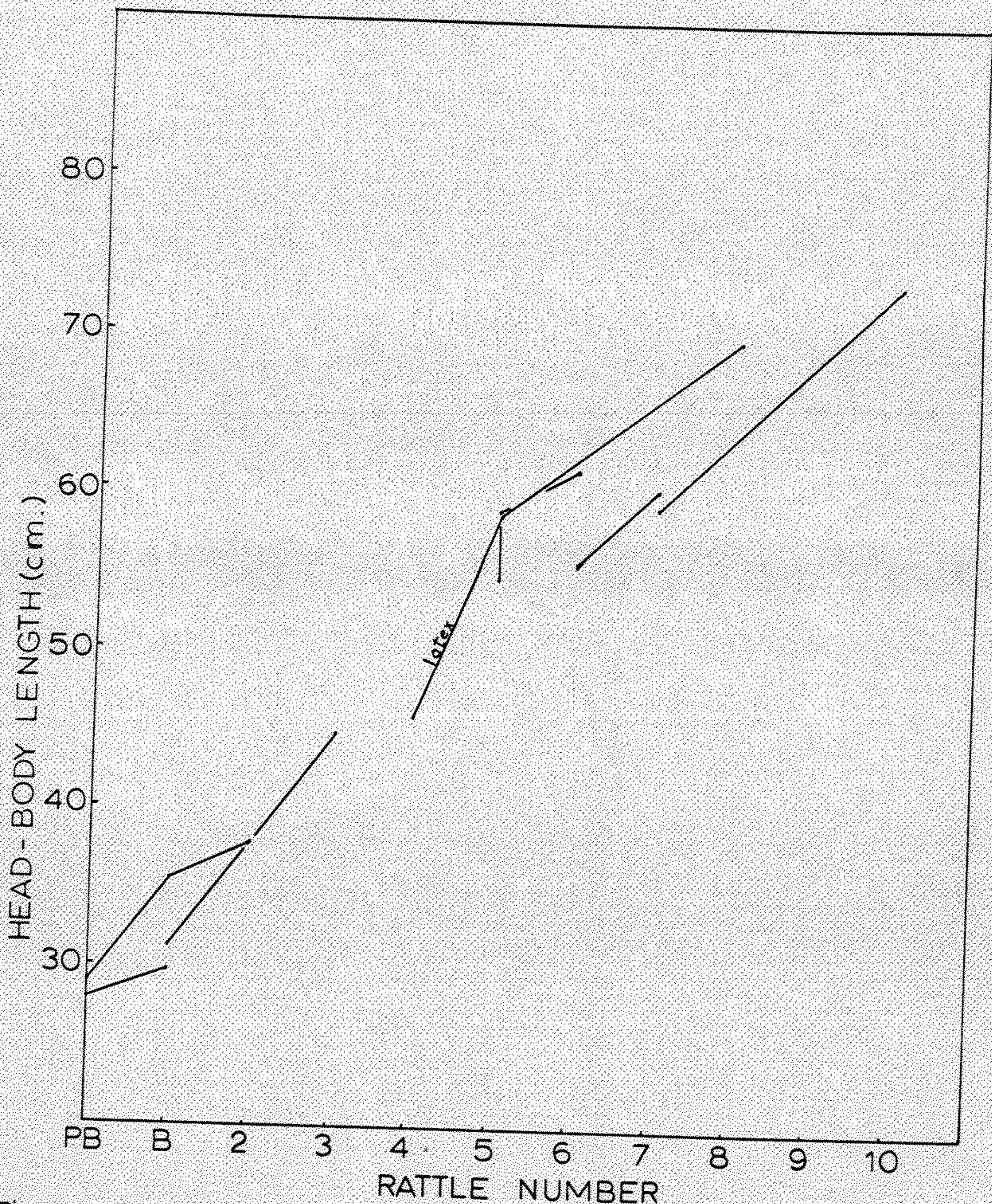

Figure 20. Increase in rattle number per unit of linear gain in male rattlesnakes. Only those whose complete rattle number was known were used.

