

THIS DISSERTATION
ENTITLED

The Natural History of Virginia valeriae pulchra
(Serpentes; Colubridae)

By

Thomas H. Cervone

has been submitted to the Department of

Biology

on the 28 day of March 1983 ,

in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

This dissertation is approved by the Major Professor and is hereby
submitted for the examination by the properly designated Readers.

Signed *Richard C. Boman*
Major Professor.

Title: The Natural History of Virginia valeriae pulchra (Serpentes; Colubridae)

Author: Thomas Henry Cervone

Major Professor: Richard C. Bothner

V. v. pulchra is discontinuously distributed in the unglaciated Allegheny Plateau of western Pennsylvania, eastern West Virginia, and western Maryland. The typical habitat is a rocky, leaf-littered, herbaceous clearing bordered by woods. V. v. pulchra was found concealed under flat-fine sandstone rocks.

Morphological studies show V. v. pulchra to be the least derived from the species' presumptive ancestral form. It is the least subterranean of the three subspecies and, in this, resembles V. v. elegans more closely than the apparently more derived V. v. valeriae.

V. v. pulchra feeds solely on earthworms. Size determines the species consumed. Gravid females fed less often than non-gravid ones.

V. v. pulchra is a thigmotherm with an ecritic temperature of $23.8 \pm 4.5^{\circ}\text{C}$. In August, gravid females prefer higher temperatures than males.

V. v. pulchra shows diurnal activity patterns and is more readily collected in the spring and the fall than in summer. Availability increases during or immediately after a rain.

Sexual maturity in males is reached in the fall of their second active season when a live snout-vent length of 158 to 168mm is achieved. Maturity in females is reached in the spring of the fourth year when a live snout-vent length of 214 to 227mm is achieved. Spermatogenesis peaks in July with mating occurring in the spring or fall. Ovulation can occur from the first week in May to mid-June. Parturition extends from 16 August to 20 September; the gestation period being approximately 105 days. Litter size ranges from 2 to 11 with an average of 6.0 ± 1.8 .

Male V. v. pulchra live 6 years or more; females, seven years or more. Growth rates for both sexes are similar from birth through the third active season. Thereafter, the females grow at a greater rate.

V. v. pulchra was found to be preyed upon by the milksnake and displayed a defense technique of biting and holding onto the lining of the milksnakes' mouth. This technique discouraged the latter from swallowing it.

TABLE OF CONTENTS

| | Page |
|---|------|
| INTRODUCTION..... | 1 |
| MATERIAL AND METHODS..... | 6 |
| General..... | 6 |
| Range..... | 7 |
| Habitat..... | 7 |
| Color and Morphology..... | 9 |
| Diet..... | 10 |
| Thermal Preference, Moisture Selection and Burrowing Activity..... | 11 |
| Time of Appearance..... | 14 |
| Reproductive Biology..... | 15 |
| Population Structure..... | 17 |
| Competitors, Predators, and Defense Mechanisms | 18 |
| OBSERVATIONS..... | 19 |
| Range..... | 19 |
| Habitat..... | 24 |
| Color and Morphology..... | 35 |
| A. Color..... | 35 |
| B. Size and Weight..... | 37 |
| C. Body Proportions..... | 38 |
| D. Body Scales..... | 39 |
| E. Degree of Keeling in the Dorsal Scales..... | 41 |
| F. Head Scutes..... | 42 |
| G. Morphological Comparison with the Other Two Subspecies..... | 44 |
| Diet..... | 50 |
| Thermal Preference, Moisture Selection and Burrowing Activity..... | 53 |
| A. Thermal Preference..... | 56 |
| B. Moisture Selection..... | 60 |
| C. Burrowing Activity..... | 62 |
| Time of Appearance..... | 62 |
| A. Seasonal..... | 63 |
| B. Daily..... | 64 |
| Reproductive Biology..... | 71 |
| A. Males..... | 71 |
| B. Females..... | 80 |
| C. Mating..... | 87 |
| D. Fat Bodies..... | 93 |

TABLE OF CONTENTS (Continued)

| | Page |
|---|------|
| Population Structure..... | 94 |
| A. Age Distribution..... | 94 |
| B. Growth Rate..... | 94 |
| Competitors, Predators, and Defense Mechanisms | 97 |
| A. Competitors..... | 97 |
| B. Predators..... | 99 |
| C. Defense mechanisms..... | 100 |
| DISCUSSION..... | 101 |
| Range..... | 101 |
| Habitat..... | 108 |
| Color and Morphology..... | 114 |
| A. Color..... | 114 |
| B. Size..... | 117 |
| C. Body Proportions..... | 117 |
| D. Body Scales..... | 120 |
| E. Degree of Keeling in the Dorsal Scales..... | 123 |
| F. Head Scutes..... | 125 |
| Diet..... | 128 |
| Thermal Preference, Moisture Selection and Burrowing Activity..... | 132 |
| A. Thermal Preference..... | 132 |
| B. Moisture Selection..... | 136 |
| C. Burrowing Activity..... | 138 |
| Time of Appearance..... | 138 |
| Reproductive Biology..... | 142 |
| Population Structure..... | 150 |
| Competitors, Predators, and Defense Mechanisms | 153 |
| SUMMARY..... | 157 |
| LITERATURE CITED..... | 159 |
| APPENDIX I..... | 175 |
| APPENDIX II..... | 178 |

LIST OF FIGURES

| <u>Figure</u> | | <u>Page</u> |
|---------------|---|-------------|
| 1 | The known ranges for the three subspecies of <u>Virginia valeriae</u> | 20 |
| 2 | The geographic distribution of <u>V. v. pulchra</u> ... | 21 |
| 3 | Photograph showing the habitat of <u>V. v. pulchra</u> across from the Sizerville State Park in Potter County, Pennsylvania..... | 24 |
| 4 | Photograph showing the habitat of <u>V. v. pulchra</u> at the Slabtown Hollow field in Potter County, Pennsylvania..... | 25 |
| 5 | Photograph showing the habitat of <u>V. v. pulchra</u> across from Thompson Island in Warren County, Pennsylvania..... | 25 |
| 6 | Photograph showing the topography of the Allegheny High Plateau near Emporium, Pa. | 26 |
| 7 | Percentage of the total number of <u>V. v. pulchra</u> collected from different aspects..... | 27 |
| 8 | Semi-log graph plotting the number of snakes collected against distance from permanent water..... | 28 |
| 9 | Percent of the total number of soil samples from collectingsites of <u>V. v. pulchra</u> , falling into the various soil texture classes of Johnson (1975)..... | 29 |
| 10 | The average percent of various types of cover surrounding 327 separate collecting sites for <u>V. v. pulchra</u> | 31 |
| 11 | Number of individuals of <u>V. v. pulchra</u> , <u>D. p. edwardsi</u> , and <u>S. occipitomaculata</u> observed per hour searching in <u>V. v. pulchra</u> habitat..... | 33 |
| 12 | Photograph of a female <u>V. v. pulchra</u> taken by Dr. M. Graham Netting on 10 July 1965.... | 36 |

| <u>Figure</u> | | <u>Page</u> |
|---------------|--|-------------|
| 13 | Head width relative to snout-vent length for 50 <u>V. v. pulchra</u> | 39 |
| 14 | Relationship between Tb and Ts for 268 <u>V. v.</u> <u>pulchra</u> | 59 |
| 15 | Relationship between water lost (mgs) per gram body weight per hour and surface area (cm ²) for 39 <u>V. v. pulchra</u> | 62 |
| 16 | Monthly captures per hour of collecting for immature and mature males and immature and mature female <u>V. v. pulchra</u> | 64 |
| 17 | The number of <u>V. v. pulchra</u> captured per time of day..... | 65 |
| 18 | Range of substrate temperatures and ground tem- peratures under test rock during seven 24-hour studies..... | 67 |
| 19 | Correlation between number of <u>V. v. pulchra</u> captured per period for seven 24-hour studies with air temperature minus ground temperature and substrate temperature minus ground temperature..... | 68 |
| 20 | Snout-vent length plotted against (a) convolu- tions of and (b) presence of sperm in vasa deferentia..... | 72 |
| 21 | Average diameter of the seminiferous tubules for 115 male <u>V. v. pulchra</u> for each month of the active season..... | 73 |
| 22 | Seasonal development of the right testis char- acterized by its length plus width and right testis length divided by snout-vent length..... | 74 |
| 23 | Spermatogenic cycle for <u>V. v. pulchra</u> | 75 |
| 24 | Seminiferous tubule in April showing spermat- ogonia, primary spermatocytes, and Sertoli cells..... | 76 |

| <u>Figure</u> | | <u>Page</u> |
|---------------|---|-------------|
| 25 | Seminiferous tubules in May showing spermatogonia, primary spermatocytes, Sertoli cells, and cellular debris..... | 77 |
| 26 | Seminiferous tubule in June showing secondary spermatocytes and spermatids..... | 77 |
| 27 | Seminiferous tubule in July showing secondary spermatocytes, spermatids, and developing spermatozoa..... | 78 |
| 28 | Seminiferous tubules in August showing secondary spermatocytes, spermatids, and spermatozoa | 78 |
| 29 | Seminiferous tubule in September showing spermatogonia, Sertoli cells, and cellular debris..... | 79 |
| 30 | Seminiferous tubules in October showing spermatogonia, Sertoli cells, and some cellular debris..... | 79 |
| 31 | A diagram of the sequence of follicular maturation in <u>V. v. pulchra</u> | 82 |
| 32 | Frequency of occurrence (%) for each type follicle for 88 mature <u>V. v. pulchra</u> | 83 |
| 33 | Photograph of an oviducal egg with follicular cells around it..... | 85 |
| 34 | Number of young born to 34 females in the laboratory plotted in 5 day periods for August and September..... | 86 |
| 35 | Presence of spermatozoa in the oviduct, oviducal eggs, embryo's, corpora lutea, and young in relation to snout-vent length in female <u>V. v. pulchra</u> | 88 |
| 36 | Spermatozoa in lumen of oviduct in July..... | 90 |
| 37 | Spermatozoa aligned along wall of oviduct in April | 91 |
| 38 | Spermatozoa aligned along wall of oviduct in October..... | 91 |

| <u>Figure</u> | | <u>Page</u> |
|---------------|--|-------------|
| 39 | Spermatozoa in lumen of oviduct in May..... | 92 |
| 40 | Spermatozoa in lumen of oviduct in September... | 92 |
| 41 | Mean comparison for abdominal fat bodies for sexually mature males and females..... | 93 |
| 42 | Age distribution for 218 male and 254 female <u>V. v. pulchra</u> | 97 |
| 43 | Snout-vent lengths (mm) for 218 male and 254 female <u>V. v. pulchra</u> plotted against their age in years..... | 98 |

LIST OF TABLES

| <u>Table</u> | | <u>Page</u> |
|--------------|---|-------------|
| 1 | Numbers of specimens of Reptile and Amphibian species found sharing the same rock cover with <u>V. v. pulchra</u> or in the immediate vicinity of this form..... | 32 |
| 2 | Summary of the dorsal scale patterns found for 352 <u>V. v. pulchra</u> | 40 |
| 3 | Number and percent of <u>V. v. pulchra</u> from the 3 populations with typical and atypical dorsal scale patterns..... | 40 |
| 4 | Number and percent of specimens with keeled and smooth anterior dorsal scales for 176 male and 176 female <u>V. v. pulchra</u> within the Sizerville, Warren, and S.Pa-Md-WV populations..... | 42 |
| 5 | Number of <u>V. v. pulchra</u> specimens demonstrating various supralabial and infralabial patterns..... | 43 |
| 6 | Number of <u>V. v. pulchra</u> specimens with various postocular scale patterns..... | 44 |
| 7 | Comparison of the 3 subspecies of <u>V. valeriae</u> for tail length expressed as a percentage of total length..... | 46 |
| 8 | Number and percent of specimens demonstrating keeled dorsal scales for the anterior and posterior areas of the body for the 3 subspecies of <u>V. valeriae</u> | 49 |
| 9 | Monthly frequency for 112 male and 103 female <u>V. v. pulchra</u> containing earthworms within the digestive tract..... | 51 |
| 10 | Earthworms identified from the stomachs of 17 <u>V. v. pulchra</u> | 51 |
| 11 | Frequency of empty stomachs found for 24 gravid and 41 non-gravid <u>V. v. pulchra</u> | 52 |

| <u>Table</u> | <u>Page</u> | |
|--------------|--|----|
| 12 | Laboratory feeding experiment comparing gravid and non-gravid <u>V. v. pulchra</u> for small earthworms..... | 53 |
| 13. | Summary of male <u>V. v. pulchra</u> thermal data..... | 56 |
| 14 | Summary of female <u>V. v. pulchra</u> thermal data... | 57 |
| 15 | Summary of field thermal data for all <u>V. v. pulchra</u> | 57 |
| 16 | Comparison of body temperatures with rock (underside), substrate, and air temperatures for eight <u>V. v. pulchra</u> | 60 |
| 17 | Rate of non-cloacal water loss per gram body weight per hour for immature and adult <u>V. v. pulchra</u> | 61 |
| 18 | Hibernacular information recorded for <u>V. v. pulchra</u> , <u>D. p. edwardsi</u> , and <u>Thamnophis brachystoma</u> from an abandoned <u>Formica exsectoides</u> mound on 1 April 1981..... | 70 |
| 19 | Effect of rainfall on number of <u>V. v. pulchra</u> per hour collecting..... | 70 |
| 20 | Types of ovarian follicles and their frequencies | 81 |
| 21 | Comparison of the number of embryos per oviduct and number of corpora lutea per ovary.... | 87 |
| 22 | The number of times <u>V. v. pulchra</u> was found with another <u>V. v. pulchra</u> under the same rock..... | 89 |
| 23 | Presence and condition of sperm in 15 females in September of 1981 demonstrated by cloacal smears..... | 89 |
| 24 | Average live snout-vent lengths (mm) per month for 254 female <u>V. v. pulchra</u> of varying ages..... | 95 |
| 25 | Average live snout-vent lengths (mm) for 218 male <u>V. v. pulchra</u> of varying ages per month..... | 96 |

| <u>Table</u> | | <u>Page</u> |
|--------------|--|-------------|
| 26 | Comparison for the 3 subspecies of <u>V. valeriae</u> for adaptations to a subterranean existence..... | 127 |
| 27 | Milligrams of non-cloacal water lost per gram body weight per hour for young and adult <u>V. v. elegans</u> , <u>V. v. pulchra</u> , <u>C. vermis</u> , <u>D. punctatus</u> , and <u>T. gracilis</u> | 137 |
| 28 | The percent soil moisture found for collecting sites for <u>V. v. elegans</u> , <u>V. v. pulchra</u> , <u>C. vermis</u> , <u>D. punctatus</u> , and <u>T. gracilis</u> . | 137 |

To

Dr. Richard C. Bothner

ACKNOWLEDGMENTS

Many people have contributed to the completion of this project. I thank Dr. David L. Carpenter of the St. Bonaventure Psychology Department for advise on statistical matters and Dr. Stephen W. Eaton and Dr. Alfred F. Finocchio for their helpful suggestions as committee members. For help in collecting *V. v. pulchra*, I thank Michael R. Eaton, Steven L. Kellogg, Dana M. McCarthy, and Dr. Russell J. Nemecek. To Dana, who accompanied me on many field excursions, I extend my deepest gratitude. I also wish to thank James G. Faharty, Mary A. Lynch, Betty A. McGinn, and John B. Rudd for their assistance in the earlier stages of this study. I thank Patricia A. Foster for her help in processing some of the reproductive tissue herein reported and Saint Francis Hospital (Olean, New York) for the use of their facilities.

I thank the following curators for access to records and collections: Dr. John M. Condit, The Ohio State University; Dr. Herbert S. Harris, Jr., Natural History Society of Maryland; Dr. Roy W. McDiarmid, National Museum of Natural History; Dr. Clarence J. McCoy, Carnegie Museum of Natural History; Dr. Michael E. Seidel and Dr. N. Bayard Green, Marshall University; and Dr. Richard G. Zweifel, American Museum of Natural History. To Dr. Clarence J. McCoy, Dr. M. Graham Netting, Dr. Thomas K. Pauley, and Dr. Neil D. Richmond, I wish to express my deepest appreciation for their suggestions and insights into this project. They are truly gentlemen and scholars. I also would like to thank Dr. John W. Reynolds, Department of Forest Resources, University of New Brunswick (Frederick, New Brunswick), for identifying the majority of the earthworms reported in this manuscript. Most of all, I would like to thank my mentor, Dr. Richard C. Bothner, for his guidance, support, confidence, and friendship throughout this project. He is not only generous and wise, but a true friend indeed. For these reasons and many more, I dedicate this work to him. I can think of no more appropriate or higher honor to bestow, than to present this work in his name. To my dear friend Theresa A. Covley, I thank her for procurement of many references cited and her thoughtful, generous way. For typing this manuscript, I thank Noel H. Riggs.

To Marie Ferrara, Rick and Marilyn Richards, their daughters (Alesia, Nicole, Ericka), and Rick and Roxanne Langianese, I extend my deepest appreciation for their support, love, and friendship throughout my graduate studies. I especially thank Marie. Also, I would like to acknowledge my parents, Richard and Helen, who are now deceased. To them I am indebted and hope my accomplishments please their everlasting dreams.

Finally, to the Biology Faculty and Graduate Students of Saint Bonaventure University, I express my humble and sincere thanks for their help and all the conveniences granted. I think very highly of the Staff and have learned much from them. May their efforts, never go unrewarded.

INTRODUCTION

The genus Virginia is a little-known group of colubrid snakes distributed in the United States from Oklahoma to the Atlantic Coast. Within this genus, two species are recognized; Virginia striatula, the Rough Earth Snake, which is a monotypic species, and Virginia valeriae, the Smooth Earth Snake. This latter species comprises three subspecies; Virginia valeriae valeriae, the Eastern Smooth Earth Snake, Virginia valeriae elegans, the Western Smooth Earth Snake, and Virginia valeriae pulchra, the Mountain Earth Snake which is the object of this present study.

Virginia valeriae pulchra (Richmond), the Mountain Earth Snake, is a small snake endemic to the Allegheny Plateau of western Pennsylvania, eastern West Virginia (to Highland Co., Va.), and western Maryland. This form has received little attention since its original description by Richmond in 1954. It is considered rare in Pennsylvania by Netting (1965) and Swanson (1952), and uncommon in Maryland by Lee (1973). Its status in West Virginia is presently under investigation by Dr. Thomas K. Pauley, University of Pittsburgh at Bradford Campus, Pennsylvania. No specimen appears to have been collected before 1928, and collecting has averaged less than one adult per year since then (Netting, 1965). Due to its secretive habits, ecological information is lacking; this warrants a thorough study of its natural history

Richmond (1954) described Virginia valeriae pulchra in Pennsylvania as a separate subspecies of the Virginia valeriae complex. All specimens collected before 1954 were classified as Virginia valeriae valeriae.

The genus Virginia has undergone a number of nomenclatural changes since 1853. Zillig (1958) has published a summary of the taxonomic history and present status of the genus Virginia.

As early as 1923, Blanchard suggested that scientists be compelled to publish any information regarding the genus Virginia since information is lacking in regards to its natural history and environmental relations. Since that time, relatively little has actually been published.

The geographic range of Virginia valeriae pulchra has been mapped by Conant (1975), McCoy (1980; 1982), and Richmond (1954). The author has used such information as well as locality records from various museums and published articles such as Bothner and Moore (Pa., 1964), Cooper (Md., 1948; 1958), Green (W.V., 1969), Harris (1969; 1975), LeMay and Marsiglia (Md., 1952), McCauley (1945), Netting (Pa., 1965), Pauley (W.V., per. com.), Pisani (Pa., 1971), Richmond (Pa., 1954), and Swanson (Pa., 1952) to map the present range for Virginia valeriae pulchra.