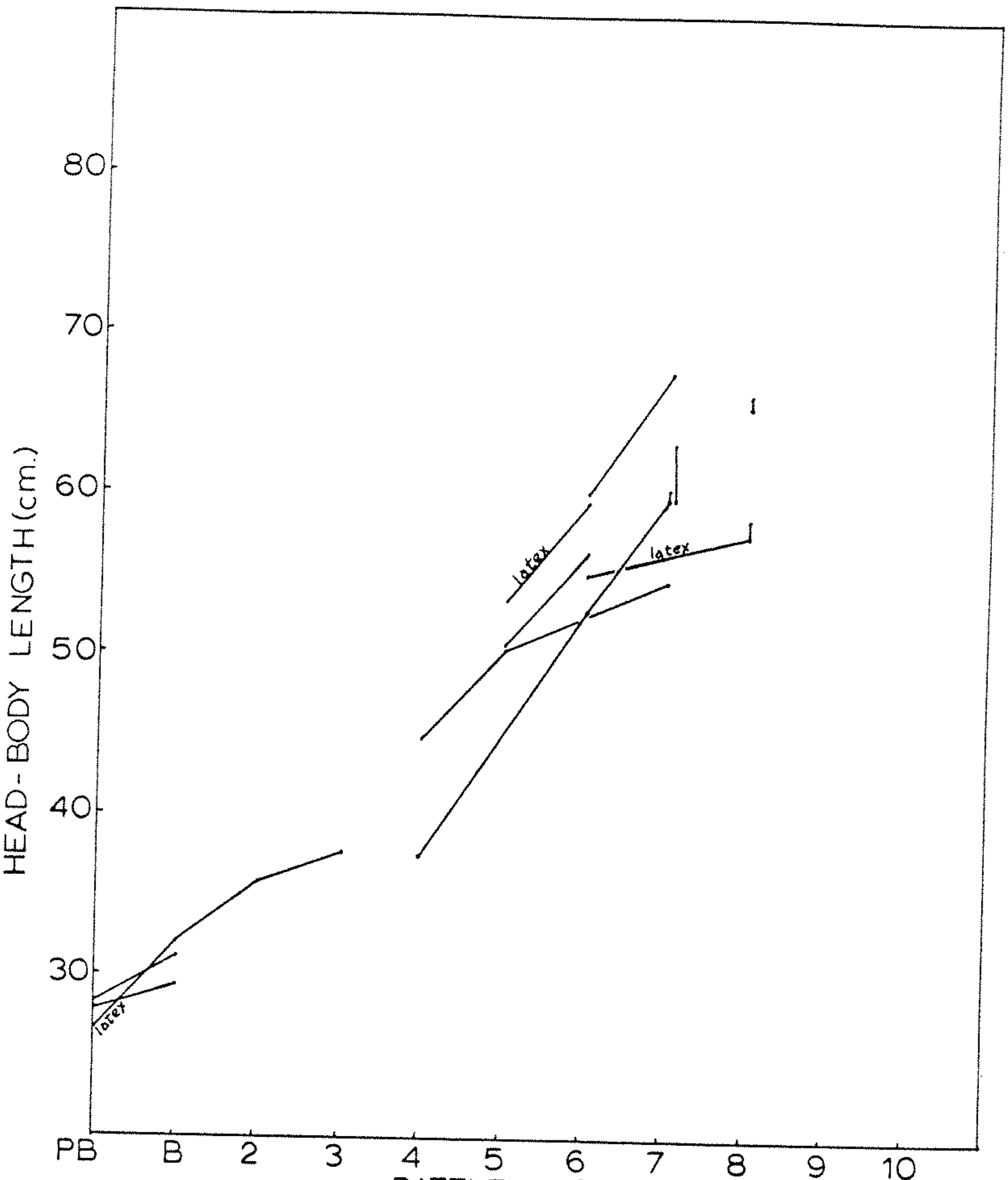

Figure 21. Increase in rattle number per unit of linear gain in female rattlesnakes. Only those whose complete rattle number was known were used.

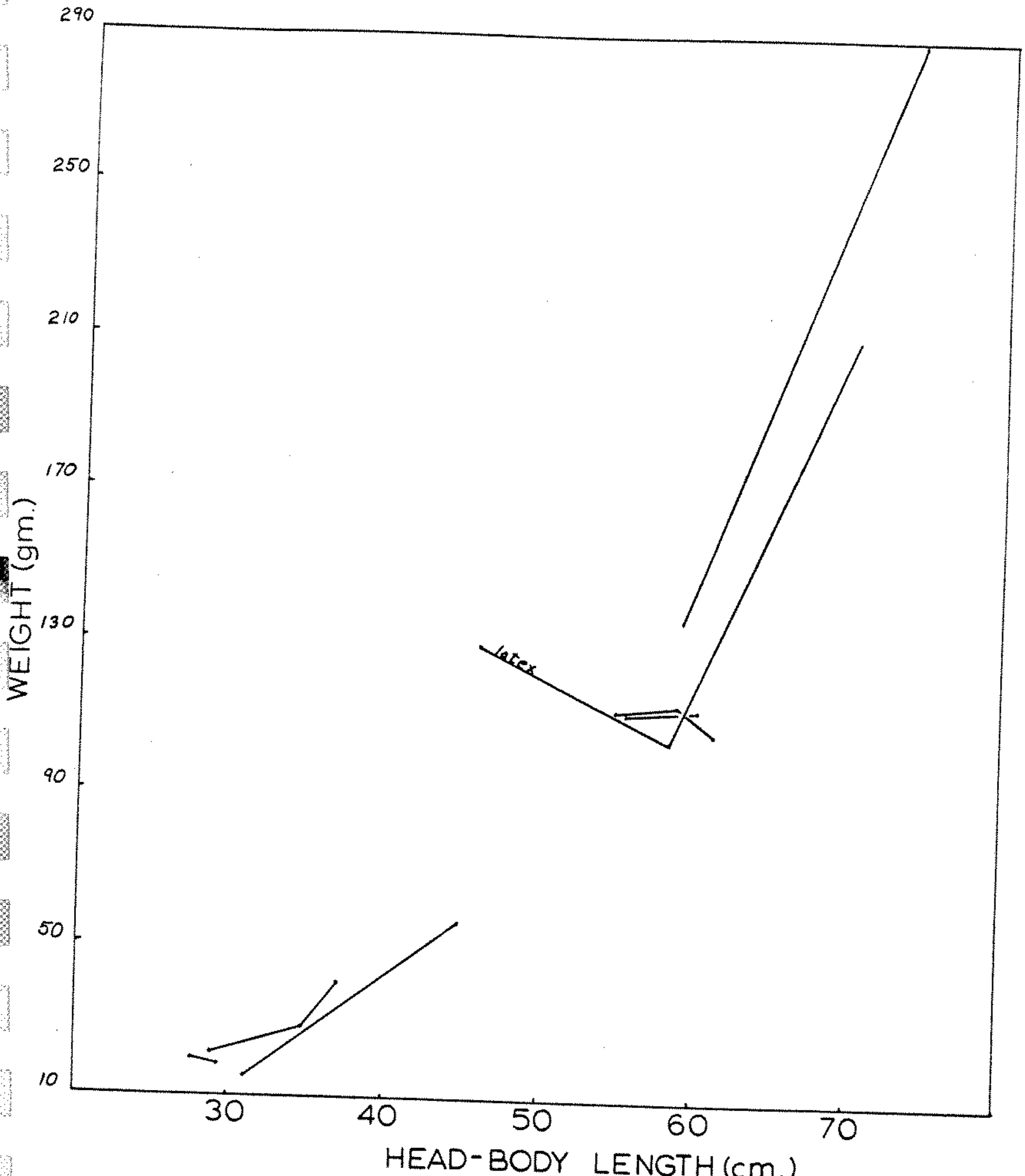

Figure 22. Growth in weight compared to growth in male rattlesnakes.

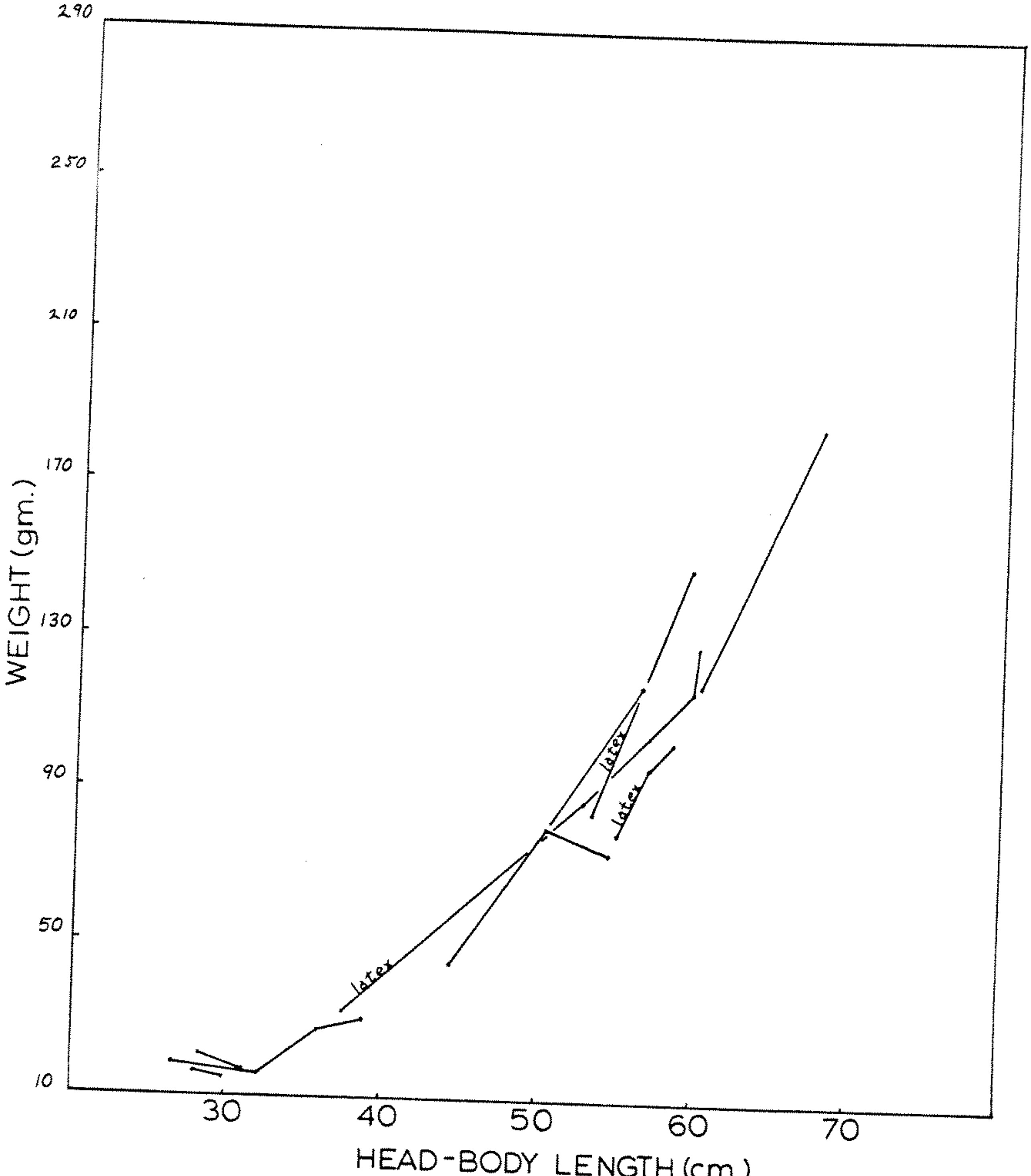

Figure 23. Growth in weight compared to growth in length in female rattlesnakes.

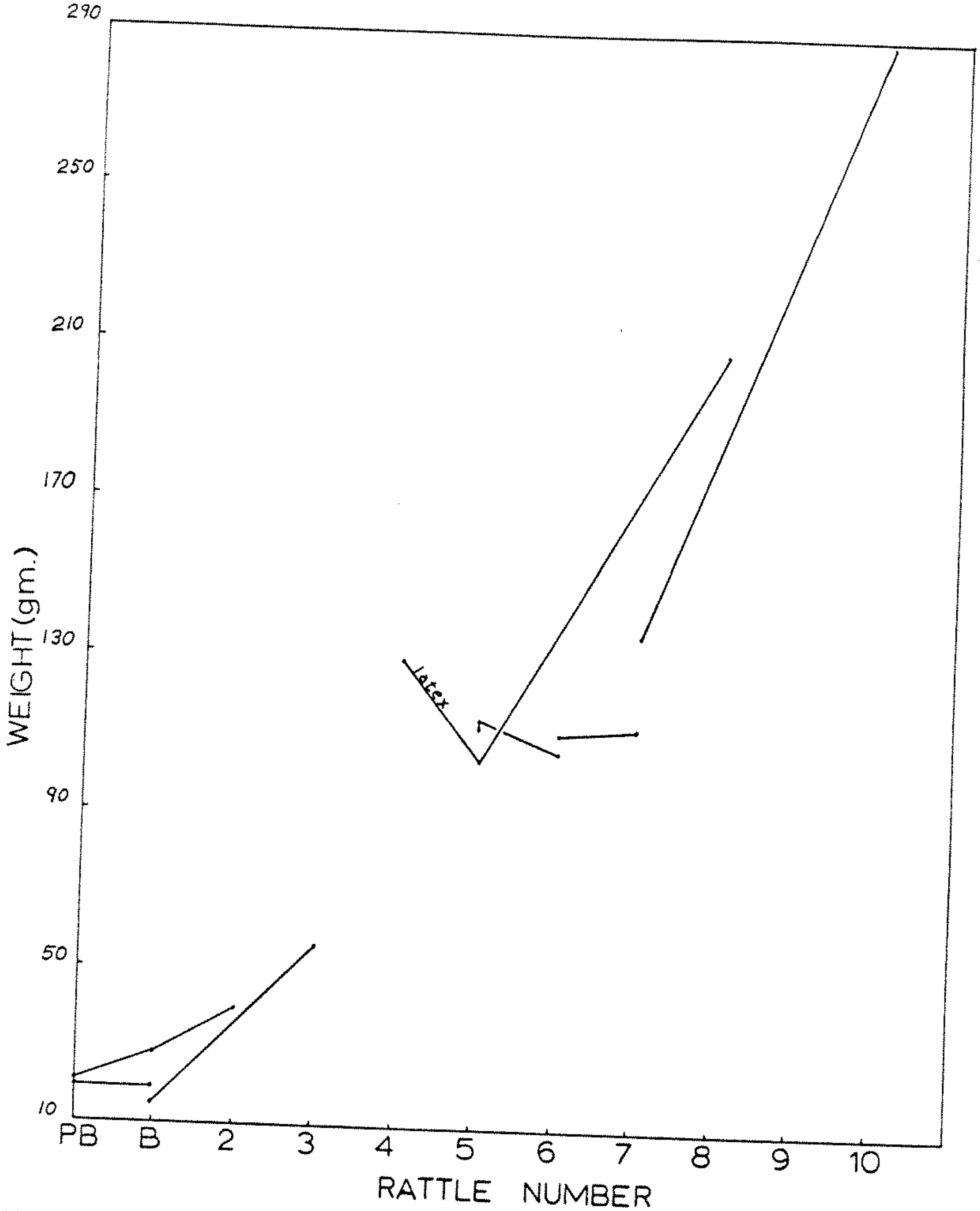

Figure 24. Increase in rattle number per unit of gain in weight in male rattlesnakes.