Habitat information for Virginia valeriae pulchra, although scanty, has been published by Bothner and Moore (Pa., 1964), Cooper (Md., 1958), LeMay and Marsiglia (Md., 1952), Netting (Pa., 1965), Richmond (Pa., 1954), and Swanson (Pa., 1952). The paucity of such

information is due to the limited number of specimens. Habitat information for Virginia valeriae elegans has been reported by Anderson (Mo., 1965), Blanchard (Gen., 1923), Brode and Allison (Miss., 1958), Christiansen (Iowa, 1973), Cliburn (Miss., 1958), Edgren and Ward (Ind., 1952), Henderson (Kan., 1974), Hurter (Mo., 1911), Minton (Ind., 1944), Myers (Mo., 1957), Pisani and Collins (Ky., 1971), Smith (Ill., 1961), Walker, J. M. (La., 1963), Westing (Ind., 1961), and Wright and Wright (Gen., 1957) while Virginia valeriae valeriae habitat has been reported by Blanchard (Gen., 1923), Campbell (Fla., 1962), Conant (Pa., 1936; Ohio, 1938), Grizzell (Md., 1949), McCauley (Md., 1945), Miller (N.J., 1916), Neill (Fla., 1948), Pisani and Collins (Ky., 1971), Werler and McCallion (Va., 1951), Wilson and Friddle (W.V., 1950), and Wright and Wright (Gen., 1957).

The external morphology for Virginia valeriae pulchra in Pennsylvania was described by Richmond (1954) while Cooper (1958) described 6 Maryland Virginia valeriae pulchra specimens. Pisani and Collins (1971) compared the external morphology for Virginia valeriae elegans specimens from western Kentucky and western Tennessee with Virginia valeriae valeriae specimens from eastern Kentucky, eastern Tennessee, Ohio, West Virginia, Virginia, and Maryland. Blanchard (1923) compared the external morphology of Virginia valeriae elegans and Virginia valeriae valeriae specimens throughout their known range except in the states of Ohio, Kentucky, Pennsylvania, Arkansas, Iowa, and Kansas. General descriptions for Virginia valeriae elegans have been published by Anderson (Mo., 1965), Bradford (Mo., 1973),

Christiansen (Iowa, 1973), Ditmars (1936), Edgren and Ward (Ind., 1952), Hurter (Mo., 1911), Pisani (1972), Smith (Ill., 1961), and Wright and Wright (1957) while descriptions for Virginia valeriae valeriae have been reported by Conant (Ohio, 1938), Ditmars (1936), McCauley (Md., 1945), Wilson and Friddle (W.V., 1950), and Wright and Wright (1957). Clark (1964) described and compared the structures of the hemipenis in the genus Virginia.

Hibernacular studies for Virginia valeriae pulchra and Virginia valeriae elegans have yet to be published. Hibernating Virginia valeriae valeriae and Virginia striatula have been described by Grizzell (Md., 1949) and Neill (Ga., 1948) respectively.

Studies of the reproductive biology of Virginia valeriae pulchra have focused, for the most part, on litter sizes and parturition dates. Bothner and Moore (1964), Cooper (1958), Pisani (1971), Netting (1950; 1965), Richmond (1954), and Swanson (1952) have contributed such information. Bradford (1973) compared the reproductive biology for Virginia valeriae elegans and Virginia striatula. General references for Virginia valeriae elegans on brood sizes and parturition dates have been reported by Anderson (1965), Christiansen (1973), Keeler (1956), Myers (1962), Pisani and Collins (1971), Smith (1956; 1961), and Wright and Wright (1957) while such information for Virginia valeriae valeriae have been reported by Ditmars (1936), Groves (1961), McCauley (1945), Walker, J.M. (1963), Wilson and Friddle (1950), and Wright and Wright (1957).

Little else has been published on the natural history of this subspecies or on its possible origin. Netting (1965) and Richmond (1954) have speculated on its zoogeography and pre-glacial existence.

The purpose of this study, therefore, is to contribute information on the natural history of this least studied subspecies of the group, Virginia valeriae pulchra, and compare this with Virginia valeriae valeriae and Virginia valeriae elegans whenever possible.

MATERIAL AND METHODS

General

Collecting trips were made at varying intervals during the period of May 1979 to October 1981. A series of Pennsylvania specimens and one Maryland specimen of Virginia valeriae pulchra were collected representing all months of the year except November, December, January, and February. Other specimens of Virginia valeriae pulchra, Virginia valeriae valeriae, and Virginia valeriae elegans examined were borrowed from various private and institutional collections. Appendix I lists museum specimens used in this study.

Appendix II lists the localities for Virginia valeriae pulchra.

Field collections were initially concentrated in areas where Virginia valeriae pulchra had been recorded. From such areas, the search was widened throughout western Pennsylvania, northeastern West Virginia, and western Maryland. Eighteen new collecting sites were added to the 44 sites previously recorded. The majority of the author's efforts were concentrated in northwestern Pennsylvania.

During the course of this study, 605 Virginia valeriae pulchra were observed in the field and detailed records are available for 519 of these. One hundred and thirty-five males and 124 females were preserved. These specimens are housed in the St. Bonaventure University collection.

Statistical methods are from Downie and Heath (1970), Ferguson (1966), Lewis (1966), and McCall (1980). Means are given with plus

or minus one standard deviation. In some cases, plus or minus one standard error of the mean was used. Levels of confidence employed in this study were 5% or greater.

The following aspects of the natural history of Virginia valeriae pulchra were studied: (1) range, (2) habitat, (3) morphology, (4) diet, (5) thermal preference, moisture selection and burrowing activity, (6) time of appearance, (7) reproductive biology, (8) population structure, and, finally, (9) competitors, predators, and defense mechanisms.

Range

The range for Virginia valeriae pulchra was determined by utilizing locality records from various public and private collections as well as the author's. All specimens not collected by the author were verified through direct examination. Literature available on localities for Virginia valeriae pulchra in western Pennsylvania have been published by Atkinson (1901), Bothner and Moore (1964), Netting (1965), Pisani (1971), Richmond (1954), and Swanson (1952); in Maryland, Cooper (1948; 1958), Harris (1969; 1975), LeMay and Marsiglia (1952), McCauley (1945); in West Virginia, Green (1969), McCoy (1965), and Pauley (pers. com.).

Habitat

- The habitat for Virginia valeriae pulchra was described, using the following parameters: (1) percent type cover, (2) angle and direction of slope, (3) soil texture, (4) proximity of collecting

site to surface water. The microhabitat was analyzed by identifying (1) the type and size of cover under which the snake lay, and (2) relative humidity at the site of capture.

When a snake was collected, a one-meter-square area was marked around the collecting site. This area was evaluated as to percent type cover for the following five categories: no cover (bare), rock, leaf litter, herbaceous cover, and woody cover. Percent type cover was estimated for each meter-square sample.

Topographic maps were used to identify rivers, streams, creeks, and runs. The distance of each collecting site away from the nearest surface water was measured. A magnetic compass was used to determine magnetic heading of the slopes exposure (called Aspect). Altitude, relief, and angle of the slope for each site were determined from topographic maps.

Soil samples were taken for 64 different collections and included all localities where the author has found Virginia valeriae pulchra. Small bottles (Volume=200ml) held surface soil samples dug from the exact spot where the snake lay. These bottles were sealed and returned to the laboratory. Here they were weighed using a Ohaus Dial-0-Gram balance accurate to ± 0.01 grams. After weighing, samples were dried for two days at 110°C and reweighed. The weight lost divided by the original weight times 100 represented the percent water in the original sample. These dried soil samples were further processed by passing them through a 2.0mm sieve which separated the gravel from the soil. The texture of this sample was tested using

the mechanical analysis method of LaMotte Chemical Company, Chestertown, Maryland. Classification of soil types followed the set standards in Johnson (1975).

Ninety-nine percent of the snakes (n=401) in this study were found under fine sandstone rocks of various sizes. This is the predominant cover in the habitat for Virginia valeriae pulchra. Every time a snake was found under one of these rocks dimensions in centimeters were measured.

Relative humidities were taken with an Atkins Model 3F01-F46 hygrometer. The humidity was taken where the snake was found. If the snake was found under an object, the object was lifted and the hygrometer barrel positioned underneath. The object was replaced and the dry bulb-wet bulb measurements recorded after a 3-5 minute wait. Relative humidities were determined using the Psychrometric Tables of Marvin (1941).

Color and Morphology

Studies in this category included (1) color, (2) size, (3) body proportions, (4) body scale counts, (5) degree of keeling in the dorsal scales, and (6) head scutes. Color was determined using the standard color keys of Smithe (1975). Size was measured in snout-vent length, total length, and body weight. All lengths are in millimeters and all weights are in grams.

Body proportions included (1) tail length as a percent of total length, and (2) head width as a percent of snout-vent length. Tail

length was measured following the method of Peters (1964). Head width was measured following the method of Clark (1970). Head widths were measured using a Finescale magnifying comparator accurate to 0.1mm.

Body scale counts studied were: (1) number of dorsal scale rows, (2) number of subcaudal scales, and (3) number of ventral scales. Ventral scales were counted following the proposed method of Schmidt and Davis (1941). Subcaudal scales were counted following the method of Peters (1964). A Bausch and Lomb (10x ocular with 1-3 zoom) binocular microscope was used in counting all scales.

Dorsal scales were determined to be either smooth or keeled. This was done for three separate regions of the body, that is, the anterior (one head length behind the occiput), midbody (midpoint between the occiput and the anal plate), and posterior (one head length cranial to the anal plate) regions.

Head scutes studied were: (1) number of supralabial scales (left and right), (2) number of infralabial scales (left and right), and (3) number of postocular scales (left and right). The relative positioning of the temporal and postocular scales was recorded.

V. v. pulchra was compared with V. v. elegans and V. v. valeriae for the above criteria.

Diet

Stomach analyses were conducted on 215 preserved specimens (112 males; 103 females). These snakes were preserved in the field immediately after collection by a intraperitoneal injection of 10% buffered

formalin. Identification and frequency of occurrence of earthworms in the stomach, including unidentified fecal matter, were recorded in the laboratory. The work of Reynolds (1977) was used to identify ingested earthworms. The majority of earthworms were digested beyond identification. However, those identifiable were recorded by the author and verified by Dr. John W. Reynolds of the Department of Forest Resources, University of New Brunswick, Fredericton, New Brunswick.

Comparative feeding studies were conducted for 35 non-gravid and 14 gravid females in the laboratory. A clean 25cm long by 15cm wide by 19cm deep aquarium was used to hold the snakes. This aquarium was cleaned before each test and individuals were given a 15-minute adjustment period before testing. After this period, a small earthworm was placed in the middle of the aquarium. The test ran 30 minutes per individual. Snakes used in this experiment were not fed for one week before each test.

Thermal Preference, Moisture Selection, and Burrowing Activity

Thermal records for Virginia valeriae pulchra included the cloacal temperature, air temperature (one inch above ground), and substrate temperature (exact site of capture). Cloacal temperatures were taken with a Schultheis quick-recording reptile thermometer (0-50°C in 0.2° increments). Each individual was held by the tail with a hemostat to prevent hand warming the snake while the cloacal temperature (T_b) was being measured. The bulb of the Schultheis

thermometer was completely inserted and allowed to equilibrate (approximately 20 seconds) before recording the temperature. The air and substrate temperatures were taken with a Model 46 Yellow Springs Tele-thermistor (0-51°C in increments of 0.2°C). A black bulb with shielding was used for the air temperature. The substrate temperature was taken where the snake was found. The cloacal temperature was taken immediately, while the other temperatures were recorded minutes later. The Yellow Springs Tele-thermistor was used instead of the Schultheis thermometer for substrate and air temperatures for two reasons. First, the Schultheis thermometer was too delicate for insertion beneath rocks and secondly, the Yellow Springs thermistor air probe was shielded on the top and sides to decrease wind effects. All temperatures were recorded only after equilibration; no significant difference existed between the two thermal methods.

Non-cloacal water loss was determined in Virginia valeriae pulchra by their desiccation rates. An apparatus similar to that used by Elick and Sealander (1972) was used whereby air was supplied from a main valve and passed through 1.93 kilograms of anhydrous calcium sulfate. A bleeder valve regulated this initial flow. The air flowed from the last desiccant bottle into an adjoining trap, thence to three drierite columns. The drierite columns, each 77cm long by 1.5cm in diameter, contained approximately 180 grams of drierite chips. From the last drierite column, air flowed through a 6-foot copper tube (0.7cm in diameter) submerged within a 25°C

water bath. Air proceeded from here to a glass column where a thermometer was suspended. Using a 4-way air stopcock, the air flow was apportioned through three latex tubes and directed to three separate flow meters. Air left these flow meters and entered corresponding desiccation chambers. The air flow leaving these chambers was standardized to 50ml/minute by displacing 50ml of water per minute in an inverted graduated cylinder.

Thirty-nine snakes were exposed to the above desiccation experiment. They were all tested within three days of collection and were housed in a container of 100% humidity for standardization purposes one day before testing. The cloaca for each snake was wrapped with parafilm to eliminate any cloacal discharge. These snakes were weighed on a Mettler P160N toploading balance accurate to ± 0.001 grams. After weighing, snakes were individually placed into one of the three desiccating chambers. The lids were applied and sealed air tight with a rubber gasket, petroleum gel, and a pressure clamp. The snakes were exposed to an air flow of 50 ± 10 ml per minute at $25 \pm 2^{\circ}\text{C}$ for 12 hours.

The milligrams of non-cloacal water lost per gram body weight per hour were recorded and plotted against the surface area (cm^2) for each snake tested. The surface area was determined by inserting the body weight of the snake into the following equation developed by Elick and Sealander (1972) for Virginia valeriae: Surface area = $9.8 \times \text{Body Wt.}^{0.76}$.

Burrowing experiments in the laboratory were designed to observe

tunneling (if any) in V. v. pulchra. A terrarium 61cm long by 3cm wide by 61cm deep was used. Peat humus soil was added to a depth of 29cm. Snakes were added to the terrarium and observed through the glass for burrowing activities. The width of the terrarium was such that any burrowing activities beneath the surface could be observed. Snakes were tested under dry and wet conditions. No surface cover was made available to the snakes.

Time of Appearance

The following data were compiled for time of appearance in V. v. pulchra: date, time of day, air temperature one inch above substrate (Ta), ground temperature (Tg), substrate temperature (Ts), and number of hours in the field. Ground temperature was taken one inch below where the snake lay. For comparative purposes, the occurrence of snakes other than V. v. pulchra also were recorded.

Climatological information was also considered important. This included (1) cloud cover, (2) rainfall, (3) recent weather, (4) weather at the time of capture, (5) atmospheric humidities at the time of capture. Rainfall and daily temperatures were recorded using data from the National Weather Service Stations in Emporium and Warren Pennsylvania. These two areas were the best collecting localities for V. v. pulchra.

Twenty-four hour studies were completed in the field to determine activity patterns for V. v. pulchra. These studies were conducted during July, August and September, 1980 and April, May, June, and

July, 1981. Each 24-hour study included six collecting periods. The time periods per day were as follows: 1200-1300 hours, 1600-1700 hours, 2000-2100 hours, 2400-0100 hours, 0400-0500 hours, and 0800-0900 hours. All 24-hour studies were completed in the Warren area, except in July of 1980, which utilized the Sizerville area. Each collecting period entailed searching for V. v. pulchra for one hour. All types of cover were inspected. After an individual was captured and its ecritic temperature recorded, it was marked using different colored oil base paints. This marking technique was adequate for daily identification and lasted, at least in one case, one month. Records were also kept as to the sex and specific location of each snake. A six volt headlamp was used during night hours.

Reproductive Biology

Male and female reproductive cycles in V. v. pulchra were studied using 135 males and 115 females.

Male snakes were evaluated for (1) sexual maturity, (2) seasonal development of the testes, and (3) spermatogenic cycle. Sexual maturity was indicated by convolutions of, and presence of spermatozoa in the vasa deferentia (Clark, 1964). Seasonal development of the testes was analyzed for mature males only. This was accomplished by (1) the average length plus width for the right testes per month (Bradford, 1973), (2) average mean diameter of the seminiferous tubules in the right testes per month (Bradford, 1973), and (3) the right testes length divided by the specimens snout-vent length plotted

per month (Clark, 1964). Testis lengths were measured using drafting dividers. Seminiferous tubules were measured using an ocular micrometer. Diameters were converted to millimeters. The stages of the spermatogenic cycle were determined by the seasonal appearance and predominance of different cell types in the seminiferous tubules.

Females were evaluated for (1) sexual maturity, (2) ovarian follicular maturation, (3) period of ovulation, (4) duration of gestation, (5) parturition dates, and (6) litter sizes. Sexual maturity was determined using the criteria of Clark (1964). They were: (1) oviducal eggs or embryos, and (2) spermatozoa in the oviducts. Ovarian follicular studies followed the methods of Betz (1963) and Pisani (1967). Period of ovulation included the appearance of Graffian follicles, while the gestational period was defined as the time interval from the earliest date of ovulation to the earliest date of parturition. Parturition dates and litter sizes were recorded as they occurred for 205 young born to 34 gravid females in the laboratory. Young were sexed by applying pressure to the tail. A Bausch and Lomb (10x ocular with 1-3 zoom) binocular microscope was used to observe the hemipenes.

The testes and oviducts were studied under greater magnification (100-1000X). They were fixed in 10% buffered formalin and all tissues were processed following the methods of Sheehan and Hrapchak (1980). Tissues were stained in Harris hemotoxylin and 1% eosin and sectioned at 5 micra.

Cloacal smears were taken in the field in the Fall of 1981.

Amphibian Ringer's Solution (100ml 0.7 & NaCl: 1ml 1%CaCl₂: 0.75ml 1% KCl: 1ml 1.9% NaHCO₃) was flushed into the cloaca of the female, extruded, and placed into a hanging drop slide. These slides were inspected for motile sperm in the field using a Bausch and Lomb light microscope (100X). The light microscope illuminator was powered by a Micronta 12 volt DC to 120 volt AC (100 watts) Power Inverter, run off the car battery.

Fat bodies from the abdomen of 85 adult males and 51 adult females were weighed on a Mettler type H6T digital capacity analytical balance accurate to ± 0.05 milligrams. These weights were divided by each snake's body weight and to obtain percent of fat in total body weight. Body weights were taken prior to fat removal and were measured on a Mettler P160N toploading Balance accurate to ± 0.001 grams. Fat weights as percent of total body weight were averaged and compared per month for both sexes.

Population Structure

Age classes were determined by plotting snout-vent length for each snake against date collected (Bradford, 1973; Jackson and Franz, 1981; Quinn, 1979). Four hundred and seventy-two snakes, 218 males and 254 females, were plotted. Growth rates were determined for males and females by averaging the snout-vent length for each age class. This is an acceptable method when growth rates are significant, but when growth rates approach zero, age classes overlap and are indistinguishable.

Competitors, Predators, and Defense Mechanisms

Predation and defense mechanisms in Virginia valeriae pulchra were observed. Predation was demonstrated in the laboratory while defense mechanisms were observed in both the field and laboratory. Competition for space and food were deduced from the habits of those snakes that co-exist with Virginia valeriae pulchra in nature.

OBSERVATIONSRange

The ranges of the three subspecies of Virginia valeriae are shown in Figure 1 (Conant, 1975). Figure 2 shows specific localities for all known specimens of V. v. pulchra. It also includes the westernmost records for V. v. valeriae in Pennsylvania, West Virginia, and Maryland (Atkinson, 1901; McCauley, 1945).