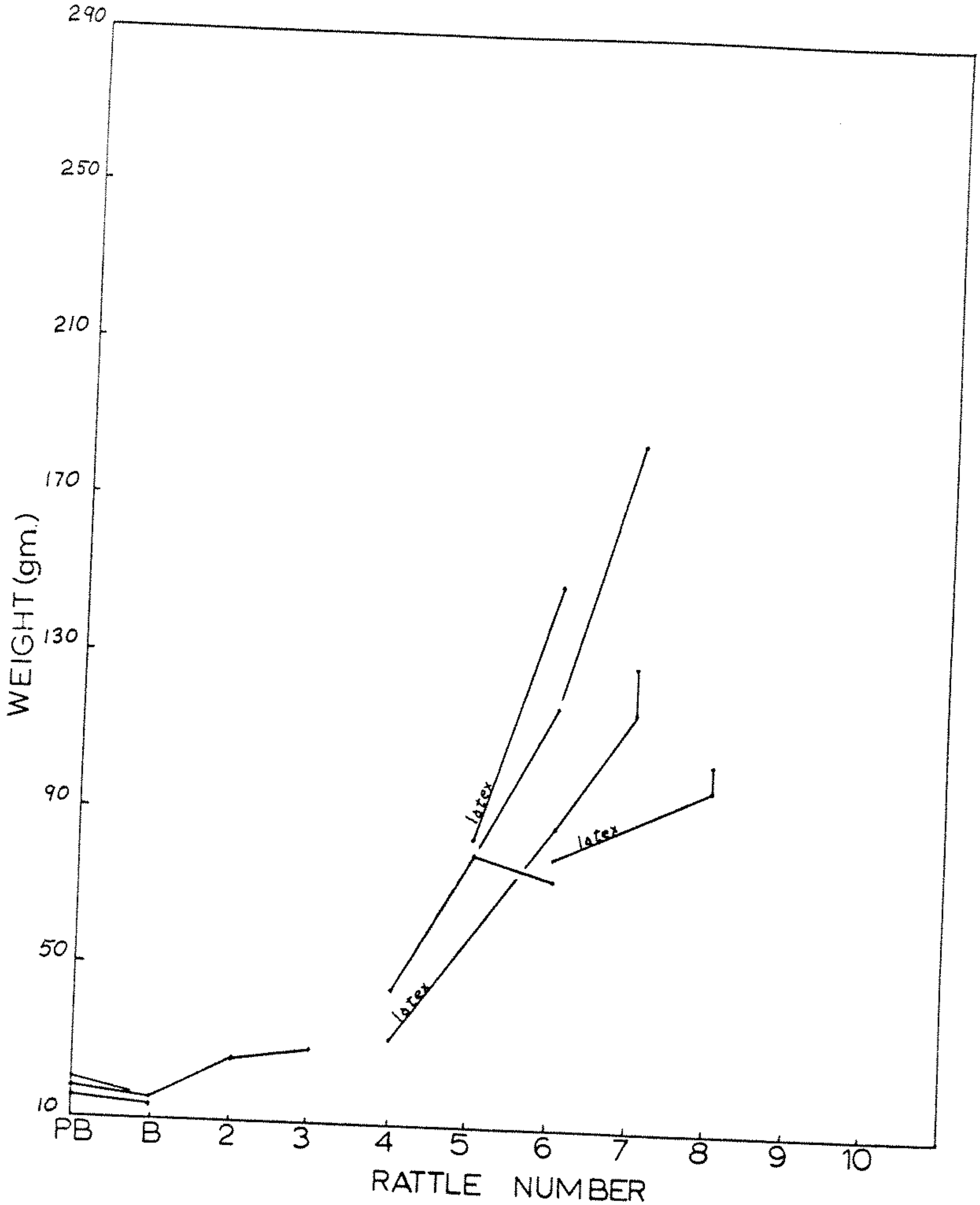

Figure 25. Increase in rattle number per unit of gain in weight in female rattlesnakes.

It has been demonstrated that a population of about 124 rattlesnakes at a density of 0.66 snakes per acre, with an abundant food supply, reveals a normal growth rate of 5.7 percent body length per growing-season-month in males under one year of age, ranging to 0.8 percent per month in old adult males. The females revealed a normal growth rate of 4.0 percent per month for those under one year of age ranging to 0.6 percent per month for the old adults.

Importance of the Facial Pit

A sensory organ, to survive, must be of some functional value to its possessor. This value in the case of the facial pit of rattlesnakes could be expressed in terms of survival or rate of growth in that snakes having non-functional pits would be expected to feed less efficiently than normal snakes. As earlier stated, it is the purpose of this project to determine the importance of this pit under natural conditions by comparison of survival, weight changes and growth rates of normal snakes with those of snakes with deleted pits.

Effect of Latex

Latex was found to be ineffective in blocking the thermoreceptive sense in that the latex plug was lost during molting. Three latex-treated snakes were recaptured before the latex was lost however, and these were treated as cauterized snakes. In other cases the duration of the latex block could not be known. Comparison of latex-treated snakes and normal snakes is discussed under the following sub-heading.

Effect of cautery:

Cautery of the pit membrane appeared to be permanent in its effect through the duration of this study. Casual observation of recaptured snakes retained in captivity about one year after cauterization indicated the pit to be yet nonfunctional. For example, on one occasion two of the snakes, one cauterized and one normal, were noticed to be resting with their heads lying in separate ventilation holes side by side in the cage. These holes are of ¾ inch diameter and bored in wood ¾ inch in thickness and are covered by window screen. When the writer's hand was waved slowly very close to their snouts, the normal snake withdrew and rattled but the cauterized snake did not respond.

On another occasion the same two snakes were again in such a position. Both flicked their tongues at the writer's hand but the normal snake rattled first and withdrew. The cauterized snake did not withdraw.

Controlled tests were conducted in order to explore further the effectiveness of cautery in extirpating the sensory activity of the facial pit. Of 18 snakes maintained in captivity for 3 months, tests revealed 2 of these to be reliable feeders, one striking 4 out of 4 mice and the other 4 out of 5. These two snakes, one cauterized and one sham-operated as previously described, were each offered a live mouse, one at a time, in the lighted test cage, 8 days after cauterization. The cauterized snake struck the mouse in 2 minutes and 30 seconds or at the rate of 24 strikes per hour. The sham-operated snake struck in 1 minute and 15 seconds or at the rate of 34 strikes per hour. This test would lead one to suspect that under ideal feeding conditions the operation would not necessarily inhibit the behaviour of the snakes.

It is suggested from the above test that cauterized snakes are able to feed successfully in a lighted cage. The same two snakes were further tested, using both lighted and light-tight boxes. The results (Table VIII) indicate unsuccessful feeding in total darkness by the cauterized snake.

Further tests were conducted using snakes recaptured in the spring of 1964. These snakes, four in number, two cauterized and two normal, were selected from 11 captives in that they showed interest in feeding, having eaten one mouse each. At the time of the tests, these snakes had been in captivity for about 2 months. Table IX reveals the results of the tests. There is no doubt that the sensory activity of the pit was destroyed.

It seems evident then that the facial pit is quite useful if not necessary in catching a mouse in absolute darkness even in a relatively small cage. Noble and Schmidt (1937) observed that two cauterized and tongueless snakes captured and ate 3 mice within 48 hours. They concluded that rattlesnakes "deprived of their pits and tongue are perfectly capable of catching and devouring prey unaided". Their experiment evidently was not carried out in total darkness. It may be that if the cauterized snakes discussed above had been left in the dark cages sufficiently long they would have captured the mice. However this experiment does indicate that the snakes with normal pits catch mice much more efficiently in total darkness than do the cauterized snakes.

In none of the recaptured cauterized snakes did the pit membrane appear to have regenerated. The pit appeared either as a cavity, the outer chamber continuous with the inner chamber, perhaps with a ring of membrane tissue or appeared to be partly closed by scar tissue. Figures 26 and 27 illustrate the cauterized right and left pits of rattler No. 22 photographed 15 months after cauterization. A vestige of the membrane can be seen in Figure 27. Figure 1 shows the right pit of a normal rattler, No. 89, in which the pit membrane is visible.

TABLE VIII. Comparing a cauterized and a Sham-operated Snake with Respect to Reactions to Mice in Lighted and Light-proof Boxes.

Treatment	Dark Box Date	Dark Box Rate of Striking	Light Box Date	Light Box Rate of Striking
Cauterized	June 11	0/hr.	June 12	40/hr.
	July 4	0/hr.	July 4	46/hr.
	July 19	0/hr.	July 19	6/hr.
Sham	June 11	15/hr.		
	July 4	0/hr.		
	July 21	60/hr.	July 4	46/hr.

TABLE IX. Comparing Normal and Cauterized Snakes with Respect to Reactions to Mice in Lighted and Light-proof Boxes.

Treatment	Dark Box Date	Dark Box Rate of Striking	Light Box Date	Light Box Rate of Striking
Normal No. 98	June 12	4/hr.		
F	July 4	30/hr.		
	July 20	10/hr.		
No. 89	July 4	30/hr.		
M	July 20	180/hr.		
Cauterized				
No. 56	July 5	0/hr.	July 5	30/hr.
M	July 20	0/hr.	July 20	12/hr.
No. 75	July 5	0/hr.	July 5	60/hr.
M	July 20	2/hr.		
	July 23	0/hr.	July 23	55/hr.

Figure 26. View of right side of head of rattlesnake Number 22 showing the cauterized pit. Scar tissue is in evidence here.

Figure 27. View of cauterized left facial pit of rattlesnake Number 22. A vestige of the destroyed membrane can be seen.

Examination of sections made from the pit regions of Nos. 64, 29, 69 and one other captive cauterized rattler revealed no noticeable damage to the tissue surrounding the pit. Remnants of the destroyed membrane were visible in No. 69 and possibly in No. 29. In general the sections were unsatisfactory with respect to indication of damage to the nervous tissue surrounding the pit.

Figure 28 compares male rattlesnakes subjected to three treatments, cautery of pits, latex blocking and normal, with respect to gain in length and date of capture. It appears that cautery has had some effect in some cases. For example No. 63 did not grow as rapidly as No. 20, of the same age, which had been treated with latex that was probably soon lost. The latex treatment appears to have had no effect, in Figure 28, having in most cases probably been lost soon after application. However No. 33, in which the latex was not lost appeared to grow as rapidly as No. 48 if not more so.

In Figure 29 in which the females are compared, effect of cautery is perhaps more evident. Again the latex appears to have had no appreciable effect. However, the cautery appears to have been more effective than in the case of the males. Three of four recaptured cauterized females, Numbers 69, 67, and 61, showed no increase in length. The slight decline shown by these three is due to measuring error. The two females that retained the latex, Numbers 30 and 34, showed slight increase in length.

Comparison of average instantaneous growth rates (Table X) reveals no major differences between the rates of the normal snakes and the latex-treated snakes with one possible exception in the 23 to 36 month old females. A cauterized 20 month old male revealed a lower growth rate than would be expected in a normal male of the same age, otherwise there were no differences

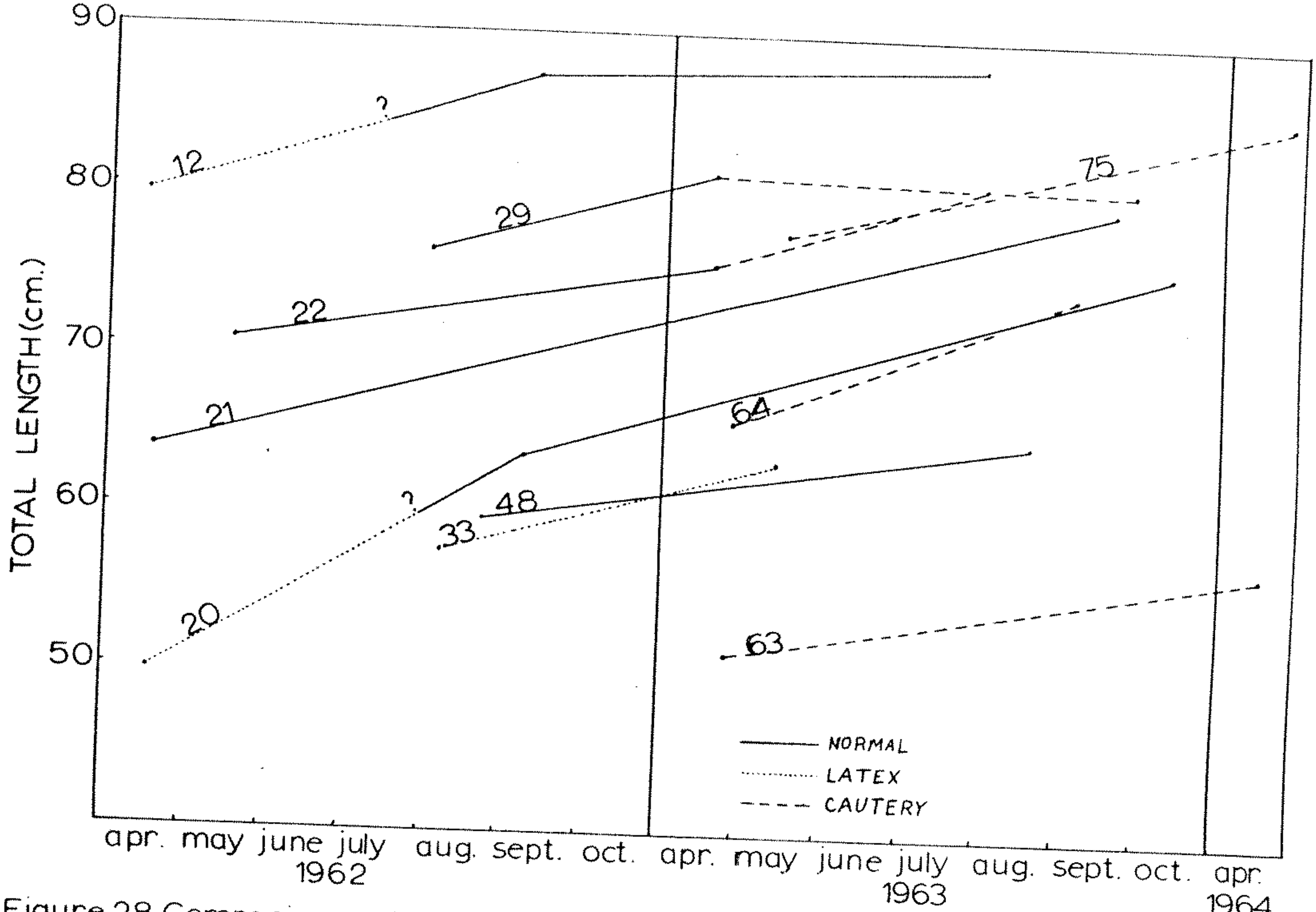

Figure 28. Comparing male rattlesnakes, treated in three ways, with respect to length and date of capture.