Intergradation has been suggested by Richmond (1954) for the southern Pennsylvania population of V. v. pulchra and the Maryland V. v. valeriae on the basis of one V. v. pulchra specimen (CM 26133) with dorsal scales in 15-15-15 rows with keels throughout. I have found atypical dorsal scale patterns in V. v. pulchra throughout its range and find no indication of intergradation today in southwestern Pennsylvania or Maryland (Swallow Falls State Park) V. v. pulchra with West Virginia (Mineral County) or Maryland V. v. valeriae. Intergradation, if it occurs, should be sought in the northeast sector of West Virginia from Romney to Spruce Knob along the Potomac River. The Spruce Knob V. v. pulchra population may be moving north along the Potomac River and entering the range of V. v. valeriae in northeastern West Virginia as indicated by specimen CM 23795 and possibly LWW 201 (Wilson and Friddle, 1950). Specimens CM 23795 and CM 23794 (V. v. valeriae) were collected along the Potomac River near Romney, West Virginia. Specimen LWW 201 was collected in Grant County, West Virginia. This specimen from Grant County has not been examined by

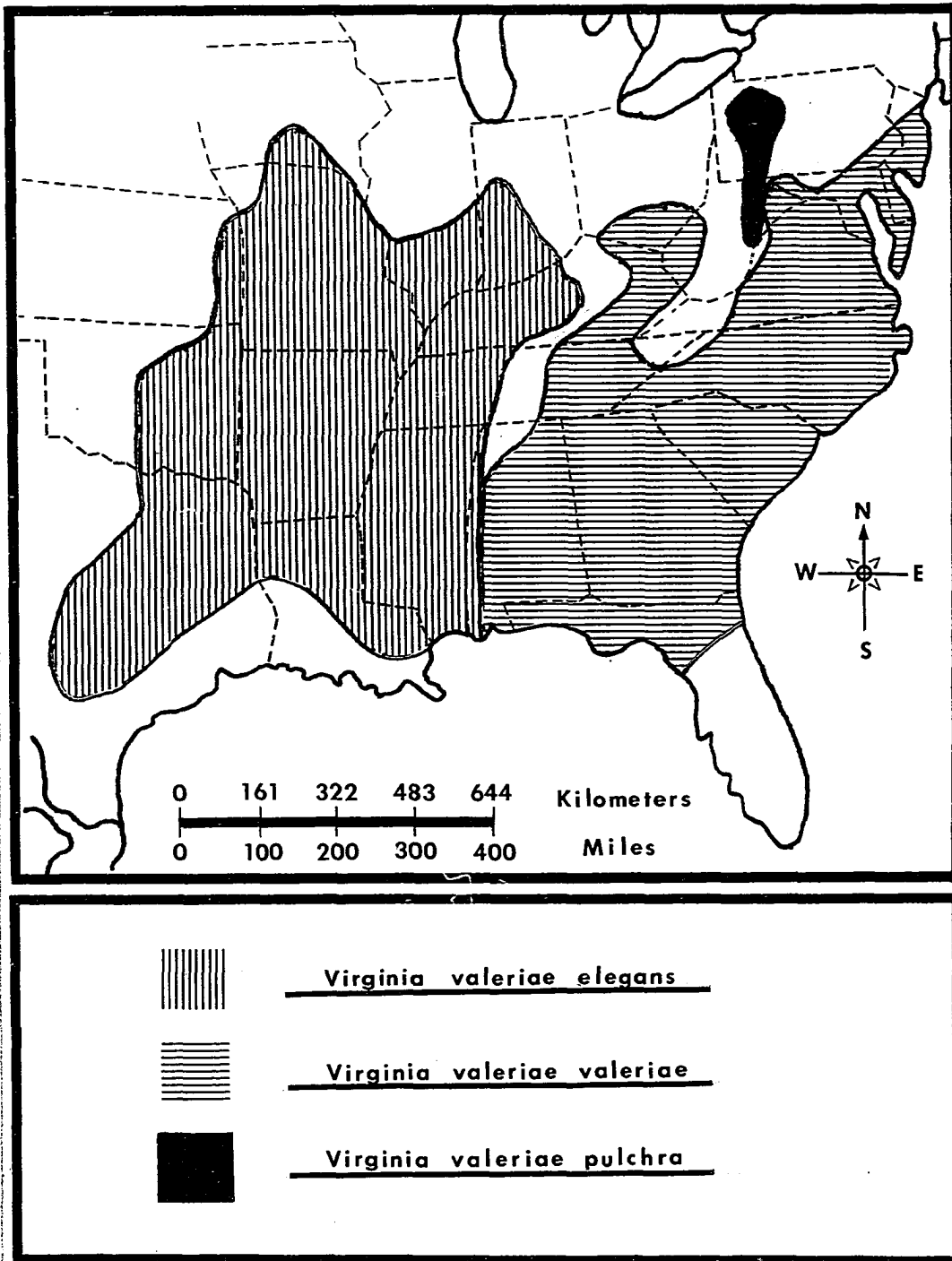


Figure 1. The known ranges for the three subspecies of *Virginia valeriae*.

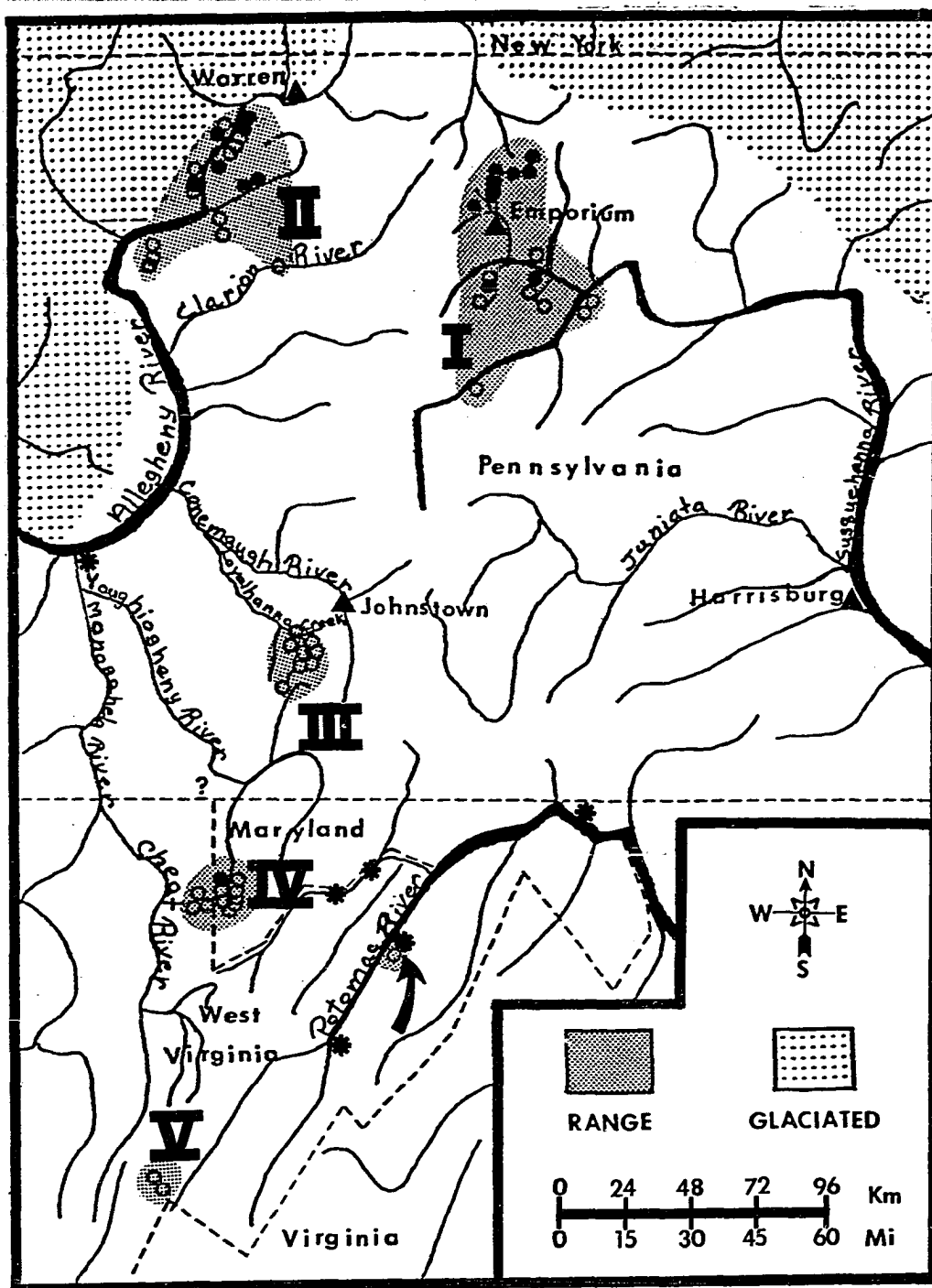


Figure 2. The geographic distribution of *V. v. pulchra*. Solid circles represent author's collecting sites; empty circles, other locality records. Arrow denotes *V. v. pulchra* and *V. v. valeriae* collected at the same locality (Romney, W.V.); triangles represent cities. Roman numerals refer to study areas defined in the discussion section.

the author; however, Wilson and Friddle (1950) report it having 17 scale rows. Specimen LWW 201 has not been plotted in Figure 2 due to its unspecified locality (See Appendix I for identification of repository for these specimens).

V. v. pulchra is confined to the unglaciated Allegheny Plateau (Fenneman, 1938; Thornbury, 1965) and shows a disjunct distribution within its range (Figure 2). The distribution appears correlated with tributaries of the Allegheny and Susquehanna Rivers. All records for V. v. pulchra demonstrate that it resides solely in unglaciated areas.

Soil studies indicate that V. v. pulchra may be found on a variety of soil types ranging from loamy sand to clay type soils. The majority (93.7%) of the snakes have been found on loamy sand to sandy clay loam type soils (n=64). Sandy to loamy type soils appear to be an influencing factor in their distribution along with wooded areas and their proximity to major drainages. Further discussion of soil types is contained in the habitat section.

The Environmental Tolerance Index (ETI), first defined by Bleakney in 1958, is determined by multiplying the number of days of the year when temperatures are above 42°F (= Growing Season) by the mean July temperature (in °F). The quotient is divided by 1000. Using climatological information by Morey (1931), the ETI for V. v. pulchra was found to range from 8.1 to 9.9 with a mean of 9.1. This index may be found throughout the range of V. v. pulchra in Pennsylvania except in the middle section of the Allegheny High Plateau (Hough and Forbes, 1943) which includes northern Potter, eastern

McKean, western Elk, and north-central Jefferson counties. In this area where V. v. pulchra has not been recorded, the ETI ranges from 5.9 to 7.5. The author believes that this area is too cool and the growing season too short to sustain healthy populations of this snake. This geographic hiatus between V. v. pulchra in northwestern Pennsylvania and those in southwestern Pennsylvania is believed to be real. Butler, Clarion, Armstrong, Jefferson, Indiana, and Cambria counties are included within this hiatus. An examination of the composite range of the three subspecies of Virginia valeriae shows several areas where they do not occur (Figure 1). These areas appear to be occupied by calcareous (limy) soils (Baker, 1936). Another important factor influencing their present distribution appears to be the availability of rock cover. My experience in collecting in the hiatus of Pennsylvania is that sandstone rocks are few. Where such rocks occur, talus slopes of shale predominate making the slope unstable. In most of these instances, these areas were overgrown with thick vegetation. Collecting records from southern Pennsylvania support the fact that few sandstone rocks are available to these snakes. Of the five recorded habitat descriptions for southern Pennsylvania V. v. pulchra specimens, only one was found under a rock. The others were found under man-made items.

Habitat

The vast majority of V. v. pulchra specimens have come from three collecting localities in northwestern Pennsylvania. They are

Locality 1: Sizerville State Park; Locality 2: Slabtown Hollow Field; and Locality 3: Warren. These are shown as typical of the habitat of V. v. pulchra (Figures 3, 4, 5).

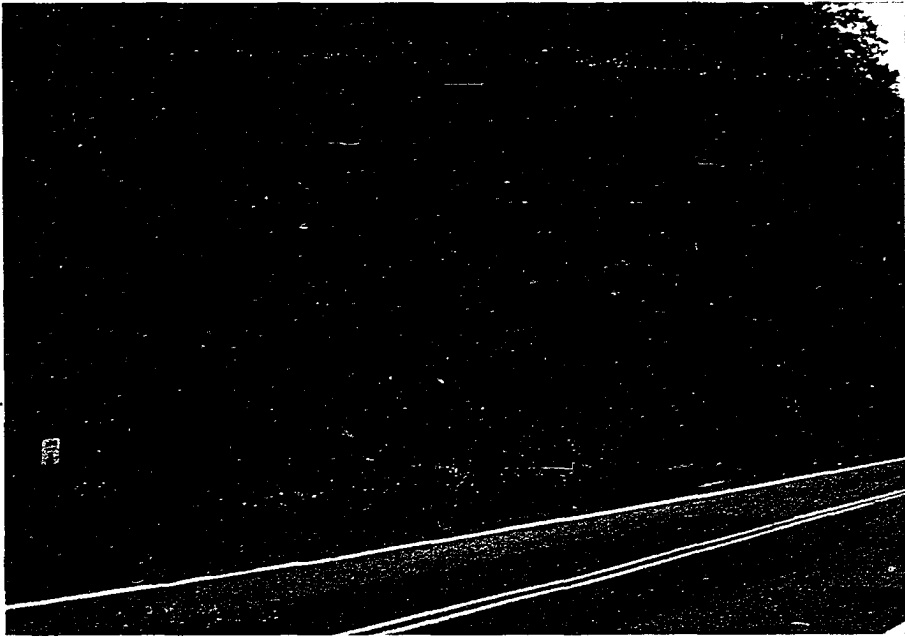


Figure 3. Photograph showing the habitat of Virginia valeriae pulchra across from the Sizerville State Park in Potter County (Portage Township, 8 miles NE of Emporium), Pennsylvania.

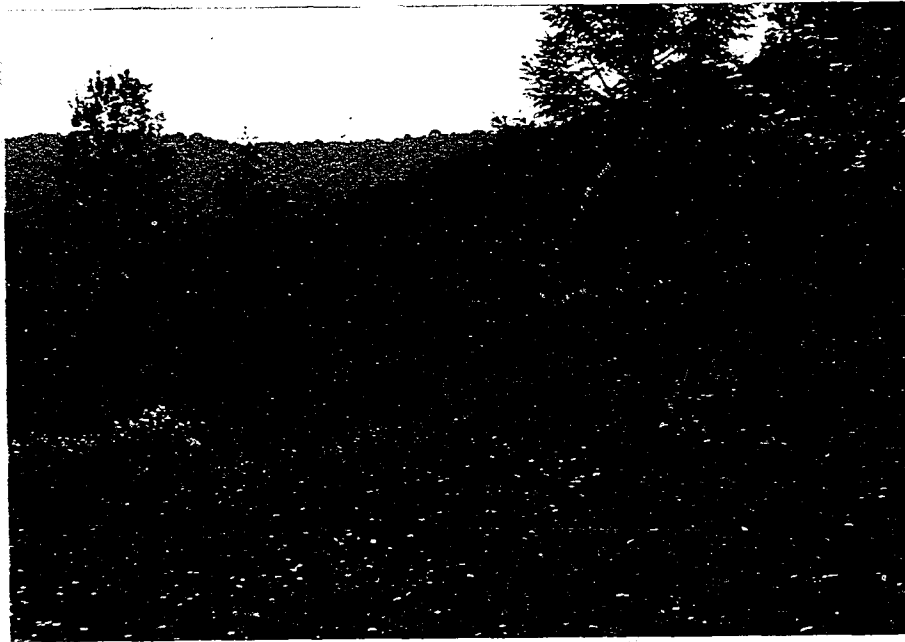


Figure 4. Photograph showing the habitat of Virginia valeriae pulchra at the Slabtown Hollow field in Potter County (Portage Township, 3.5 miles S of Keating Summit), Pennsylvania.

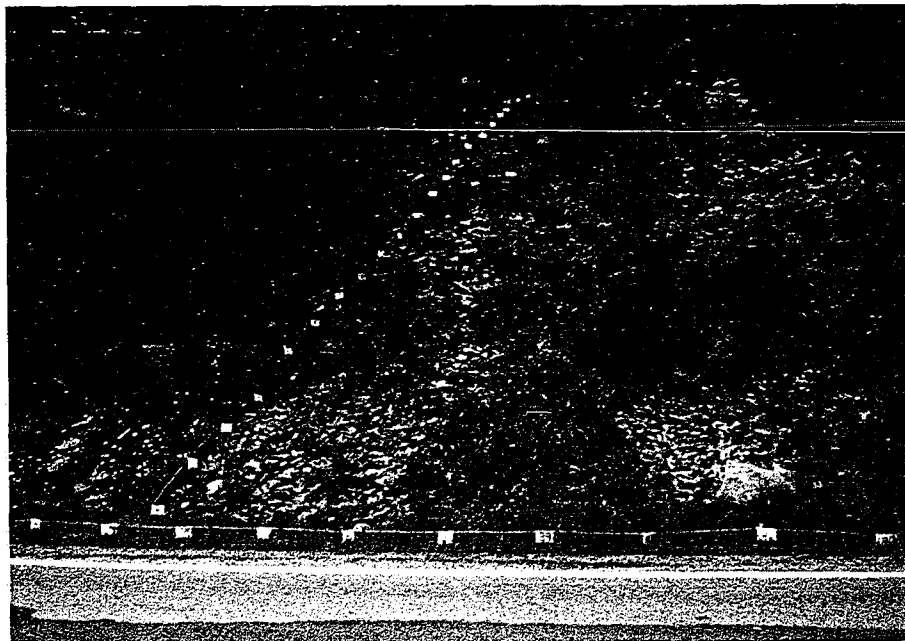


Figure 5. Photograph showing the habitat of Virginia valeriae pulchra across from Thompson Island in Warren County (Pleasant Township, 8 miles SW of Warren), Pennsylvania.

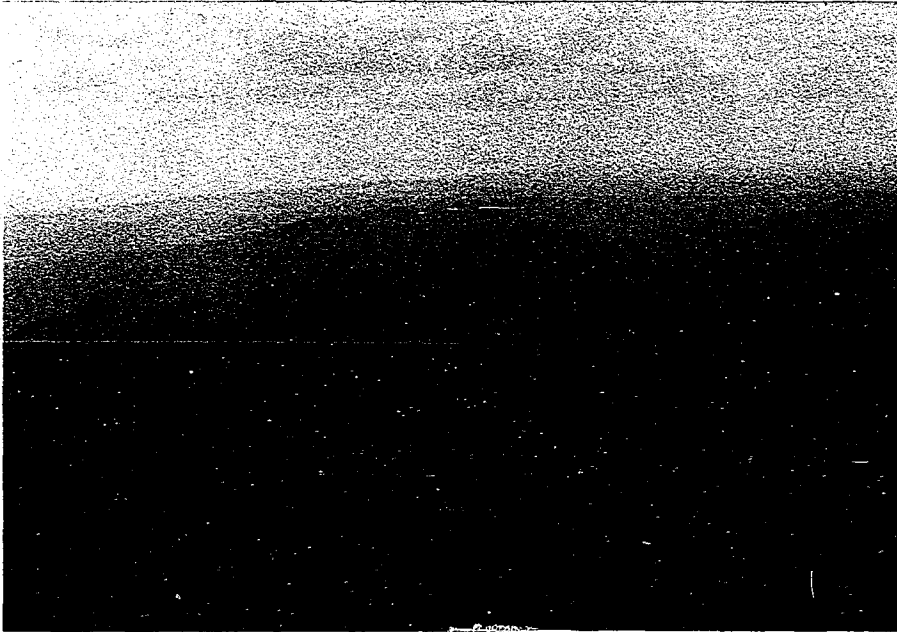


Figure 6. Photograph showing the topography of the Allegheny High Plateau near Emporium, Pennsylvania.

The topography within the range of Virginia valeriae pulchra is that of a maturely dissected Cretaceous peneplain (Figure 6). Nineteen collecting areas within northwestern Pennsylvania record altitudes from 274 to 1183 meters above sea level. The relief ranged from 0 to 34 meters above valley floor.

The slope angle for Virginia valeriae pulchra collecting sites is flat to moderate ranging from 0 to 30 degrees (Mean = 13.6). The direction the slope faces is referred to as aspect by foresters (Braun, 1950), and was determined for a total of 560 individuals captured. The percentage of the total number of snakes collected from different aspects is shown in Figure 7. Virginia valeriae pulchra

avoids north facing slopes.

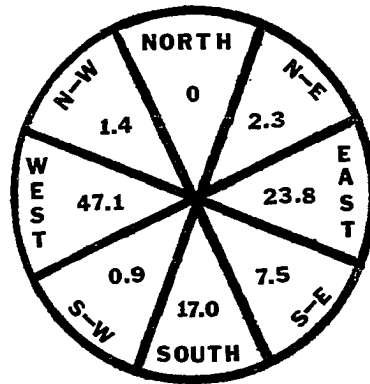


Figure 7. Percentage of the total number of Virginia valeriae pulchra collected from different aspects (N = 560).

Distance from permanent surface water was measured for a total of 346 snakes and was plotted on semi-log paper (Figure 8). The results indicate that the number of snakes collected decreases with distance from permanent water. However, no significant correlations appeared between distance from permanent water and either relative humidity of microhabitat or percent moisture (by weight) of soil at point of capture. The distance of these collecting sites for Virginia valeriae pulchra were in all cases within 15 meters from the forest edge.

The soil composition for 16 collecting localities characterizes the soil in the northern areas of the range of Virginia valeriae

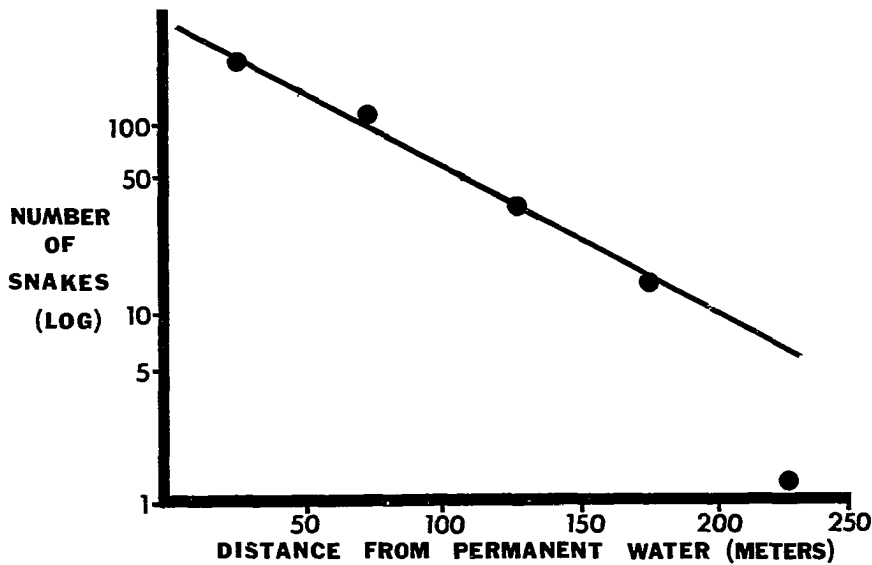


Figure 8. Semi-log graph plotting the number of snakes collected against distance from permanent water ($r = -0.987$; $N = 346$)

pulchra, where all but one of the specimens were collected. Within these areas, 64 soil samples were taken. Each sample was drawn from the exact site where a specimen was discovered. The soil texture of the samples varied from clay to loamy sand (Figure 9). However, using the criteria of Johnson (1975), 95.3% (61 of 64) can be classified as sandy or loamy. Such samples are characterized as being well- to very well drained soils (Goodman, 1958).

The soil moisture content was determined for these 16 collecting localities. Seventy-six sites were evaluated. The percentage water (by weight) of the soils ranged from 3.2 to 30.3 with a mean of 10.6. This level of soil moisture is compatible with the soil type (well to moderately well drained).

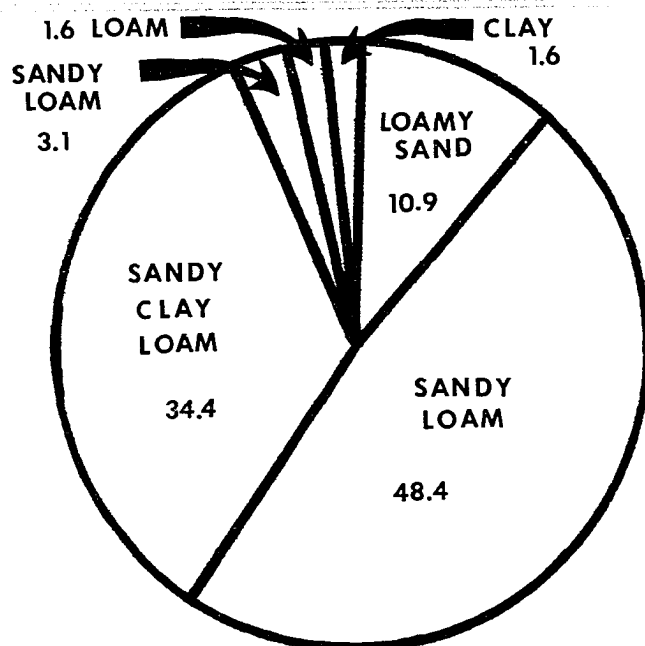


Figure 9. Percent of the total number of soil samples from collecting sites of Virginia valerianae pulchra, falling into the various soil texture classes of Johnson (1975). N = 64.

The microhabitat of Virginia valerianae pulchra is under fine sandstone rocks of various sizes. Of a total of 519 specimens recorded during this study, only three of these were discovered in the open; one was on top of some leaf litter and the other 2 were road kills. The 516 remaining specimens were concealed beneath the following: rocks, 506; leaf litter, 5; piece of sheet metal, 3; board, 1; and a piece of auto tire, 1.

The size of these rocks were evaluated since they represent the overwhelmingly selected type of cover (98.1%). A total of 354 rocks were measured for surface area, thickness, and volume. Rock area ranged from 6.3 to 4,337.1 square centimeters with a mean of 528.2 square centimeters; rock thickness ranged from 0.6 to 25.4 centimeters

with a mean of 3.6 centimeters; and rock volume ranged from 6.3 to 28,434.5 cubic centimeters with a mean of 2,031.7 cubic centimeters.

The V. v. pulchra specimens were divided into the following categories to determine if there existed any differences among them regarding microhabitat selection: gravid females, non-gravid females, adult males, immature females, and immature males. The gravid females demonstrated a preference for larger rocks than the other four categories combined. Since live gravid females can only be recognized as gravid from June through September, the following comparisons apply only for June, July, August, and September. The gravid females prefer thicker rocks ($t = 3.16$; $df = 205$; $p < .01$), rocks with greater surface area ($t = 2.20$; $df = 212$; $p < .05$), and rocks with greater volume ($t = 2.83$; $df = 205$; $p < .01$) than the other four categories combined for the months of June, July, August, and September. In order to explain this selective difference, the relative humidity and soil moisture under rocks chosen by gravid females were compared with those chosen by the other categories. No significant differences were found. Thermal considerations were suspected as the causal agent, thus an evaluation of the thermal measurements under these rocks were undertaken. No significant correlation was found between rock volume and substrate temperature (T_s).

The relative humidity under these rocks was rather high and demonstrated a range of 44% to 100% (Mean = 86.2%) for 163 snakes. No significant preferences for relative humidity among the five populational components were observed.

The immediate habitat for V. v. pulchra was described by the cover occurring within a one square meter area surrounding the site of capture. This was accomplished by estimating the percentage of the plot that contained (a) no cover (bare), (b) woody cover, (c) herbaceous cover, (d) leaf litter, and (e) rock. All months of the active season (except a single March record) are represented in these determinations. Figure 10 represents the habitat cover for 327 specimens of V. v. pulchra. It shows the habitat to be primarily short, grassy slopes strewn with many rocks and some leaf litter.

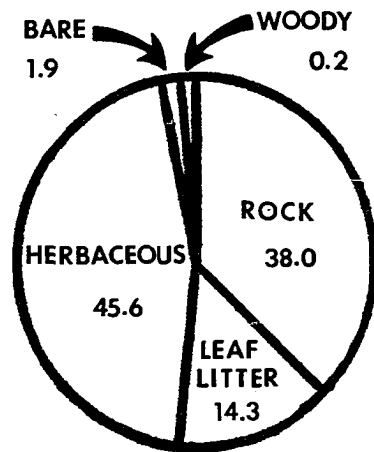


Figure 10. The average percent of various types of cover surrounding 327 separate collecting sites for Virginia valeriae pulchra.

During the course of this study, the amount of time spent collecting was recorded as were the identity and number of reptiles and amphibians found in association with Virginia valeriae pulchra.

These data give a helpful estimate of the relative abundance of these species as compared with V. v. pulchra and also yeild information on the types of animals that share its habitat. The most commonly associated forms may be divided into three groups: reptiles, amphibians, and ants (Hymenoptera; Formicidae)

| Species | Number Observed Sharing Same Rock With <u>V. v. pulchra</u> | Number Observed In Immediate Vicinity of <u>V. v. pulchra</u> |
|-------------------------------------|---|--|
| <u>Diadophis punctatus edwardsi</u> | 16 | 917 |
| <u>Virginia valeriae pulchra</u> | 24 | *605 |
| <u>Storeria occipitomaculata</u> | 10 | 360 |
| <u>Thamnophis brachystoma</u> | 6 | 190 |
| <u>Thamnophis sirtalis</u> | 3 | 122 |
| <u>Nerodia sipedon</u> | 1 (Young) | 45 |
| <u>Plethodon cinereus</u> | 0 | 37 |
| <u>Eumeces anthracinus</u> | 0 | 27 |
| <u>Storeria dekayi</u> | 1 | 15 |
| <u>Eurycea longicauda</u> | 1 | 13 |
| <u>Lampropeltis triangulum</u> | 0 | 7 |
| <u>Plethodon glutinosus</u> | 0 | 7 |
| <u>Bufo americanus</u> | 0 | 3 |
| <u>Rana palustris</u> | 0 | 1 |
| <u>Rana sylvatica</u> | 0 | 1 |
| <u>Crotalus horridus</u> | 0 | 1 |

Table 1. Numbers of specimens of Reptile and Amphibian species found sharing the same rock cover with Virginia valeriae pulchra or in the immediate vicinity of this form. * Data are for 605 separate observations of Virginia valeriae pulchra.

The reptiles and amphibians associated with V. v. pulchra are listed in Table 1. Figure 11 shows the relative abundance (by month of active season) for V. v. pulchra and its two commonest associated reptiles, i.e., Diadophis punctatus edwardsi and Storeria occipitomaculata. This figure shows that V. v. pulchra can be collected with greater ease (approximately 3 times) earlier and later in the active

season than can the other two species. All three species demonstrated a mid-summer decline in collectability.

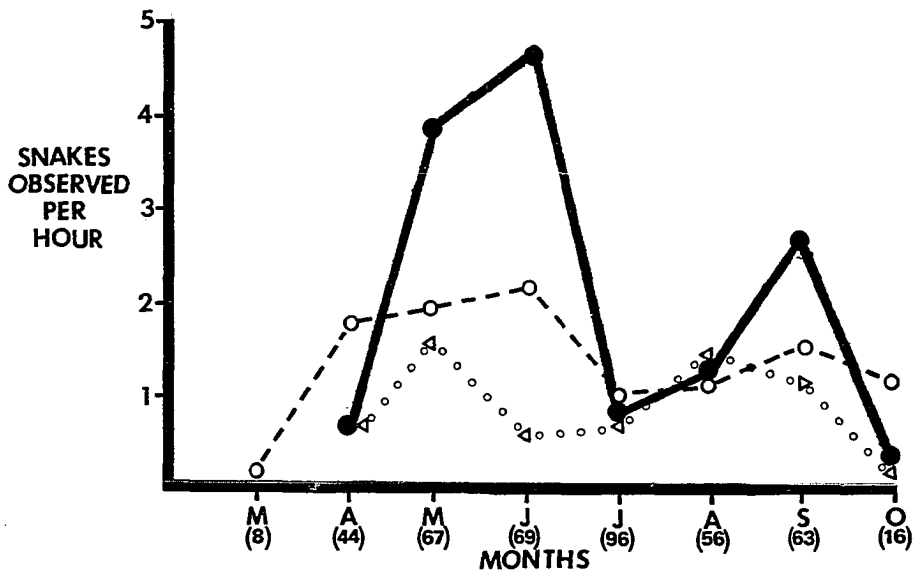


Figure 11. Number of individuals of *Virginia valeriae pulchra* (O--O), *Diadophis punctatus edwardsi* (●—●), and *Storeria occipitomaculata* (△◦◦△) observed per hour searching in *Virginia valeriae pulchra* habitat. Total collecting hours = 419. Number in parentheses indicates hours searching per month.

Ant colonies are very common throughout the range and habitat of *Virginia valeriae pulchra*. It is not surprising, therefore, to find a high correlation between signs of ant activity and the presence of this snake. The question arises; however, of whether it is also the result of some additional phenomenon, viz. a biological interaction. Since this relationship did not become apparent until well into this study, it was necessary to return and reassess all collecting areas and sites where *Virginia valeriae pulchra* had been collected. All showed large numbers of galleries and tunnels that

emerged beneath the same type of flat rocks that are sought by V. v. pulchra. Furthermore, all additional snake specimens that were collected were found to be under rocks that also covered these tunnels or galleries. In 15 separate instances specimens of V. v. pulchra were observed to use these tunnels as a means of escape.

Of the several different types of ants associated with V. v. pulchra, one species, Formica exsectoides, is readily identifiable by both its bicolored appearance and by its very large mounds. It also is the most pugnacious local species and readily bites when disturbed. A dozen of these Formica exsectoides ants were put in a terrarium with a V. v. pulchra. The snake withdrew its head abruptly and attempted to avoid these ants when they approached it. When the ants mounted the body of the snake and began biting it, the snake violently thrashed around in an attempt to unseat them. When confronted in the laboratory with other species of ants with which it shares its habitat, the snakes were never observed to be bitten and appeared to tolerate these ants.

Field observations suggest a similar pattern - one does not find V. v. pulchra under the same rock with specimens of Formica exsectoides but it may share its habitat with other species of ants. However, V. v. pulchra will utilize tunnels or galleries of Formica exsectoides and other ants when these have been abandoned. There is a large ant mound in the Warren, Pennsylvania area that was populated by an active colony of Formica exsectoide in the first year of this study. This population had become greatly decreased by the second year and in the third year a different species of ant was occupying the mound in modest

numbers. I excavated this mound and two others in April of 1982 before the weather had warmed sufficiently for any snakes to emerge. Four hibernating V. v. pulchra were unearthed (two immature males, one immature female, and one adult male). They were still torpid and were all coiled up within ant tunnels at depths from 40 to 60 centimeters from the surface. In addition, one adult Thamnophis brachystoma and three Diadophis punctatus edwardsi (all young) were uncovered. The other two ant mounds that were excavated did not contain any snakes.

During the course of this study, I have often seen ants in areas where there were no V. v. pulchra; however, I can recall no instance of ever finding V. v. pulchra without ants and tunnels in the same site. This ant-snake relationship is interesting and merits further study.

Color and Morphology

V. v. pulchra is a diminutive colubrid snake with a small head only slightly distinct from the neck. Figure 12 depicts a typical individual. This photograph was taken by Dr. M. Graham Netting and is used with his kind permission.

(A) Color

The dorsal color for live Virginia valeriae pulchra (using Smithe, 1975) is burnt umber to smoke gray. The most common dorsal

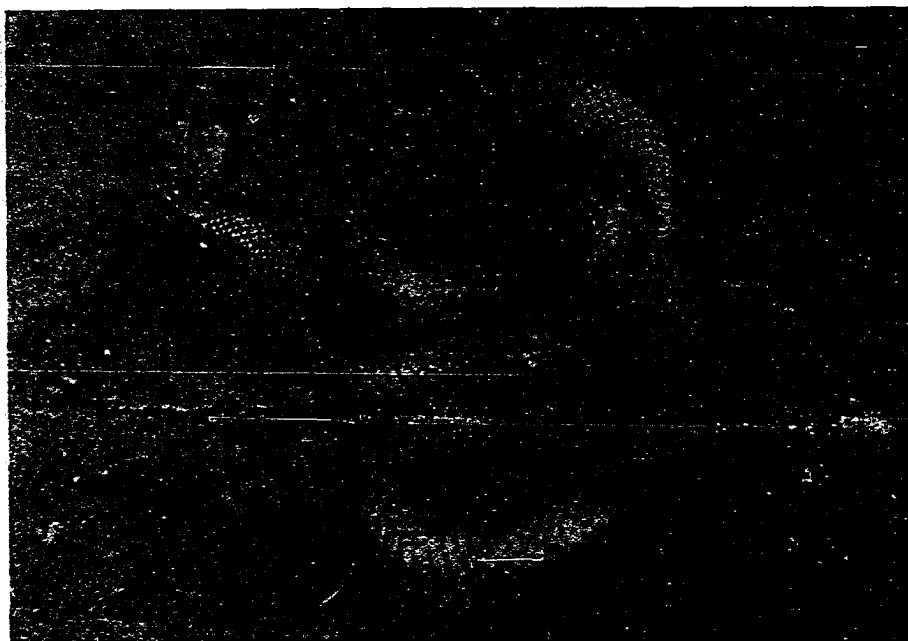


Figure 12. Photograph of a female Virginia valeriae pulchra taken by Dr. M. Graham Netting on 10 July 1965.

color is an olive-brown to fuscous brown suffused with vinaceous pink color intensifying towards the ventral plates and including the lateral ends of these. In most specimens the dorsum is also flecked with small dark spots arranged in 4 lines. These spots are almost non-existent in some specimens as seen in Figure 12. These spots usually border a tan, raw umber, or russet-orange middorsal stripe. This stripe is absent in all neonates and inconspicuous in some adults. The venter may be cream to greenish-sulfur yellow. The loreal and postocular areas of the head are rather heavily pigmented with black and present a mask-like appearance. The infralabials, supralabials, and mentum are usually immaculate white; some specimens

show a dusky stippling on the lips and chin. Neonates have a dusky brown dorsum with a buff white venter. Prior to their first molt; however, they display a dull gray color.

(B) Size and Weight

Most of the measurements of V. v. pulchra that were taken, were made by carefully stretching out the living specimen. However, some preserved specimens had to be measured for comparisons with preserved specimens of the other two subspecies. To check the amount of shrinkage due to the preserving process, I have compared both live and preserved measurements for 116 V. v. pulchra and found the decrease in snout-vent length to be $6.4 \pm 1.5\%$ after one day in 10% buffered formalin. This factor did not significantly change after a total of 43 days. The equation that may be used to convert from preserved to live snout-vent measurements ($r = 0.995$) is: Live snout-vent length = 1.064 times preserved snout-vent length in millimeters + 0.972. Museum preserved V. v. pulchra specimens were converted to their live lengths in this study. Snout-vent lengths were used rather than total body lengths because some V. v. pulchra specimens (7.1%) examined demonstrated incomplete tails.

Male Virginia valeriae pulchra ranged from 94mm to 296mm in total body length and 72mm to 237mm in snout-vent length ($n = 344$). Female Virginia valeriae pulchra range from 89mm to 338mm in total body length and 75mm to 290mm in snout-vent length ($n = 401$). Adult female Virginia valeriae pulchra were longer in total body lengths

($t = 17.2$; $df = 315$; $p < .001$) and longer in snout-vent lengths ($t = 24.3$; $df = 342$; $p < .001$) than adult male specimens. However, female neonates did not significantly differ from neonate males in snout-vent lengths, but were shorter in total body lengths ($t = 4.59$; $df = 265$; $p < .001$).