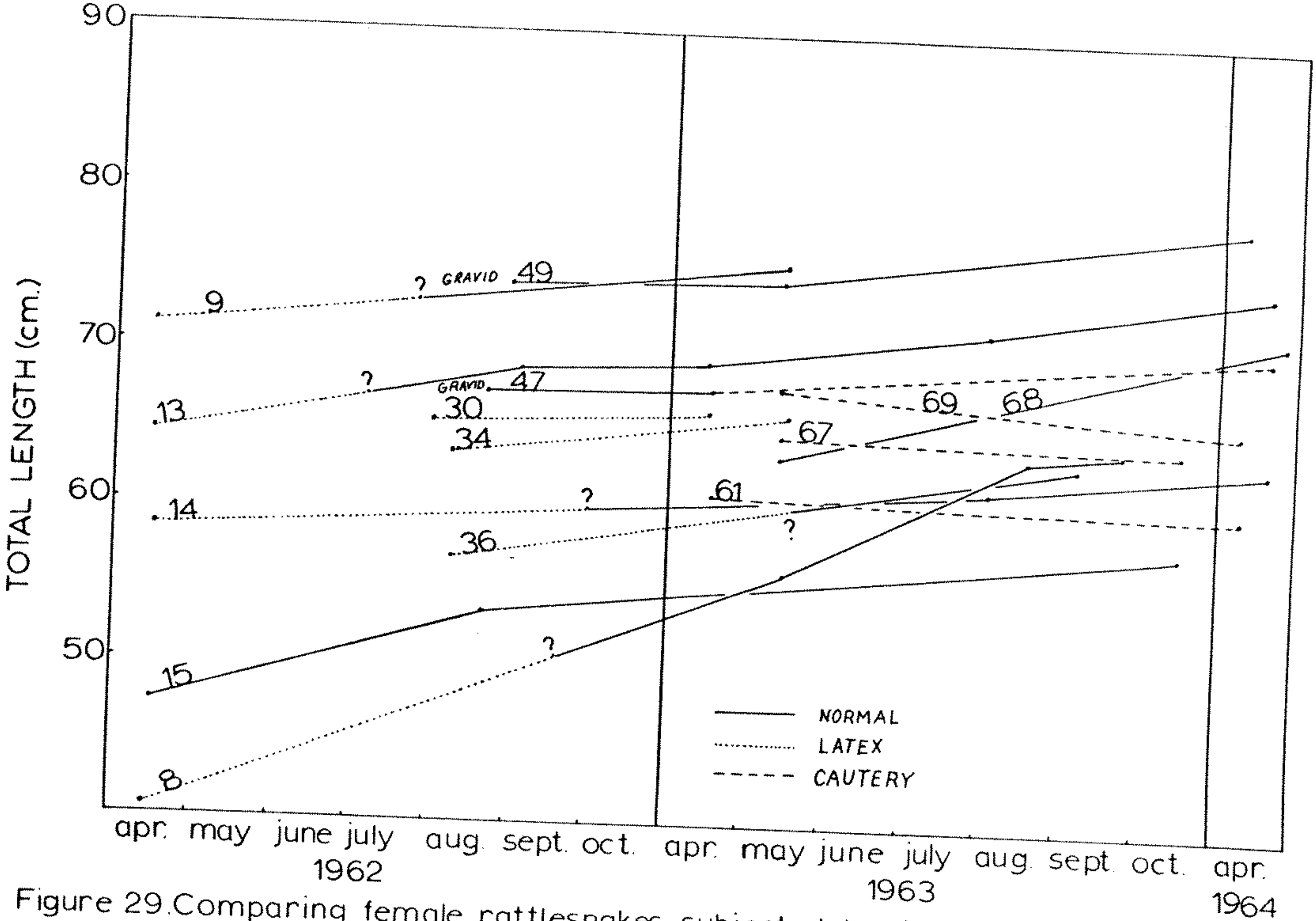

Figure 29. Comparing female rattlesnakes, subjected to three treatments, with respect to length and date of capture.

TABLE X. Comparison of Growth Rates in Terms of Percent Head-body length per Growing-season-month of Snakes Subjected to Three Different Treatments. Numbers in Parentheses Indicate Sample Size.

MALES

	Age (Mo.)	8	20	23-32	Adult	
	Head-body (cm.)	31.0		54.6-59.0	70.0-75.1	76.6-85.6
Normal	%/Mo.	6.7(1)		2.4(4)	1.2(4)	.8(5)
Latex	%/Mo.		5.7(1)	1.6(2)		
Cauterized	%/Mo.		1.8(1)	3.0(2)	1.1(4)	.8(2)

FEMALES	Age (Mo.)	8	20	23-36	Adult
	Head-body (cm.)		44.6	50.3-52.8	59.7-66.6
Normal	%/Mo.		3.1(1)	2.2(4)	1.2(6)
Latex	%/Mo.		5.7(1)	1.0(2)	1.0(2)
Cauterized	%/Mo.			0(1)	.5(5)

in the males. In the females, however, a major difference did appear between cauterized and normal snakes.

In order to obtain better figures for statistical analysis the slope of the growth curve was obtained by dividing the length at recapture (L_2) by the initial length (L_1). To straighten the curve the logarithm was taken of this ratio, $\log(L_2/L_1)$, and to eliminate the effect of age, $\log(L_2/L_1)$ was divided by the logarithm of the age ratio, $\log(T_2/T_1)$. The figures obtained, $\log(L_2/L_1)/\log(T_2/T_1)$(Table XI) were subjected to an analysis of variance. Only snakes of which the ages were known were used and only the first recaptures were used, in an attempt to eliminate all variation except that due to the three different treatments and individual variation which, of course, cannot be eliminated. If the snakes of all three treatments were compared there is no apparent difference in the differently treated males and no significant difference in the females. If the latex-treated snakes except ;those in which the latex was retained, were discarded and the cauterized and normal snakes compared, there is still no difference in the males, but the females reveal a significant difference at the 2.5 percent level. Individual variation in growth rate probably overweighed any differences in the males that might occur due to the loss of the heat sense. Also, the sample size is perhaps much too small to reveal a consistent difference between the differently treated snakes.

Figures 30 and 31 compare the weight changes with respect to time of the same snakes for which data were presented in Figures 28 and 29. In the males (Figure 30) there appears to be no definite pattern with respect to treatment. Number 20 lost weight after latex treatment and then gained weight after the latex had been lost. Number 29, not treated at first, also lost weight but gained weight after the second capture at which time he was cauterized. The females (Figure 31) again show no definite pattern with respect to weight change. It is probable that individual variation again outweighs the effect of the deletion of the thermoreceptive sense on growth through feeding.