Body weights for live V. v. pulchra ranged from 0.54 grams to 12.77 grams ($n = 274$). Males and females at birth demonstrated no significant difference for live body weights (Males: $n = 104$; Range = 0.54 grams to 0.91 grams; Females : $n = 99$; Range = 0.57 grams to 0.94 grams) while adult males and females demonstrated similar growth-weight relations. The growth-weight equation for males ($n = 38$; $r = 0.985$) was : Log weight in grams = 2.52 times log live snout-vent length in millimeters - 5.11; Females ($n = 23$; $r = 0.995$): Log weight in grams = 2.62 times log live snout-vent length in millimeters - 5.29. Post-ovulatory and post-partum females were not included in the above growth-weight relations. These two groups were excluded because of their reproductive condition which produced (for their size) above or below average ("normal") weights.

(C) Body Proportions

Male Virginia valeriae pulchra ranged from 17.5% to 24.2% (Mean = 20.1%; SD = 1.0) in tail length expressed as a percentage of total length ($n = 327$). Female Virginia valeriae pulchra ranged from 12.2% to 18.5% (Mean = 15.9%; SD = 0.94) in tail length expressed as a

percentage of total body length ($n = 383$). Adult female Virginia valeriae pulchra demonstrated shorter tail lengths expressed as a percentage of total body length than did adult male specimens ($t = 45.9$; $df = 315$; $p < .001$). Female neonates also showed shorter tail lengths expressed as a percentage of total body length than did male neonates ($t = 30.3$; $df = 265$; $p < .001$).

Head widths were taken for 50 Virginia valeriae pulchra and was expressed as a percentage of snout-vent length. It was measured along the posterior suture of the parietal plates (the widest part of the head). Figure 13 shows head width expressed as a percentage of snout-vent length for Virginia valeriae pulchra. No difference between males or females appears for this trait. However, the young showed higher percents in both cases than do the adults.

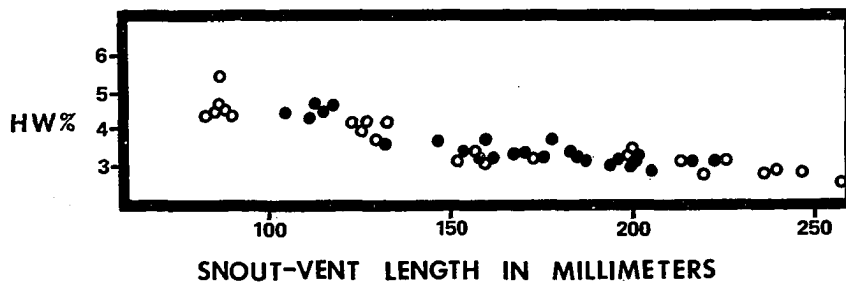


Figure 13. Head width relative to snout-vent length for 50 Virginia valeriae pulchra. Solid circles - males; Open circles - females. HW% = Head width in millimeters divided by snout-vent length in millimeters multiplied by 100. Snakes were chosen at random.

D. Body Scales

Male Virginia valeriae pulchra specimens ranged from 107 to 125 ventral plates ($n = 173$; Mean = 118.1) and 39 to 47 subcaudal scales

(n = 158; Mean = 41.8). Females ranged from 112 to 133 ventral plates (n = 179; Mean = 122.6) and 29 to 37 subcaudal scales (n = 170; Mean = 33.2). The males have significantly fewer ventral plates (t = 14.1; df = 350; p < .001), yet a greater number of subcaudal scales (t = 44.1; df = 326; p < .001).

| <u>Dorsal Scale Pattern</u> | <u>Number Examined</u> | <u>% of Total Examined</u> |
|-----------------------------|------------------------|----------------------------|
| 17-17-17 | 7 | 2.0% |
| 16-17-17 | 9 | 2.5% |
| *15-17-17 | 281 | 79.8% |
| 14-17-17 | 1 | 0.3% |
| 15-17-16 | 17 | 4.8% |
| 15-17-15 | 32 | 9.1% |
| 15-16-17 | 1 | 0.3% |
| 15-16-16 | 1 | 0.3% |
| 15-16-15 | 2 | 0.6% |
| 15-15-15 | 1 | 0.3% |

Table 2. Summary of the dorsal scale patterns found for 352 Virginia valeriae pulchra. * denotes typical pattern.

| | <u>FEMALES</u> | | | <u>MALES</u> | | |
|------------|----------------|-----------------|------------------|----------------|-----------------|------------------|
| | <u>Typical</u> | <u>Atypical</u> | <u>%Atypical</u> | <u>Typical</u> | <u>Atypical</u> | <u>%Atypical</u> |
| Sizerville | 58 | 13 | 18.3% | 38 | 24 | 38.7% |
| Warren | 70 | 10 | 12.5% | 84 | 17 | 16.8% |
| S.Pa-Md-WV | 21 | 5 | 19.2% | 10 | 2 | 16.7% |

Table 3. Number and percent of Virginia valeriae pulchra from the 3 populations with typical (15-17-17) and atypical dorsal scale patterns. Males examined = 175; Females = 177.

The typical dorsal scale count for Virginia valeriae pulchra is 15-17-17. In 352 specimens (both sexes combined), 281 specimens (79.8%) demonstrated the typical 15-17-17 pattern while the remaining specimens demonstrated atypical combinations (Table 2). Variability

within the three previously mentioned body areas (anterior, midbody, posterior - See Material and Methods) was found to be greatest in the posterior (15.3%), less variable in the anterior (4.8%), and least variable (most stable) at the midbody (1.1%). Males in the Sizerville population showed a significantly greater percent variability from the typical pattern than do the females ($\chi^2 = 6.3$; $df = 1$; $p < .02$) and males from the other two populations ($\chi^2 = 9.5$; $df = 1$; $p < .01$). This difference was found among the 3 female populations in dorsal scale variations. Table 3 shows the number of specimens demonstrating typical and atypical dorsal scale patterns. It includes the sexes from the 3 populations of V. v. pulchra.

(E) Degree of Keeling in the Dorsal Scales

The dorsal scales of V. v. pulchra may be smooth or keeled. In 352 specimens, the dorsal scales examined within the anterior area were faintly keeled in 299 specimens (84.9%), whereas 53 specimens demonstrated smooth dorsal scales in this area. Table 4 shows the number and percent of specimens with smooth and keeled anterior dorsal scales for the male and female V. v. pulchra within the 3 populations. Females from the Sizerville population had significantly higher number with atypically smooth anterior dorsal scales than either the males from the Sizerville population ($\chi^2 = 9.7$; $df = 1$; $p < .01$) or the females from the other two populations combined ($\chi^2 = 13.1$; $df = 1$;

$p < .001$). No difference was found between females from the Warren and Southern Pennsylvania-Maryland-West Virginia populations. The dorsal scales near the midbody and posterior areas were always noticeably keeled. All dorsal scales had a terminal notch and definitive free margins. There are no apical pits.

| <u>Anterior Dorsal Scales</u> | <u>Sizerville Population</u> | | <u>Warren Population</u> | | <u>S.Pa-Md-WV Population</u> | |
|---------------------------------------|----------------------------------|------------------------|------------------------------|------------------------|----------------------------------|------------------------|
| | <u>Male N(%)</u> | <u>Female N(%)</u> | <u>Male N(%)</u> | <u>Female N(%)</u> | <u>Male N(%)</u> | <u>Female N(%)</u> |
| Keeled | 56(89.9) | 47(66.2) | 92(92.0) | 68(86.1) | 11(84.6) | 25(96.2) |
| Smooth | 7(11.1) | 24(33.8) | 8 (8.0) | 11(13.9) | 2(15.4) | 1 (3.8) |

Table 4. Number and percent of specimens with keeled and smooth anterior dorsal scales for 176 male and 176 female Virginia valeriae pulchra within the Sizerville, Warren, and S.Pa-Md-WV populations.

F. Head Scutes

Head scutes of Virginia valeriae pulchra are of the typical pattern for colubrid snakes. These have been described by Richmond (1954). I have found some variation in the number of supralabial, infralabial, and postocular scales. The typical numbers of supralabial and infralabials are 6 for each side. However, atypical supralabial and infralabial patterns were found in 9.3% (33 of 354) specimens examined (Table 5). Infralabial scales demonstrated a greater variation from the typical pattern of 6 than did the supralabials ($X^2 = 7.6$; $df = 1$; $p < .01$). No sexual or regional differences in this variation were observed in Virginia valeriae pulchra.

The typical count for postocular scales is 2 left, 2 right;

however, other patterns are not uncommon. Postocular scales usually vary from 1 to 3 per side of head and in rare instances some specimens showed 4. In one rare case, no postocular scale was found. In this case, the supraoccipital scale extended behind the eye. Table 6 shows the various postocular patterns found in 354 Virginia valeriae pulchra specimens.

| <u>Supralabial</u> | | <u>Infralabial</u> | | <u>Number of Specimens</u> |
|--------------------|--------------|--------------------|--------------|----------------------------|
| <u>Left</u> | <u>Right</u> | <u>Left</u> | <u>Right</u> | |
| 7 | 6 | 7 | 7 | 1 |
| 7 | 6 | 6 | 6 | 1 |
| 6 | 7 | 6 | 6 | 1 |
| 6 | 6 | 7 | 7 | 2 |
| 6 | 6 | 7 | 6 | 3 |
| 6 | 6 | 6 | 7 | 6 |
| *6 | 6 | *6 | 6 | 321 |
| 6 | 5 | 6 | 6 | 5 |
| 6 | 6 | 5 | 5 | 3 |
| 6 | 6 | 5 | 6 | 3 |
| 6 | 6 | 6 | 5 | 8 |

Table 5. Number of Virginia valeriae pulchra specimens demonstrating various supralabial and infralabial patterns. Total number of specimens examined = 354. * denotes typical pattern.

The postocular scales are usually in contact with the anterior temporal scale. In some specimens these two scales were separated by the interposition of the lateral edge of the parietal plate and the dorsal tip of the fifth supralabial. It was found that only 13 of 354 specimens examined (3.7%) showed this atypical separation between the postocular scale and the anterior temporal on either or both sides of the head.

| <u>Postocular Scale Pattern</u> | | <u>Number of Specimens</u> |
|---------------------------------|-------|----------------------------|
| Left | Right | |
| 1 | 0 | 1 |
| 1 | 3 | 6 |
| 2 | 1 | 12 |
| 1 | 1 | 21 |
| 1 | 2 | 22 |
| *2 | *2 | 154 |
| 2 | 3 | 56 |
| 3 | 3 | 53 |
| 3 | 2 | 23 |
| 3 | 1 | 2 |
| 3 | 4 | 2 |
| 4 | 4 | 2 |

Table 6. Number of Virginia valeriae pulchra specimens with various postocular scale patterns. Total number examined = 354. * denotes typical pattern.

(G) Morphological Comparison With The Other Two Subspecies

For purposes of comparison, the author examined 22 preserved Virginia valeriae elegans (11 males and 11 females) and 62 Virginia valeriae valeriae (30 males and 32 females) along with the previously mentioned Virginia valeriae pulchra specimens for: total length, tail length as a percentage of total length, head width as a percentage of snout-vent length, number of ventral scales, number of subcaudal scales, dorsal scale counts, degree of keeling on the dorsal scales, infralabial and supralabial counts, number of postocular scales, and finally the contact or lack of contact of the postocular scale with the anterior temporal scale.

Total lengths for male Virginia valeriae pulchra ranged from 87mm to 277mm (n = 344); Virginia valeriae elegans, 121mm to 259mm (n = 11); and Virginia valeriae valeriae, 81mm to 241mm (n = 29).

Female Virginia valeriae pulchra ranged from 83mm to 317mm (n = 401); Virginia valeriae elegans, 112mm to 317mm (n = 11); and Virginia valeriae valeriae, 85mm to 280mm (n = 31) in total length. Both sexes of Virginia valeriae pulchra attain total lengths closer to Virginia valeriae elegans than Virginia valeriae valeriae.

Tail length expressed as a percentage of total length for male Virginia valeriae pulchra ranged from 17.5% to 24.2% (n = 327; Mean = 20.1; SD = 1.0); Virginia valeriae elegans, 18.2% to 21.2% (n = 11; Mean = 19.4; SD = 0.9); and Virginia valeriae valeriae, 16.4% to 23.4% (n = 25; Mean = 18.7; SD = 1.5); Female Virginia valeriae pulchra ranged from 12.2% to 18.5% (n = 383; Mean = 15.9; SD = 0.9); Virginia valeriae elegans, 13.9% to 17.0% (n = 10; Mean = 14.9; SD = 0.9); and Virginia valeriae valeriae, 11.0% to 16.3% (n = 32; Mean = 13.6; SD = 0.9). Male Virginia valeriae pulchra have significantly longer tail lengths expressed as a percentage of total length than male Virginia valeriae valeriae ($F = 41.7$; $df = 1,350$; $p < .01$); however, no difference was found between male Virginia valeriae pulchra and Virginia valeriae elegans for this measurement. Female Virginia valeriae pulchra have significantly longer tail lengths expressed as a percentage of total length than female Virginia valeriae elegans ($F = 11.2$; $df = 1,391$; $p < .01$) and female Virginia valeriae valeriae ($F = 179.3$; $df = 1,413$; $p < .01$).

Table 7 summarizes the results for the three subspecies of Virginia valeriae for tail length expressed as a percentage of total length and provides the Coefficient of Divergence (CD) for the three

forms. The Coefficient of Divergence devised by Klauber (1943) is defined as the difference between the mean tail length (expressed as a percentage of total length) for males and the mean tail length (expressed as a percentage of total length) for females divided by half their sum. High CD values correlate well with burrowing snakes (Clark, 1966).

| | <u>MALES</u> | | <u>FEMALES</u> | | <u>CD</u> (X100) |
|-----------------------------------|--------------|-------------|----------------|-------------|---------------------|
| | <u>N</u> | <u>Mean</u> | <u>N</u> | <u>Mean</u> | |
| <u>Virginia valeriae pulchra</u> | 327 | 20.1% | 383 | 15.9% | 23.3 |
| <u>Virginia valeriae elegans</u> | 11 | 19.4% | 10 | 14.9% | 26.2 |
| <u>Virginia valeriae valeriae</u> | 25 | 18.7% | 32 | 13.6% | 31.6 |

Table 7. Comparison of the 3 subspecies of Virginia valeriae for tail length expressed as a percentage of total length. N = sample size; CD = Coefficient of Divergence.

Head width expressed as a percentage of snout-vent length is shown for Virginia valeriae pulchra in Figure 13. No difference was found among the three subspecies for this character. The young though demonstrated higher percentages than the adults in all three forms.

The number of ventral plates for male Virginia valeriae pulchra ranged from 107 to 125 (n = 173; Mean = 118.1; SD = 2.6); Virginia valeriae elegans, 115 to 124 (n = 11; Mean = 119.5; SD = 3.1); and Virginia valeriae valeriae, 112 to 121 (n = 25; Mean = 116.6; SD = 2.4). The number of ventral plates for female Virginia valeriae pulchra ranged from 112 to 133 (n = 179; Mean = 122.6; SD = 11.2); Virginia valeriae elegans, 119 to 131 (n = 10; Mean = 124.3;

SD = 10.2); and Virginia valeriae valeriae, 115 to 133 (n = 37; Mean = 122.0; SD = 11.5). Male Virginia valeriae pulchra (F = 7.3; df = 1,196; p < .05) as well as male Virginia valeriae elegans (F = 9.5; df = 1,34; p < .01) have more ventral scales than male Virginia valeriae valeriae. No significant difference between male specimens of Virginia valeriae pulchra and Virginia valeriae elegans for number of ventral scales was observed. Females of the 3 subspecies did not differ significantly among themselves for number of ventral plates. The females have significantly more ventral plates than do the males for all 3 subspecies (Virginia valeriae pulchra: t = 14.1; df = 350; p < .001; Virginia valeriae elegans: t = 3.5; df = 19; p < .01; Virginia valeriae valeriae: t = 6.9; df = 60; p < .001).

The number of subcaudal scales for male Virginia valeriae pulchra ranged from 39 to 47 (n = 158; Mean = 41.8; SD = 1.8); Virginia valeriae elegans, 37 to 40 (n = 11; Mean = 38.5; SD = 1.0); and Virginia valeriae valeriae, 30 to 40 (n = 26; Mean = 34.7; SD = 2.4) while female Virginia valeriae pulchra ranged from 29 to 37 (n = 170; Mean = 33.2; SD = 1.7); Virginia valeriae elegans, 28 to 33 (n = 9; Mean = 29.7; SD = 1.7); and Virginia valeriae valeriae, 22 to 31 (n = 32; Mean = 26.2; SD = 1.9). Both sexes of Virginia valeriae pulchra have significantly more subcaudal scales than Virginia valeriae elegans (Males: F = 32.0; df = 1,167; p < .01; Females: F = 35.0; df = 1,177; p < .01) and Virginia valeriae valeriae (Males: F = 322.1; df = 1,182; p < .01; Females: F = 433.6; df = 1,200;

$p < .01$). Male Virginia valeriae have significantly more subcaudals than female Virginia valeriae (Virginia valeriae pulchra: $t = 44.1$; $df = 326$; $p < .001$; Virginia valeriae elegans: $t = 14.5$; $df = 18$; $p < .001$; Virginia valeriae valeriae: $t = 15.1$; $df = 56$; $p < .001$).

The typical dorsal scale counts found for Virginia valeriae pulchra specimens are 15-17-17. The 21 Virginia valeriae elegans specimens examined for dorsal scale counts showed 17-17-17 ($n = 20$) dorsal scales to be the typical pattern. One specimen (CM 8301) demonstrated a 15-17-17 pattern. Dorsal scale patterns for Virginia valeriae valeriae specimens showed the 15-15-15 pattern to be the typical; however, 6.3% (4 of 63 specimens) demonstrated 15-16-15 (CM 21681), 14-15-15 (RS 230 HSH; R 219 HSH), 14-15-13 (CM 9529) counts. From the above, it appears that Virginia valeriae elegans demonstrated variations only in the anterior area, while Virginia valeriae valeriae showed variations within all three body areas (anterior, midbody, posterior). Variability for Virginia valeriae pulchra in dorsal scale counts for the 3 body areas was found to be the greatest in the posterior, less variable in the anterior, and least variable (most stable) at the midbody.

The anterior and posterior dorsal scales may be either keeled or smooth in all 3 subspecies of Virginia valeriae. The middorsal scales do not show such variation; they are always keeled in Virginia valeriae pulchra and Virginia valeriae elegans and are always smooth in Virginia valeriae valeriae. Table 8 illustrates the percentage of specimens per subspecies that show variation in anterior and posterior

dorsal scale structure.

| | Keelcd Anterior Dorsal Scales | | Keelcd Posterior Dorsal Scales | |
|-----------------------------------|--|-------|---|--------|
| | N | % | N | % |
| <u>Virginia valeriae pulchra</u> | 299 | 84.9% | 352 | 100.0% |
| <u>Virginia valeriae elegans</u> | 3 | 14.3% | 18 | 85.7% |
| <u>Virginia valeriae valeriae</u> | 3 | 4.8% | 21 | 33.3% |

Table 8. Number and percent of specimens demonstrating keeled dorsal scales for the anterior and posterior areas of the body for the three subspecies of Virginia valeriae. Total number of Virginia valeriae pulchra examined = 352; Virginia valeriae elegans = 21; and Virginia valeriae valeriae = 63.

The infralabials and supralabials typically number 6 (left), 6 (right) for the 3 subspecies of Virginia valeriae. In the Virginia valeriae pulchra examined (n = 354) the infralabial counts showed a significantly greater percent of deviation ($X^2 = 7.6$; df = 1; $p < .01$) from the norm (7.3%) than did the supralabials (2.3%). This variation was not demonstrated by either Virginia valeriae elegans or Virginia valeriae valeriae.

The typical number of postocular scales for the three subspecies of Virginia valeriae is 2 left, 2 right; however, other combinations are not uncommon. No significant differences appear among the three subspecies for this feature.

The anterior temporal scale may be either in contact with or separated from the postocular scale in all three subspecies, although in all 3 forms these two scales are normally in contact. Virginia

valeriae pulchra showed the least departure from the norm here with 13 of 354 specimens (3.7%) bearing the atypical separation of these two scales. In Virginia valeriae elegans 5 of 21 specimens (23.8%) showed this atypicality and in Virginia valeriae valeriae 10 of 37 specimens (27.0%) did likewise. Virginia valeriae pulchra demonstrated more specimens with these two scales in contact than did specimens of Virginia valeriae elegans ($X^2 = 17.8$; $df = 1$; $p < .001$) and Virginia valeriae valeriae ($X^2 = 32.6$; $df = 1$; $p < .001$). Larger numbers of specimens of Virginia valeriae elegans and Virginia valeriae valeriae would be desirable for purposes of comparison; however, the above data do suggest the Virginia valeriae pulchra shows significantly less variability for this trait than do the other two subspecies.

Diet

The only identifiable food remains ever discovered in Virginia valeriae pulchra were earthworm parts. It is reasonable, therefore, to suggest that Virginia valeriae pulchra feeds solely on earthworms. Table 9 shows the monthly frequency for male and female Virginia valeriae pulchra containing earthworms and unidentified fecal matter (UFM). The number of stomachs examined was 215 (Males: $n = 112$; Females: $n = 103$) which included all months of the active season except March.

Of the 215 stomachs examined, only 17 snakes had earthworm fragments that could be identified to genus or below. Table 10 lists

| <u>Months</u> | <u>MALES</u> | | <u>Total</u> <u>Examined</u> | <u>FEMALES</u> | | <u>Total</u> <u>Examined</u> |
|---------------|-------------------------------------|-----------------------------------|---------------------------------|-------------------------------------|-----------------------------------|---------------------------------|
| | <u>Number (%)</u> <u>c Worms</u> | <u>Number (%)</u> <u>c UFM</u> | | <u>Number (%)</u> <u>c Worms</u> | <u>Number (%)</u> <u>c UFM</u> | |
| April | 2(22.2%) | 5(55.6%) | 9 | 6(60.0%) | 7(70.0%) | 10 |
| May | 13(46.4%) | 21(75.0%) | 28 | 10(55.6%) | 14(77.8%) | 18 |
| June | 9(32.1%) | 19(67.9%) | 28 | 7(29.2%) | 13(54.2%) | 24 |
| July | 4(36.1%) | 7(63.6%) | 11 | 6(35.3%) | 10(58.8%) | 17 |
| August | 0 | 7(70.0%) | 10 | 3(37.5%) | 2(25.0%) | 8 |
| September | 7(33.3%) | 13(61.9%) | 21 | 8(36.4%) | 14(63.6%) | 22 |
| October | 4(80.0%) | 4(80.0%) | 5 | 1(25.0%) | 1(25.0%) | 4 |

Table 9. Monthly frequencies for 112 male and 103 female Virginia valeriae pulchra containing earthworms within the digestive tract.

the earthworm species found in these 17 snakes and their dates of collection. Most of the Lumbricus species could only be identified to genus. During August no remains were complete enough to allow identification to genus or species.

| <u>Date of Collection</u> | <u>Earthworm Identification</u> |
|---------------------------|---------------------------------|
| 2 April 1981 | <u>Aporrectodea turgida</u> |
| 2 April 1981 | <u>Lumbricus sp.</u> |
| 3 April 1980 | <u>Lumbricus terrestris</u> |
| 26 April 1980 | <u>Lumbricus sp.</u> |
| 30 April 1981 | <u>Dendrodrilus rubidus</u> |
| 3 May 1981 | <u>Aporrectodea tuberculata</u> |
| 25 May 1981 | <u>Aporrectodea tuberculata</u> |
| 31 May 1981 | <u>Lumbricus sp.</u> |
| 31 May 1981 | <u>Lumbricus sp.</u> |
| 4 June 1981 | <u>Lumbricus sp.</u> |
| 5 June 1981 | <u>Lumbricus sp.</u> |
| | <u>Aporrectodea tuberculata</u> |
| 7 June 1981 | <u>Lumbricus sp.</u> |
| 27 July 1981 | <u>Dendrodrilus rubidus</u> |
| 7 September 1981 | <u>Lumbricus sp.</u> |
| 9 September 1981 | <u>Lumbricus sp.</u> |
| 20 September 1981 | <u>Dendrobaena octaedra</u> |
| 20 September 1981 | <u>Dendrobaena octaedra</u> |

Table 10. Earthworms identified from the stomachs of 17 Virginia valeriae pulchra. The total number of specimens examined = 215. All earthworms other than Lumbricus were identified by Dr. John Reynolds.

Gravid Virginia valeriae pulchra were compared with non-gravid females for frequency of feeding during the time period of 31 May through to 12 September (gestation period). This was done to test the hypothesis that gravid Virginia valeriae pulchra feed less often than non-gravid ones as was shown for Thamnophis elegans atratus (Fox, 1948). Table 11 shows the frequency of earthworms and UFM found within the stomachs for 24 gravid and 41 non-gravid females collected during the gestation period. Gravid females had a significantly higher frequency of empty stomachs than did non-gravid females ($\chi^2 = 8.8$; $df = 1$; $p < .01$).

| <u>Condition of Female</u> | <u>Number (%) of Specimens with Empty Stomachs</u> | <u>Total Number of Specimens Examined</u> |
|----------------------------|--|---|
| Gravid | 16 (66.6%) | 24 |
| Non-gravid | 12 (29.3%) | 41 |

Table 11. Frequency of empty stomachs found for 24 gravid and 41 non-gravid Virginia valeriae pulchra collected during gestation (31 May to 12 September). $N = 65$.

Laboratory experiments were conducted on the feeding frequency for gravid and non-gravid females. This was done for the purpose of checking the previous field findings. Fourteen gravid and 35 non-gravid females were tested. Each individual was housed within a small terrarium for 15 minutes. After this adjustment period, the snake was presented a small earthworm and results on feeding were recorded. All individuals were tested but once and each test ran 30 minutes. Prior to testing, each snake was deprived of food for one week. All

containers used were thoroughly washed, rinsed, and dried before each test.

Laboratory results shown in Table 12 demonstrate that gravid females do indeed feed less often than non-gravid females ($X^2 = 21.1$; $df = 1$; $p < .001$). No significant difference was found for these two groups in the spring; however, a tendency was observed for the spent females in the fall to feed more often than the other females.

| Condition of Female | Number of Specimens that Fed | Number of Specimens that Didn't Feed(%) |
|---------------------|------------------------------|---|
| Gravid | 3 | 11(79.6%) |
| Non-gravid | 31 | 4(11.4%) |

Table 12. Laboratory feeding experiment comparing gravid and non-gravid Virginia valeriae pulchra for small earthworms. N = 49.

Of the 215 stomach analysed, 117 (54.4%) contained earthworms and/or UFM. This UFM is of the same nature as that of the soil ingested by these earthworms and therefore represents earthworm remains. The above percent imply that feeding in Virginia valeriae pulchra is frequent as was suggested for Virginia striatula (Clark, 1964).

Thermal Preference, Moisture Selection, and Burrowing Activity

Body (T_b) and environmental temperatures (T_a, T_s, T_g) for 268 Virginia valeriae pulchra were studied and were recorded only for those snakes greater than 145mm in snout-vent length. (The bulb of the Schultheis thermometer was too large for proper insertion into

specimens smaller than this.) Thermal data for Virginia valeriae pulchra have come solely from the northwestern Pennsylvania populations.

The ecritic temperature is defined as the mean of all the body temperatures for a particular species over a given time (Cowles and Bogert, 1944). Brattstrom (1965) defines the ecritic temperature (=mean; =preferred; =optimum) as the narrow range of temperatures at which some reptiles are found carrying on their normal activity. In practice it equals the average of all body temperatures for active snakes. The normal activity range as defined by Brattstrom (1965) is the range of body temperatures of active individuals from the voluntary minimum to the voluntary maximum.

Temperature and moisture relations are interrelated. In the past, reptilian skin was considered impermeable to water. However, more recent studies show that it is much more permeable than was once thought (Bentley and Schmidt-Nielsen, 1966; Chew and Dammann, 1961; Claussen, 1967; Dawson et al., 1966; Gans et al., 1968; Krakauer et al., 1968; Schmidt-Nielsen and Bentley, 1966; Schmidt-Nielsen and Dawson, 1964).

Water maintenance in reptiles is an extremely important process. An animal unable to regulate its metabolic water would soon die. An alternative measure would be selecting a habitat moist enough to keep water loss within tolerable limits. The rate of water loss in reptiles has been correlated with habitat selection. Laboratory studies of aquatic and burrowing snakes have shown these animals to

lose more water per unit time than terrestrial or arboreal snakes (Bogert and Cowles, 1947). Clark (1967) found burrowing snakes preferred wetter soils than non-burrowing snakes. Water loss in reptiles may be cloacal, cutaneous or respiratory.

The rates of non-cloacal water loss in thirty-nine Virginia valeriae pulchra were studied. These snakes were desiccated in an apparatus similar to that designed by Elick and Sealander (1972; See Material and Methods) for 12 hours at a 50 ml per minute air flow (less than 10% relative humidity) at $25 \pm 2^{\circ}\text{C}$. The purpose for this experiment was threefold. First was to determine the rate of non-cloacal water loss in young and adult V. v. pulchra of each sex. Second was to compare the rate of non-cloacal water loss for V. v. pulchra with all published information on its conspecifics (only V. v. elegans) and to compare it with other small secretive snakes in its range (Diadophis punctatus). A comparison was also made with known burrowing forms (Tantilla gracilis, Carphophis vermis). Finally, a comparison of soil moisture(%) information with V. v. pulchra was made with published information for the above five forms. Since the rate of water loss in a snake is related to habitat preference and burrowing (fossorial) snakes prefer wetter soils, it is expected that a less subterranean form such as V. v. pulchra would show a mean rate of non-cloacal water loss and preferred soil moisture significantly less from those of Carphophis vermis and Tantilla gracilis. Data for Carphophis vermis, Tantilla gracilis, Virginia valeriae elegans, and Diadophis

punctatus have come from Elick and Sealander (1972). Comparisons between Virginia valeriae pulchra and the four other forms for (1) non-cloacal water loss, and (2) percent soil moisture are contained in the discussion on moisture selection.

A. Thermal Preference

Body and environmental temperatures for male Virginia valeriae pulchra are shown in Table 13 and for females in Table 14. Combined male and female data are in Table 15. These tables include the field ecclitic temperature for the active season. Note how the males and females differ for ecclitic temperatures for the month of August.

| Month | High Tb | Low Tb | \bar{T}_b | \bar{T}_s | \bar{T}_a | \bar{N} |
|-----------|---------|--------|----------------|----------------|----------------|-----------|
| March | | | 16.8 | 15.8 | 14.8 | 1 |
| April | 27.8 | 8.8 | 21.5 \pm 5.6 | 18.3 \pm 4.7 | 19.6 \pm 5.4 | 16 |
| May | 28.6 | 16.6 | 23.0 \pm 3.9 | 21.4 \pm 3.8 | 22.8 \pm 4.3 | 28 |
| June | 31.0 | 19.7 | 23.4 \pm 4.0 | 22.2 \pm 3.7 | 24.7 \pm 5.4 | 13 |
| July | 32.8 | 16.4 | 25.3 \pm 3.8 | 24.7 \pm 4.2 | 24.9 \pm 6.6 | 18 |
| August | 25.8 | 19.4 | 22.8 \pm 2.3 | 22.6 \pm 1.5 | 22.3 \pm 3.0 | 13 |
| September | 30.8 | 17.4 | 24.8 \pm 3.5 | 24.4 \pm 3.5 | 23.3 \pm 3.9 | 24 |
| October | | | 20.8 | 20.7 | 21.3 | 1 |
| Total | 32.8 | 8.8 | 23.5 \pm 4.1 | 22.3 \pm 4.2 | 22.9 \pm 5.0 | 114 |

Table 13. Summary of male Virginia valeriae pulchra thermal data. Tb = body temperature, \bar{T}_b = mean body temperature, \bar{T}_s = mean substrate temperature, \bar{T}_a = mean air temperature, N = number of snakes sampled; All temperatures are expressed in degrees Centigrade and all means are listed \pm one standard deviation unit.

| Month | High Tb | Low Tb | \overline{Tb} | \overline{Ts} | \overline{Ta} | n |
|-----------|---------|--------|-----------------|-----------------|-----------------|-----|
| April | 29.2 | 8.6 | 19.9 \pm 7.0 | 18.5 \pm 6.6 | 19.4 \pm 6.4 | 20 |
| May | 31.6 | 14.2 | 23.4 \pm 4.2 | 22.8 \pm 5.1 | 22.9 \pm 5.0 | 21 |
| June | 30.2 | 17.4 | 23.0 \pm 2.9 | 22.6 \pm 3.1 | 22.8 \pm 4.9 | 25 |
| July | 33.0 | 17.2 | 24.6 \pm 4.4 | 24.1 \pm 5.4 | 23.2 \pm 6.1 | 26 |
| August | 32.2 | 18.4 | 26.4 \pm 3.9 | 25.5 \pm 4.0 | 25.0 \pm 5.7 | 40 |
| September | 32.4 | 19.4 | 25.5 \pm 3.6 | 24.5 \pm 3.3 | 24.3 \pm 4.7 | 21 |
| October | | | 17.8 | 18.2 | 21.2 | 1 |
| Total | 33.0 | 8.6 | 24.1 \pm 4.8 | 23.3 \pm 5.0 | 23.2 \pm 5.7 | 154 |

Table 14. Summary of female Virginia valeriae pulchra thermal data (See Table 13 for explanation of abbreviations).

| Month | High Tb | Low Tb | \overline{Tb} | \overline{Ts} | \overline{Ts} | n |
|-----------|---------|--------|-----------------|-----------------|-----------------|-----|
| March | | | 16.8 | 15.8 | 14.8 | 1 |
| April | 29.2 | 8.6 | 20.6 \pm 6.4 | 18.4 \pm 5.7 | 19.5 \pm 5.9 | 36 |
| May | 31.6 | 14.2 | 23.2 \pm 4.0 | 22.0 \pm 4.4 | 22.9 \pm 4.5 | 49 |
| June | 31.0 | 17.4 | 23.1 \pm 3.2 | 22.4 \pm 3.3 | 23.4 \pm 5.1 | 38 |
| July | 33.0 | 16.4 | 24.9 \pm 4.1 | 24.3 \pm 4.9 | 23.9 \pm 6.3 | 44 |
| August | 32.2 | 18.4 | 25.5 \pm 3.9 | 24.8 \pm 3.7 | 24.3 \pm 5.3 | 53 |
| September | 32.4 | 17.4 | 25.1 \pm 3.6 | 24.4 \pm 3.4 | 23.8 \pm 4.3 | 45 |
| October | 20.8 | 17.8 | 19.3 \pm 2.1 | 19.5 \pm 1.8 | 21.3 \pm 0.1 | 2 |
| Total | 33.0 | 8.6 | 23.8 \pm 4.5 | 22.9 \pm 4.7 | 23.1 \pm 5.4 | 268 |

Table 15. Summary of field thermal data for all Virginia valeriae pulchra (See Table 13 for explanation of abbreviations).

Male Virginia valeriae pulchra (n = 114) demonstrated a field Tb of $23.5 \pm 4.1^{\circ}\text{C}$ with a range of 8.8°C to 32.8°C . The Ts averaged $22.3 \pm 4.2^{\circ}\text{C}$ with a range of 9.0°C to 34.2°C . The Ta averaged $22.9 \pm 5.0^{\circ}\text{C}$ with a range of 8.6°C to 42.0°C . No significant differences were observed among the mean Tb, Ts, and Ta by month nor for the entire active season when these data were subjected to an F-test.

Female Virginia valeriae pulchra (n = 154) demonstrated a field Tb of $24.1 \pm 4.8^{\circ}\text{C}$ with a range of 8.6°C to 33.0°C . The Ts averaged $23.3 \pm 5.0^{\circ}\text{C}$ with a range of 8.6°C to 35.7°C . The Ta averaged $23.2 \pm 5.7^{\circ}\text{C}$ with a range of 8.5°C to 42.0°C . No significant differences were observed among the mean Tb, Ts, and Ta by month nor for the entire active season.

The mean Tb for male and female Virginia valeriae pulchra did not significantly differ for the entire active season. However, gravid females demonstrated a higher Tb than did the males for the month of August (F = 10.6; df = 1; p < .01). Non-gravid Virginia valeriae pulchra showed no difference from males or gravid females for body temperatures in August.

Combined male and female data (n = 268) showed a Tb of $23.8 \pm 4.5^{\circ}\text{C}$ with a range of 8.6°C to 33.0°C . The Ts averaged $22.9 \pm 4.7^{\circ}\text{C}$ with a range of 8.6°C to 35.7°C . The Ta averaged $23.1 \pm 5.4^{\circ}\text{C}$ with a range of 8.5°C to 42.0°C . Virginia valeriae pulchra demonstrated a voluntary maximum temperature of 33.0°C and a voluntary minimum temperature of 8.6°C in the field.

Figure 14 shows the relationship between Tb and Ts for 268

snakes ($r = 0.872$; $df = 266$; $p < .001$). Tb and Ta were also correlated with each other ($r = 0.716$; $df = 266$; $p < .001$); however, the Tb:Ts relationship showed a higher order of correlation than did the Tb:Ta relationship. In the Tb:Ts relationship, 76.1% of the records may be attributed to this correlation while in the Tb:Ta relationship only 51.3% of the records agree. For this reason, only the Tb:Ts relationship is shown (Figure 14).

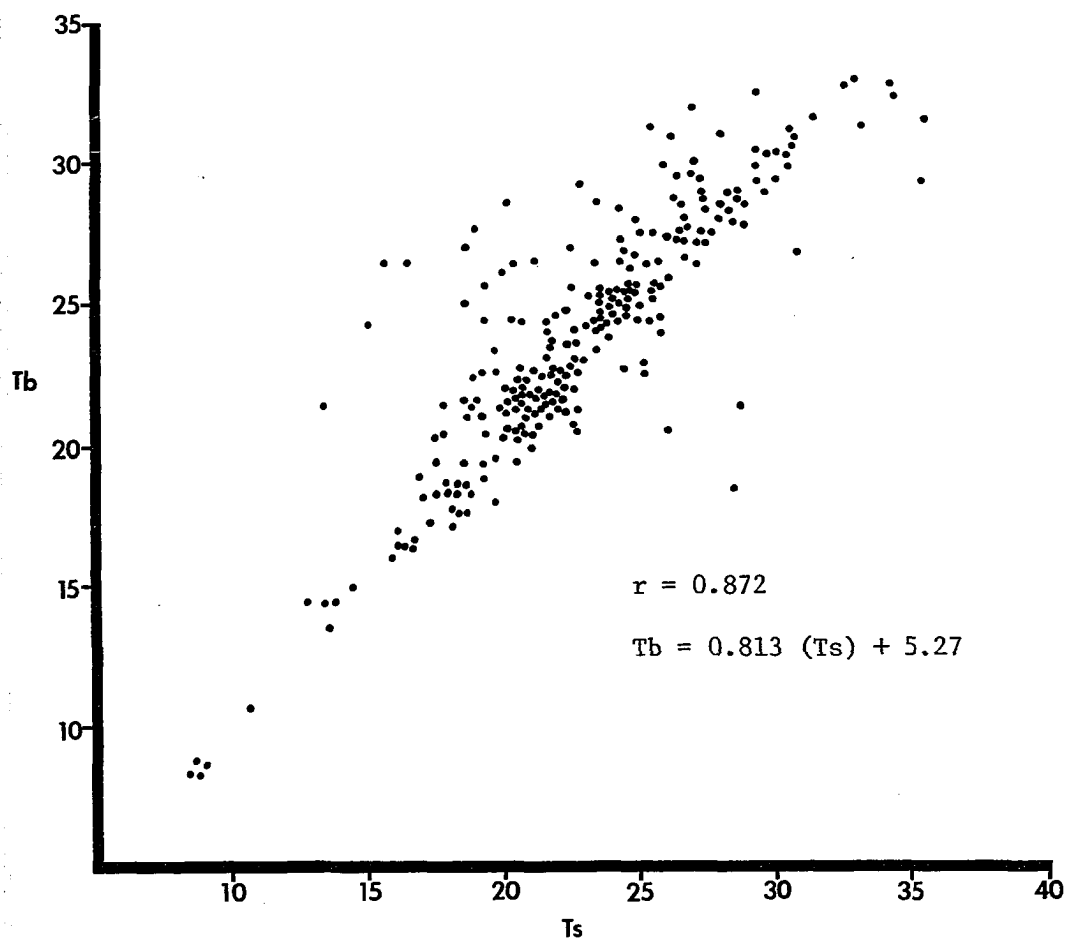


Figure 14. Relationship between Tb and Ts for 268 Virginia valeriae pulchra. All temperatures are in degrees Centigrade.