TABLE XI (a). Statistical Comparison of the Snakes Subjected to the Three Treatments

Snake	Head-body length(M) L_1	L_2	Pit Deleted	L_2/L_1	Log (L_2/L_1)	Age in months T_1	Months between captures	T_2	T_2/T_1	Log (T_2/T_1)	$\frac{\text{Log}(L_2/L_1)}{\text{Log}(T_2/T_1)}$
MALES											
20	45.8	58.4	Latex	1.2751	.1055	20	4.8 5.4[1] = 10.2	30.2	1.5100	.1790	.59
	58.4	69.7		1.1935	.0770	24.8	13.2	38	1.5323	.1853	.42
33	53.2	59.1	Latex retained	1.1109	.0457	24	9.3	33.3	1.3875	.1425	.32
48	55.3	60.0		1.0850	.0355	24	12	36	1.5000	.1761	.20
21	59.0	73.6		1.2475	.0962	32	17.3	49.3	1.5406	.1878	.51
64	61.1	68.6	caut.	1.1227	.0503	32	4.3 5.4[1] = 9.7	46.0	1.4375	.1577	.32
63	47.3	52.8	caut.	1.1163	.0476	20	11.9	31.9	1.5950	.2028	.23

[1]Since these snakes had not hibernated between captures, 5.4 months was added to the time interval to eliminate the effect a period of hibernation (5.4 months) might have on the growth time.

[2]L_1 cannot be larger than L_2, therefore it must at least have remained the same.

TABLE XI (b). Statistical Comparison of the Snakes Subjected to the Three Treatments

Snake	Head-body length(M) L_1	L_2	Pit Deleted	L_2/L_1	Log (L_2/L_1)	Age in months T_1	Months between captures	T_2	T_2/T_1	Log (T_2/T_1)	$\frac{\text{Log}(L_2/L_1)}{\text{Log}(T_1/T_2)}$
FEMALES											
8	37.4	52.8	Latex	1.4118	.1496	20	13.2	33.2	1.6600	.2201	.68
	52.8	59.9		1.1345	.0550	33.2	3.1 5.4[1] = 8.5	44.8	1.3494	.1300	.42
15	44.6	50.3		1.1276	.0522	20	4.2 5.4[1] = 9.6	33.8	1.6900	.2279	.23
26	50.6	56.4		1.1146	.0472	23	12.8	35.8	1.5565	.1923	.25
10	52.2	58.2		1.1149	.0472	32	13.1	45.1	1.4094	.1488	.32
36	53.3	59.4	Latex	1.1145	.0472	24	13.1	37.1	1.5458	.1892	.25
14	55.0	57.8	Latex	1.0509	.0216	32	15.8	47.8	1.4938	.1744	.12
	57.8	58.5		1.0121	.0051	47.8	8.4	56.2	1.1757	.0705	.07
67	61.2	60.6	caut.	1.0000[2]	.0000	33	5.2 5.4[1] = 10.6	43.8	1.4788	.1700	.00
68	60.0	67.4		1.1233	.0503	32	11.6	43.6	1.3625	.1345	.37
61	57.6	57.0	caut.	1.0000[2]	.0000	32	12.0	44.0	1.3750	.1383	.00

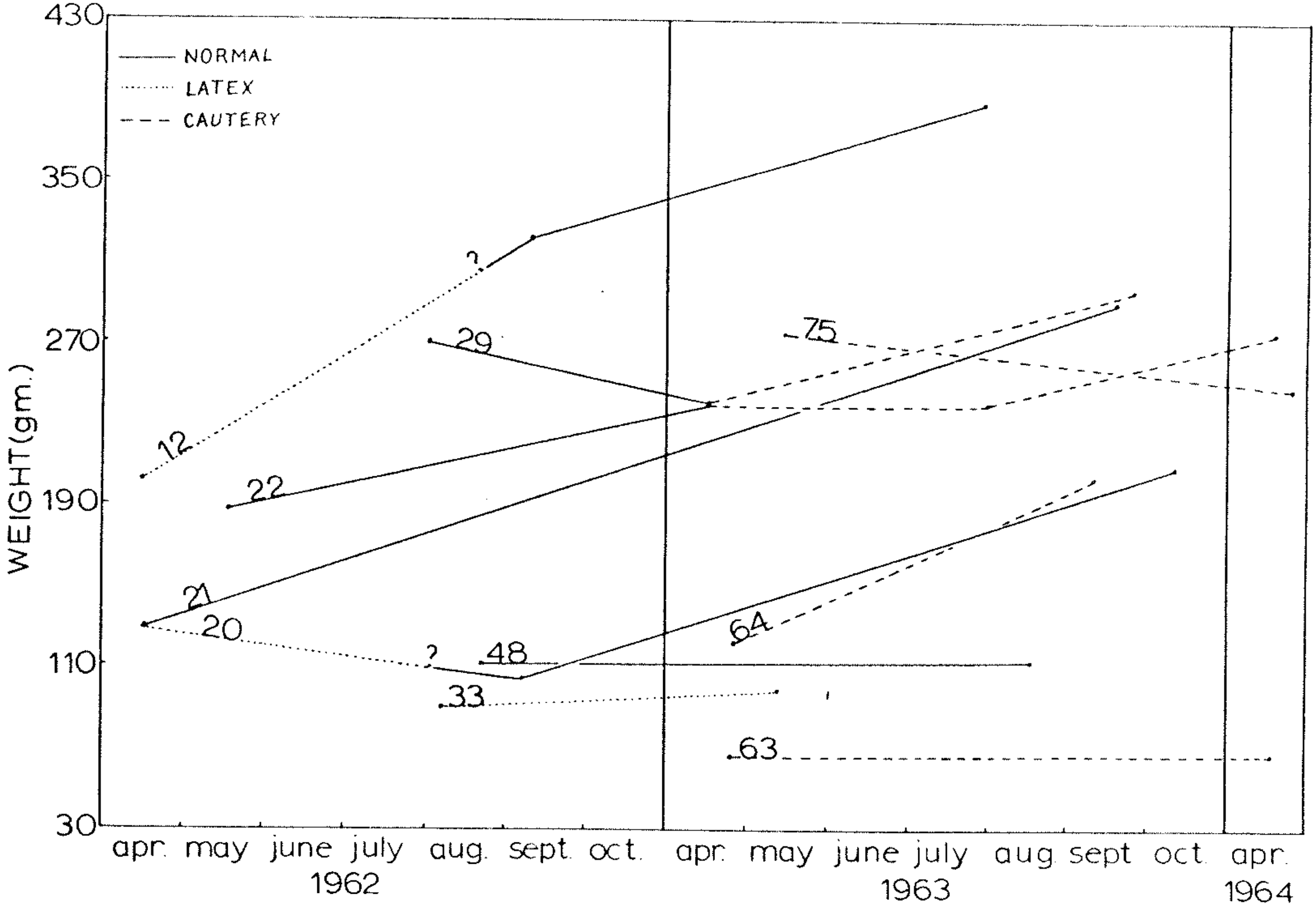

Figure 30. Comparing male rattlesnakes, subjected to three treatments, with respect to weight and date of capture.