In Figure 14, 68 of the 268 records (25.4%) demonstrated Tb's that ranged from 1°C to 10.8°C higher than their associated Ts. Of these 68 records, 54 (79.4%) showed the Ta to be lower than the associated Ts. Therefore, these elevated Tb's can not be attributed to the surrounding air. Observations in the field (Table 16) suggest that when both the snakes' Tb's and the temperatures of the overlying rocks are greater than the Ts's, then the snakes are absorbing heat via direct contact with the underside of the rock. Table 16 shows the Tb, Underside rock temperature, Ts, and Ta for 8 snakes of the 68 mentioned. No difference existed between Tb and the underside rock temperature; however, the Tb was significantly higher than either the Ts ($t = 4.83$; $df = 6$; $p < .01$) or the Ta ($t = 5.00$; $df = 6$; $p < .01$).

| <u>Specimen</u> | <u>Tb</u> | <u>Underside Rock Temperature</u> | <u>Ts</u> | <u>Ta</u> |
|-----------------|-----------|---|-----------|-----------|
| TC-166 | 22.4 | 22.0 | 21.4 | 21.2 |
| TC-210 | 21.0 | 21.0 | 19.6 | 16.8 |
| TC-233 | 29.2 | 30.8 | 22.8 | 23.0 |
| TC-251 | 28.4 | 28.5 | 24.4 | 32.6 |
| TC-278 | 27.9 | 27.5 | 25.8 | 26.1 |
| TC-322 | 25.3 | 25.1 | 23.1 | 22.6 |
| TC-328 | 20.2 | 20.2 | 17.8 | 14.6 |
| TC-383 | 23.3 | 22.3 | 19.7 | 20.8 |
| Total | 24.7+3.5 | 24.7+3.9 | 21.8+2.7 | 22.2+5.5 |

Table 16. Comparison of body temperatures with rock (underside), substrate, and air temperatures for eight Virginia valeriae pulchra. Totals are in mean \pm one standard deviation unit. All temperatures are in degrees Centigrade.

B. Moisture Selection

Thirty-nine Virginia valeriae pulchra (19 males; 20 females)

were desiccated for 12 hours at 50ml/minute air flow (less than 10% relative humidity) at $25 \pm 2^{\circ}\text{C}$. Table 17 shows the rate of non-cloacal water loss per gram body weight per hour. Figure 15 shows the same data plotted against surface area. Surface area was determined using the equation for Virginia valeriae elegans as devised by Elick and Sealander (1972): Surface Area = $9.8 \times \text{Body Wt.}^{0.76}$.

Male Virginia valeriae pulchra demonstrated no significant difference in their rate of non-cloacal water loss when compared with similar sized female Virginia valeriae pulchra. However, immatures combined showed significantly higher rates of non-cloacal water loss than did adult Virginia valeriae pulchra combined ($t = 5.76$; $df = 37$; $p < .001$).

| | <u>Immatures</u> | | | <u>Adults</u> | | |
|---------|------------------|---------------|---------|---------------|---------------|---------|
| | N | Mean \pm SD | Range | N | Mean \pm SD | Range |
| Males | 8 | 4.9 \pm 1.3 | 2.8-6.3 | 11 | 3.3 \pm 0.6 | 2.9-4.4 |
| Females | 7 | 4.8 \pm 1.4 | 3.4-7.3 | 13 | 2.5 \pm 0.9 | 1.1-3.7 |
| Totals | 15 | 4.8 \pm 1.2 | 2.8-7.3 | 24 | 2.9 \pm 0.9 | 1.1-4.4 |

Table 17. Rate of non-cloacal water loss per gram body weight per hour for immature and adult Virginia valeriae pulchra. Snakes were exposed for 12 hours to a 50ml/minute air flow (less than 10% relative humidity) at $25 \pm 2^{\circ}\text{C}$. N = sample size; SD = one standard deviation unit.

Two snakes, not included in Figure 15 or Table 17 were tested while in the process of ecdysis. Each snake showed a 2 to 2.5 fold greater water loss than the average amount for a similar sized snake.

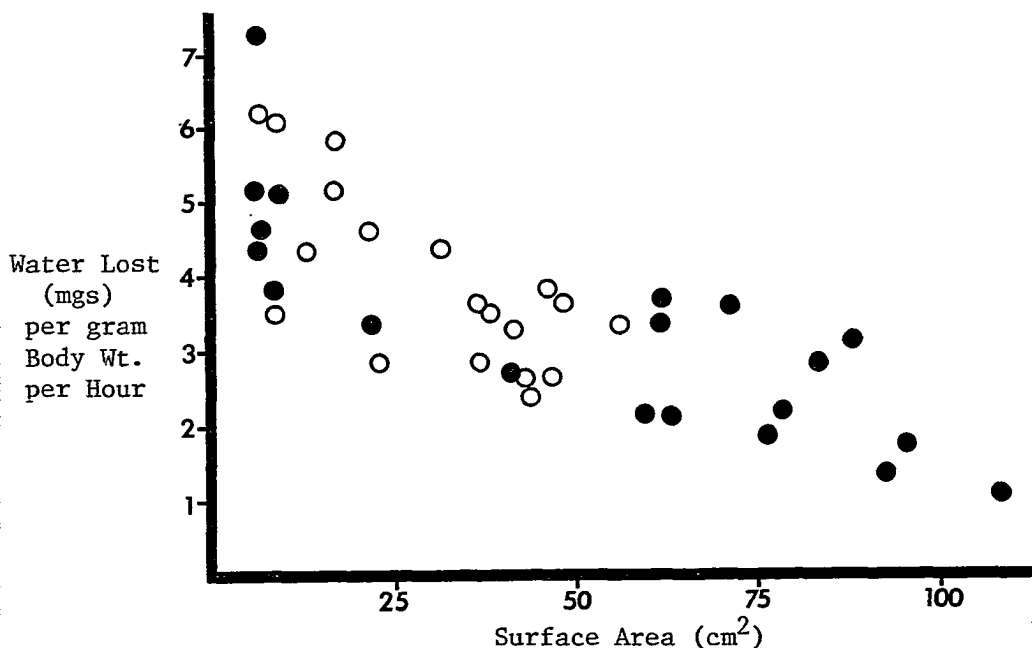


Figure 15. Relationship between water lost (milligrams) per gram body weight per hour and surface area (cm²) for 39 Virginia valeriae pulchra. Snakes were exposed for 12 hours to a 50ml/minute air flow (less than 10% relative humidity) at 25±2°C. Solid circles represent females; open circles represent males.

C. Burrowing Activity

Burrowing experiments were conducted in the laboratory (See Material and Methods). Observations showed no tendency for Virginia valeriae pulchra to tunnel even in loose potting soil. Animals were found either exposed or covered by loose soil. Those snakes that were covered simply wriggled themselves into this soil until covered.

Time of Appearance

Time of appearance refers to the specimens occurrence at the soil surface (almost invariably under rocks). The number of specimens found per hour searching was recorded. Whether this correlates with

their actual activity rhythms is unknown since telemetric methods were not used. Both seasonal and daily appearances for Virginia valeriae pulchra were studied.

A. Seasonal

The earliest spring collecting date for Virginia valeriae pulchra was 28 March. This specimen happened to be an adult male; however, no difference was found between the sexes for times of early appearance. The latest collecting date recorded in this study was 23 October 1980. However, R. C. Bothner (per. com.) found a Virginia valeriae pulchra specimen in the Warren area of Pennsylvania during the first week of November in 1967. This did not surprise him since the weather had been quite mild all that week.

The seasonal availability of Virginia valeriae pulchra is shown in Figure 11 (See Habitat). This snake was found more readily in the spring (1.9 snakes/hour) than in the fall (1.4 snakes/hour). A decline in numbers was observed for the summer (1.0 snakes/hour), especially for the latter part of July and first part of August. Storeria occipitomaculata and Diadophis punctatus edwardsi also showed declines in numbers captured during the summer.

This summer decline in occurrence was analyzed by separating the monthly records into the following categories: immature males, adult males, immature females, and adult females. Figure 16 depicts the availability of Virginia valeriae pulchra throughout the active season. All four categories showed a decrease in July. However, the adult females were found to be more abundant in August than either the adult

males or immatures.

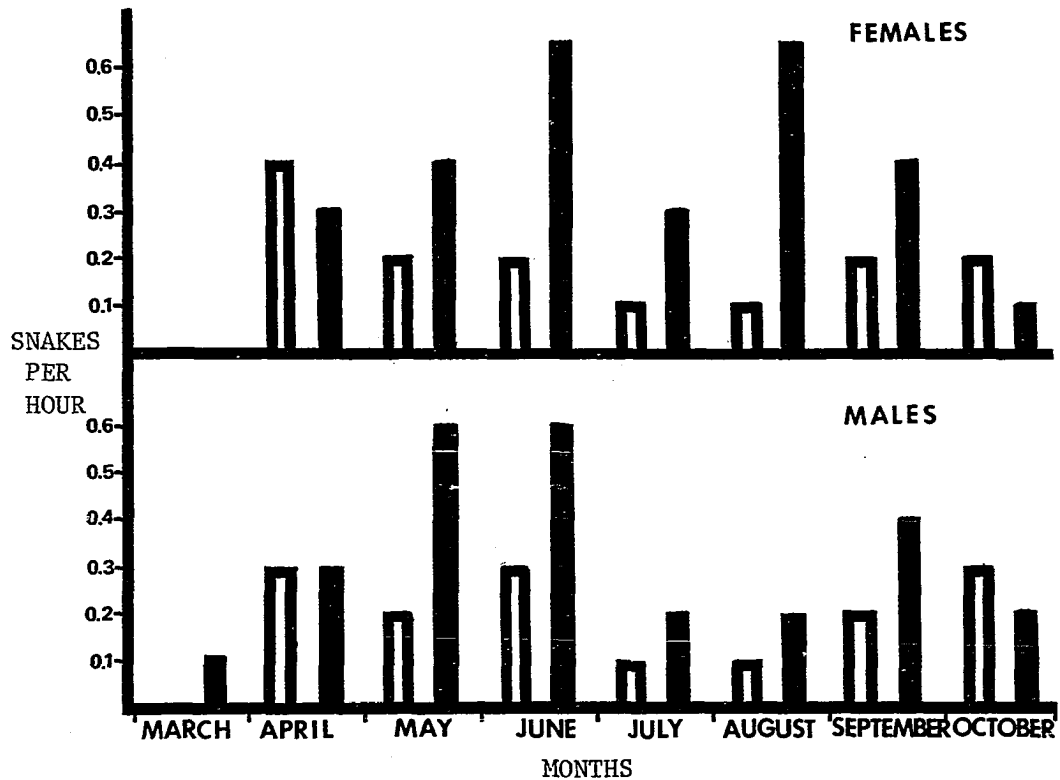


Figure 16. Monthly captures per hour of collecting for immature (N = 78) and mature (N = 153) males and immature (N = 76) and mature (N = 174) females. Immature Virginia valeriae pulchra are represented by open bars while mature Virginia valeriae pulchra are represented by solid bars.

B. Daily

This was done to determine during what part of a given day the snakes were most available. Figure 17 (Part A - Open bars) shows the total number of snakes caught per time of day over the whole season. In all months the time period of 1400 to 1800 showed the best results (judged by the number of snakes collected).

The possibility of a collecting bias was considered, i.e., did

the author do most of the collecting during a specific time period? This was tested by a series of seven studies of 24 hour duration each. These took place during the following dates: 16-17 April, 18-19 May, 4-5 June, 11-12 July, 23-24 July, 23-24 August, and 18-19 September. The results of these 24 hour studies are shown in Figure 17 (Part B - Solid bars) and represent equal amounts of collecting time over a one day period. They show the periods of 1200 to 1300 and 1600 to 1700 as best. The best collecting then for Virginia valeriae pulchra would be mid-afternoon to early evening hours.

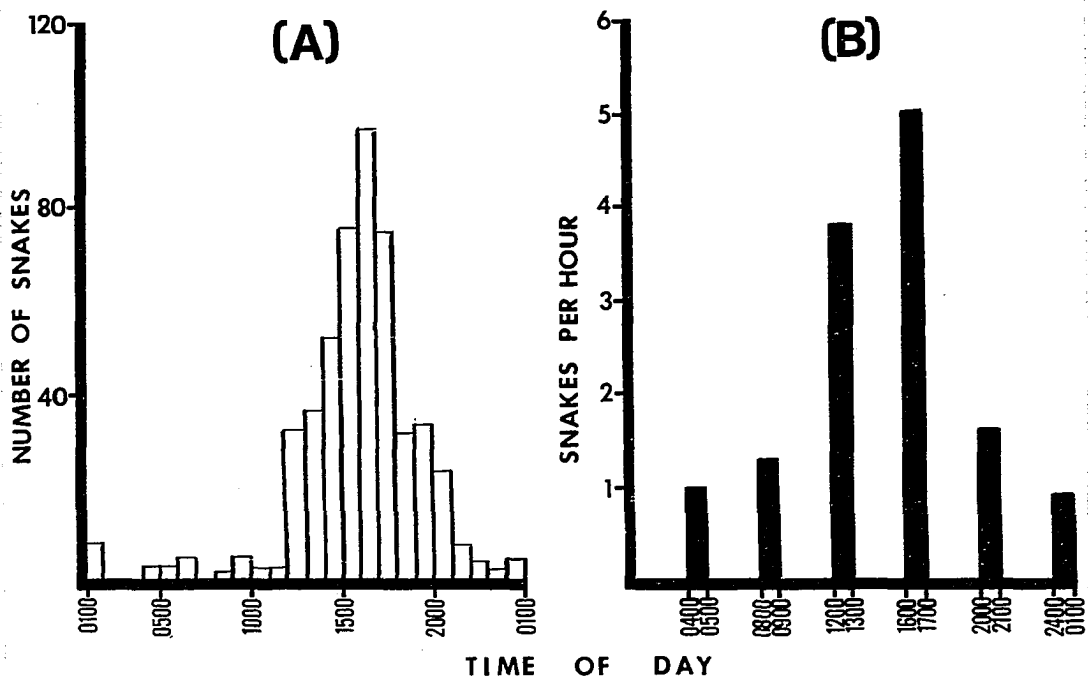


Figure 17. The number of Virginia valeriae pulchra captured per time of day. (A) Total number of snakes captured in the field over three active seasons (n = 514); (B) Average number of snakes captured per hour during seven 24-hour studies (n = 108).

It is believed that the thermal regimen of the area is the prime determinant of the period of availability for these snakes. To test this hypothesis a series of temperature measurements under rocks (Ts, Ta, Tg) was needed. It was realized that the above temperatures would not be exactly the same for all rocks in the area (shade, thickness, moisture, etc. would cause modifications). However, it would be impossible to apply the above temperature measurements for every rock in the area. Thus, a test rock, considered as a reasonable indicator of the general temperature relations of the area was selected. This rock was of average size of all rocks ever found concealing Virginia valeriae pulchra. This test rock was studied for Ta, Ts, and Tg for each time period for seven 24-hour studies. These measurements plus the previously determined thermal measurements for Virginia valeriae pulchra (voluntary maximum, voluntary minimum, ecritic) appear together in Figure 18. It will be seen that during the warmer months of the year (July - August), the Ts approaches or exceeds the voluntary maximum of Virginia valeriae pulchra. During these times, the animal retraheres into the soil. This explains the reduction in available snakes during July and August (Figure 16). Gravid females; however, have a higher ecritic Tb for August than males and thus are evident in greater numbers (Figure 16).

It becomes apparent that Virginia valeriae pulchra is found on the surface (under rocks) under two conditions only. First, when Ts is closer to ecritic than is the Tg and secondly, when Ts is between the voluntary maximum and voluntary minimum for this snake. Figure 19

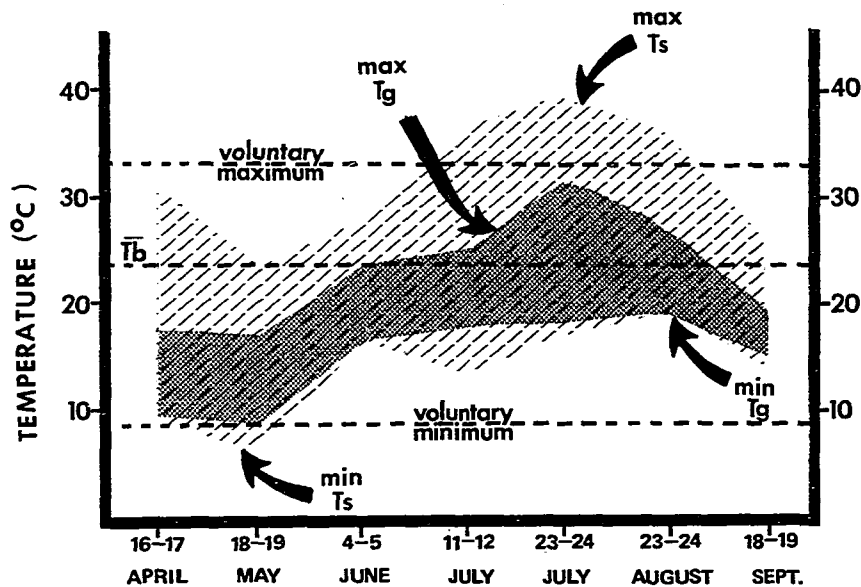


Figure 18. Range of substrate temperatures (Hatched Area) and ground temperatures (Solid Area) under test rock during seven 24-hour studies. Voluntary minimum and maximum body temperatures for *Virginia valeriae pulchra* with their preferred temperature (T_b) are included for reference.

demonstrates this point. It shows differences in temperatures between T_a and T_g and differences in temperature between T_s and T_g superimposed on them is a line showing the number of snakes observed per time of day over a whole season. The information shown in Figure 19 demonstrate that when air temperatures rise, the substrate temperatures (T_s) under the test rock rose, thus warming the ground below this rock. This produces a gradient with higher temperatures toward the surface which would be a heat source during the mid-afternoon and early evening hours. When substrate temperatures were greater than or equal to those of the ground, snakes were found on the surface under

rocks. However, when ground temperatures rose above those of the substrate, snakes were not found on the surface under rocks and are presumably using the ground as a heat source. Substrate temperatures above 33.0°C (voluntary maximum) as shown in Figure 18, would force these snakes to seek more preferred (cooler) temperatures in the ground.