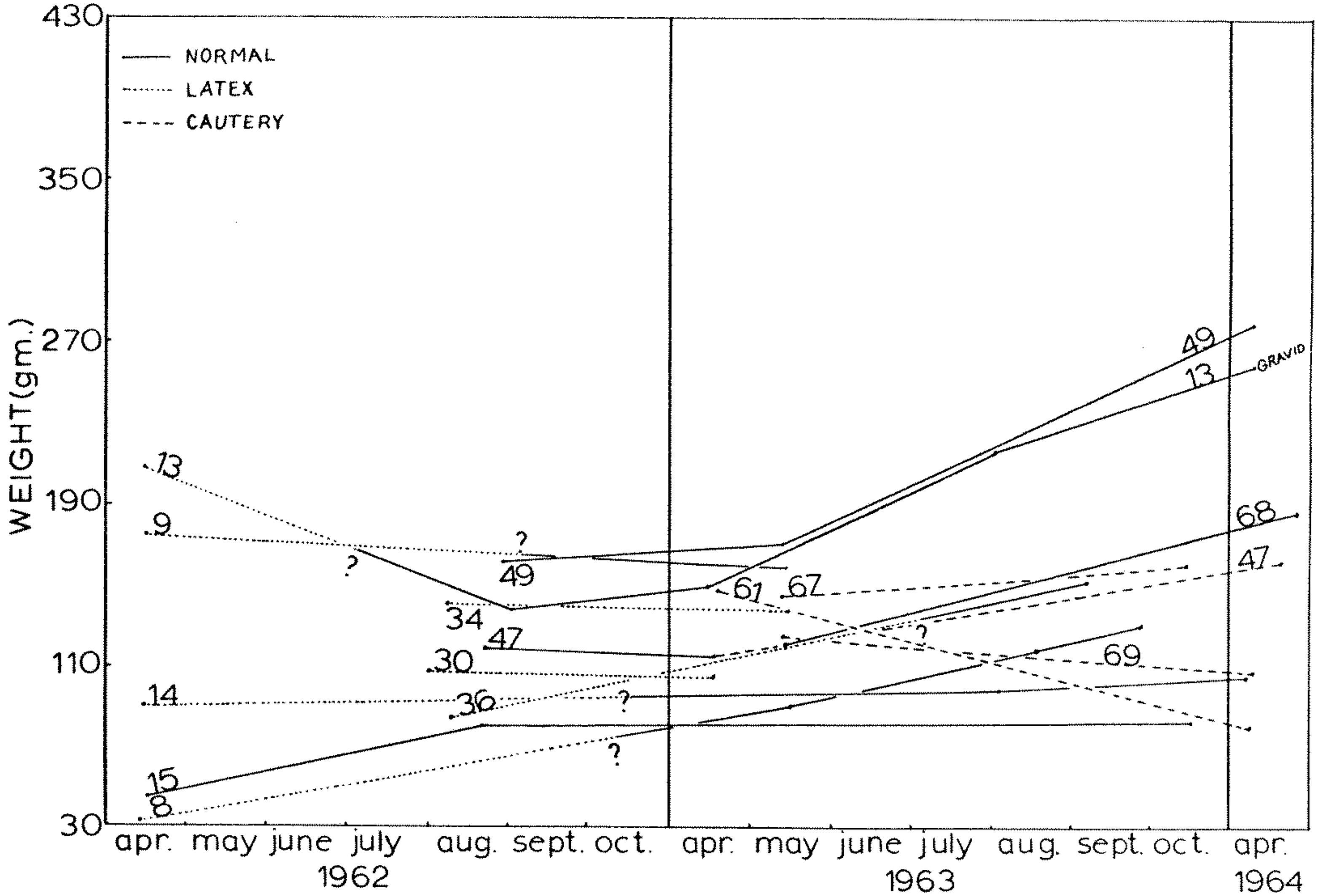

Figure 31. Comparing female rattlesnakes, subjected to three treatments, with respect to weight and date of capture.

During the spring of 1963 one male less than one year old was captured and cauterized, but has not been subsequently recaptured. On the other hand, of the 9 males 20 months old and older, captured and cauterized in the spring of 1963, seven were recaptured either in the fall of 1963 or the spring of 1964. None of the 8 normal males captured at the same time have been recaptured. This does not indicate a differential survival in favour of the normal snakes.

In the case of the females neither of the 2 cauterized young-of-the-year were recaptured subsequent to the time they were cauterized in spring 1963. One third of the normal young were recaptured, however. Four of the eight cauterized older snakes and six of the ten normal older snakes were recaptured. A differential survival of cauterized and non-cauterized young may be indicated in the case of the females but the numbers are too small to be definite. In the case of the older females 4/8 versus 6/10 may indicate a differential survival but to a slight degree only. Actually an additional cauterized female found dead at the den site in April, 1964, if included would bring the ratio to 5/8 compared to 6/10 in favour of the cauterized snakes. Death appeared to be due to predation, as only a section of the tail was found. Whether death in this case could be attributed indirectly to the cautery of the facial pits through reduction in wariness or through loss of condition is not certain. It is perhaps most likely that death to that particular female came purely by chance.

CONCLUSIONS

Summing up, the importance of the facial pit in locating prey in absolute darness is definitely indicated by the behavioural tests comparing cauterized and normal snakes. Statistical tests revealed a significant difference in the growth rates of the females, the cauterized snakes growing more slowly than the normal ones. No difference at all was revealed in the males. The fact that there was a significant difference indicated in the case of the females and not in the males may suggest that the pits may be more important to the one sex than the other. Indeed, it has been pointed out that males tend to wander more than the females (Fitch, 1949) and perhaps hunt more actively. The thermoreceptive sense then may be more important to snakes that tend to lie in wait for their prey as may do the less nomadic females. However, the controlled behaviour tests indicated the pits to be important to males.

On the other hand, the thermoreceptive sense may be more important in a particular age class. For example, one 20 month old male showed a growth rate lower than that to be expected in this age class (Table X). Also, no cauterized young-of-the-year was recaptured. The data are too meagre to support this suggestion of difference with age, however.

In conclusion, to overcome the effect of individual variation in growth rate a much larger sample is required, preferably with equal numbers of cauterized, sham operated and normal snakes. In addition, observation of cauterized snakes over a longer period, of at least two growing seasons, would be desirable. To settle the question regarding the importance of facial pits under natural conditions further study is required. Even then growing rates, particularly in the older snakes, may be much too variable to reveal a differential success in feeding as a result of pit deletion.

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