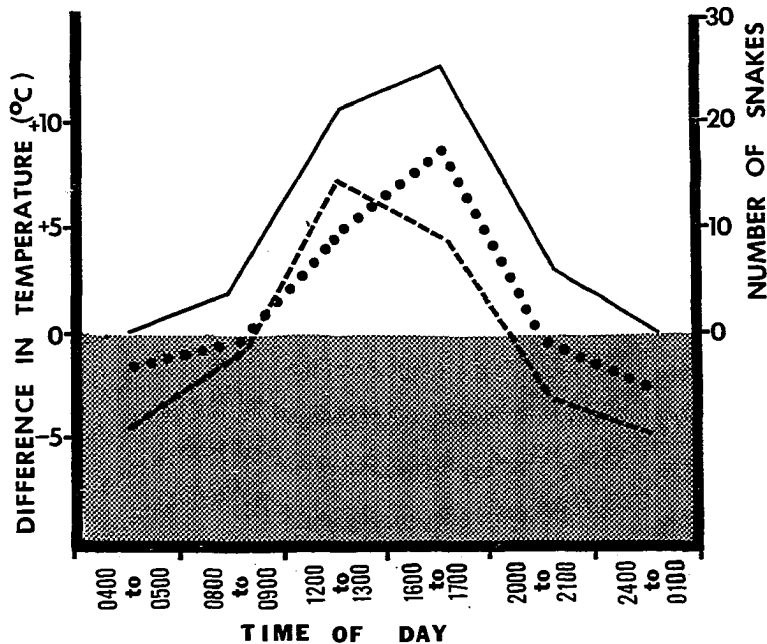


Figure 19. Correlation between number of *Virginia valeriae pulchra* captured per period for seven 24-hour studies (solid line) with air temperature minus ground temperature (broken line) and substrate temperature minus ground temperature (dotted line).

In addition to recording the environmental temperatures and occurrence of specimens, twenty-eight snakes were additionally marked during this study. This was done by color coding (with oil based paints) each snake captured. The objective was to determine how far the snake moved during a 24-hour period. Eight snakes (28.6%) of

those marked were recaptured and demonstrated daily movements from 0 to 6.4 meters. One snake (female) was recaptured 33 days later and moved but 9.1 meters. These data suggest that this form moves for short distances; and lends support to the contention that the snakes thermoregulate by vertical rather than horizontal movement.

During this study, snakes found in late March and early April appeared in proximity to the perimeter of ant mounds. These mounds were later excavated to see if they were used as hibernacula. Virginia valeriae pulchra was found on one occasion (1 April 1982) to be hibernating in an abandoned Formica exsectoides (Hymenoptera: Formicidae) mound at depths of 40 to 50 centimeters from the ground surface (80 to 90 centimeters below top of mound). The dimensions of the mound were 147 cm long by 75 cm wide by 40 cm high. Table 18 shows hibernaculum information for Virginia valeriae pulchra, Diadophis punctatus edwardsi, and Thamnophis brachystoma removed from this mound. Substrate temperatures in Table 18 may be higher than those prior to their discovery due to the subsoil being exposed to air temperatures ranging from 14.4°C to 18.2°C. All snakes were in ant tunnels in the subsoil under the north through east facing sides of the mound. These exposures were appreciably cooler than the south or west facing sides, suggesting that any specimens that used warmer exposures of the mound had already emerged.

Three other ant mounds were excavated during this study (1-2 February 1981; 28 March 1982); however, no snakes were found. Two of these mounds harbored Formica exsectoides while one was

completely devoid of any ants.

| Species | Sex | Snout-Vent Length | Depth from Surface | Substrate Temperature |
|-------------------------------------|--------|-------------------|--------------------|-----------------------|
| <u>Virginia valeriae pulchra</u> | | | | |
| | Male | 105 mm | 50 cm | 6.5°C |
| | Male | 176 mm | 40 cm | 5.2°C |
| | Female | 107 mm | 40 cm | 5.2°C |
| | Male | 110 mm | 40 cm | 5.2°C |
| <u>Diadophis punctatus edwardsi</u> | | | | |
| | Female | 110 mm | 15 cm | 7.3°C |
| | - | 116 mm | 19 cm | 5.3°C |
| | - | 127 mm | 19 cm | 5.3°C |
| <u>Thamnophis brachystoma</u> | | | | |
| | Male | 235 mm | 63 cm | 4.7°C |

Table 18. Hibernacular information recorded for Virginia valeriae pulchra, Diadophis punctatus edwardsi, and Thamnophis brachystoma from an abandoned Formica exsectoides mound on 1 April 1981.

Rainfall also seems to have some subordinate effect on the appearance of Virginia valeriae pulchra under rocks on the surface. Table 19 shows the effect of time of rainfall on number of Virginia valeriae pulchra captured per hour collecting. Their scarcity appears to increase with the number of days after a rain.

| | | | | | | |
|--|----------------|----------------|---------------|----------------|------------------|-----------------|
| Number of Snakes Collected / Hour | 1.1 | 1.8 | 1.5 | 1.6 | 1.2 | 1.1 |
| Number of Days Before and After a Rain | One Day Before | On Day of Rain | One Day After | Two Days After | Three Days After | Four Days After |

Table 19. Effect of rainfall on number of Virginia valeriae pulchra captured per hour collecting.

Reproduction Biology

A. Males

The right testis is located cranial of the left and is centered over the 75 ± 4 gastrosteges. The left testis is centered above the 84 ± 4 gastrosteges ($n = 135$). Both are white ellipsoid bodies. The right testis was significantly longer than the left in 130 of 135 (96.3%) specimens ($t = 20.8$; $df = 133$; $p < .001$). Such asymmetry is not uncommon in snakes (Fox, 1977). The right and left testes were found to increase in length with an increase in snout-vent length (right testis: $r = 0.775$; $df = 133$; $p < .001$; left testis: $r = 0.811$; $df = 133$; $p < .001$).

During the course of this study, the reproductive tracts of 135 male snakes were examined. A state of sexual maturity was considered to have been attained when the vasa deferentia were convoluted and/or contained spermatozoa. These criteria were applied to the right side only (Clark, 1964). Figure 20 shows the number of snakes demonstrating the above criteria. Sexual maturity in male Virginia valeriae pulchra is first attained during the fall of their second active season when they reach a snout-vent length of 147mm to 157mm (preserved) or 158mm to 168mm (live). Of the above 135 specimens, 115 were sexually mature. These 115 mature specimens were used to study seasonal testicular development and spermatogenesis.

The seasonal development of the testes for mature males was analyzed by using the following criteria: (1) length plus width for

the right testes (Bradford, 1973); (2) mean diameter (average of five readings) of the seminiferous tubules in the right testes (Bradford, 1973); and (3) the right testis length divided by the specimens snout-vent length (Clark, 1964). Figure 21 shows the average diameter of the seminiferous tubules in the right testes per month while Figure 22 depicts the other two criteria. These measurements demonstrate that the testes reach maximum size in July.

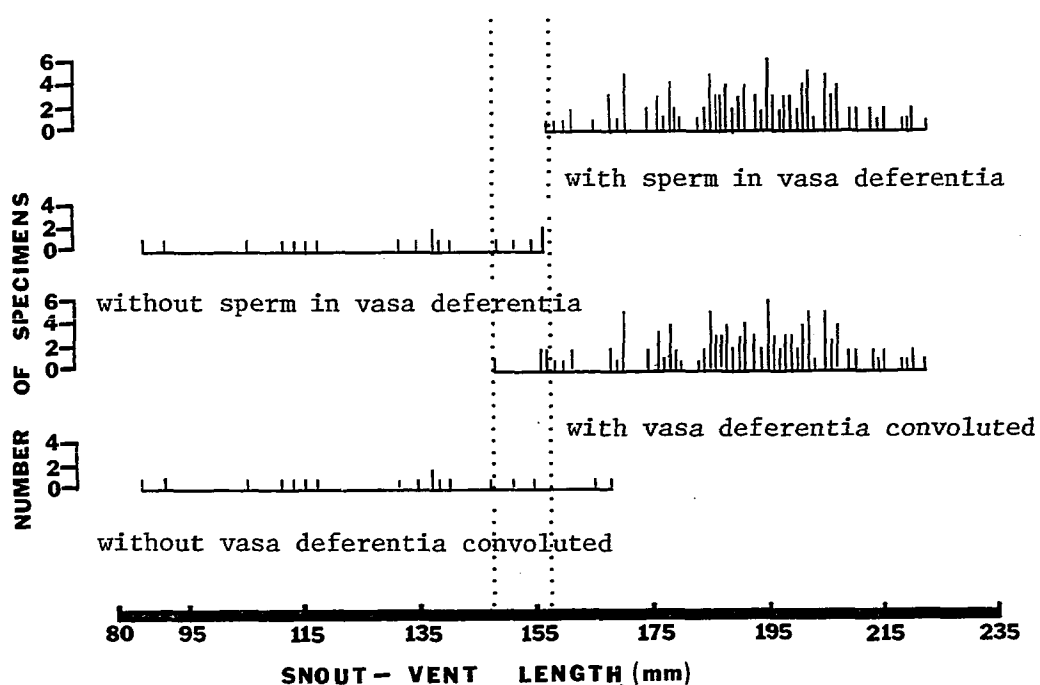


Figure 20. Snout-vent length (preserved) plotted against (a) convolutions of and (b) presence of sperm in vasa deferentia. The area included between the dotted lines denotes the snout-vent length range for onset of sexual maturity in male V. v. pulchra (n = 135).

Virginia valeriae pulchra shows a pattern of spermatogenesis which begins upon the snake's emergence in late March-early April with spermatogonial cells and primary spermatocytes present. Secondary spermatocytes, formed in May, give rise to spermatids by late May-

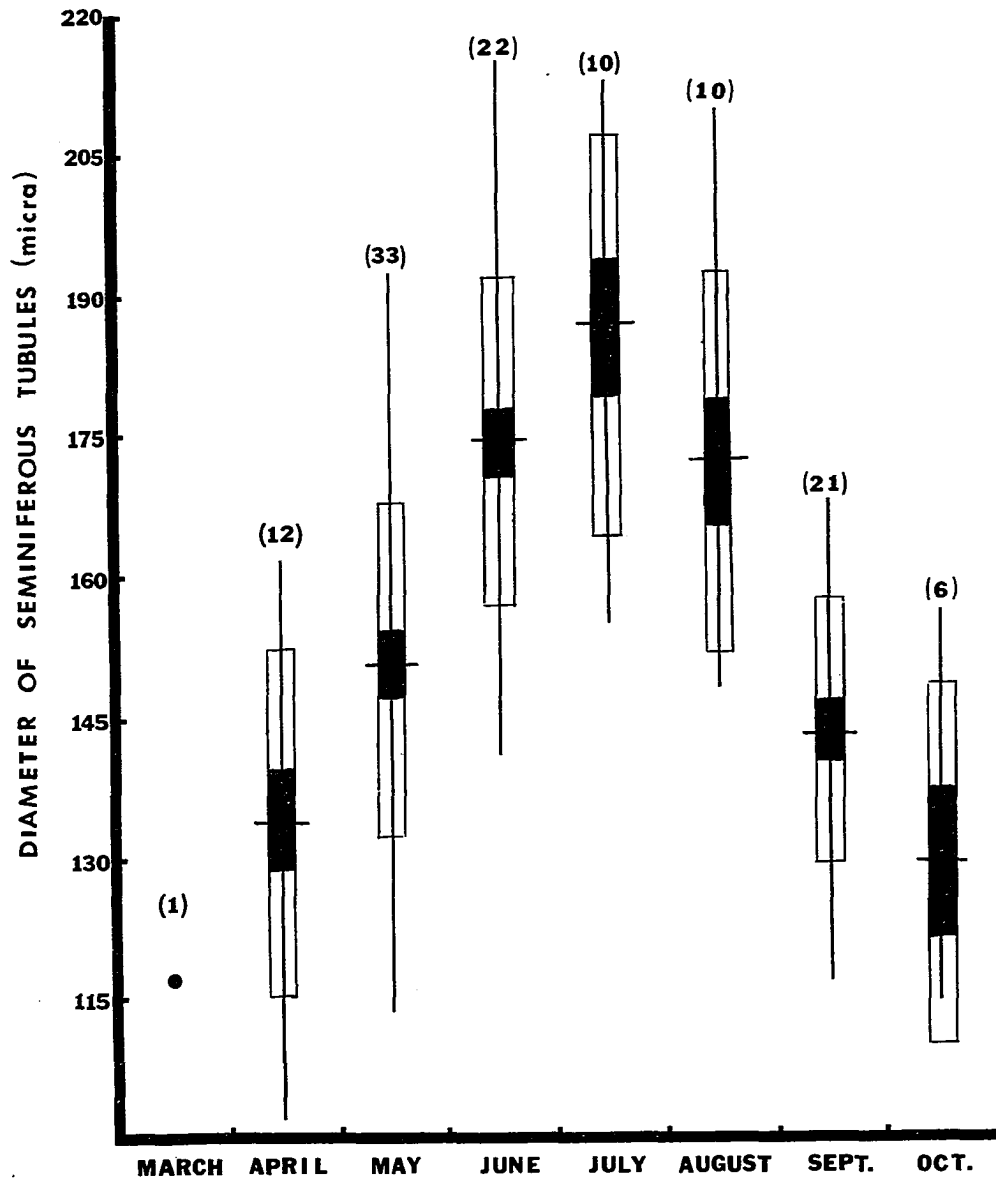


Figure 21. Average diameter of the seminiferous tubules for 115 male *Virginia valeriae pulchra* for each month of the active season. Numbers in parentheses represent the number of snakes examined. Vertical lines = range; horizontal lines = mean; open rectangles = \pm one standard deviation unit; and solid rectangles = \pm one standard error of the mean.

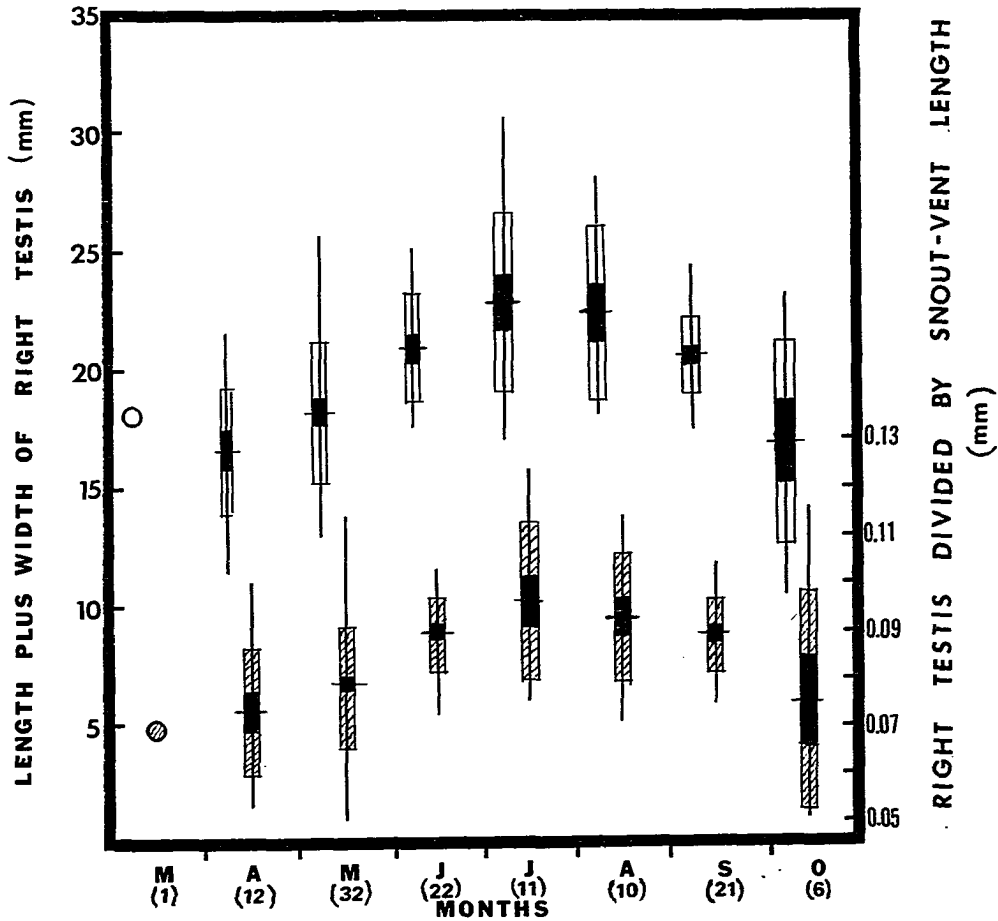


Figure 22. Seasonal development of the right testis characterized by its length plus width (upper open series of bars) and right testis length divided by snout-vent length (lower hatched series of bars). Vertical lines = range; horizontal lines = mean; open or hatched bars = \pm one standard deviation unit; and solid bars = \pm one standard error of the mean. Numbers in parentheses denote number of specimens examined (n = 115).

early June. Spermatids are the predominant cell type in July.

Spermatozoa begin to form in the seminiferous tubules by the first week of July and remain there until mid-August when they begin to migrate into the epididymi. The spermatozoa are then stored in the vasa deferentia concurrent with a regression in seminiferous tubule

diameter. The vasa deferentia were found to store sperm throughout the year in mature males.

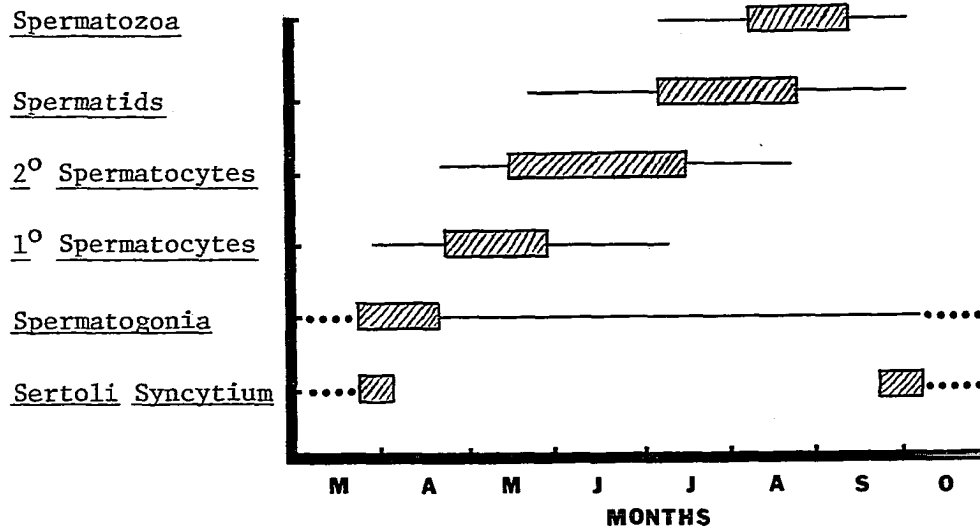


Figure 23. Spermatogenic cycle for *Virginia valeriae pulchra*. Lines span the time interval when cell types were present in the seminiferous tubules while bars indicate their predominance ($n = 115$). Dotted lines are time of hibernation which was not studied and is therefore unknown.

Figure 23 shows a monthly range and predominance for each cell type found in the seminiferous tubules from 28 March to 6 October. Sertoli cells were found throughout this time but were most abundant in late March and April and in September-October. Evidence from late March-early April tubules, which had a degenerating Sertoli syncytium and September-October tubules, which had a developing Sertoli syncytium suggest that the winter tubules are probably made up of a Sertoli syncytium and remain unchanged during hibernation. Sertoli cells were least abundant during the summer. Figures 24, 25, 26, 27, 28, 29 and 30 show typical cell types and their abundance in the seminiferous tubules for April, May, June, July, August, September,

and October respectively.

For Figures 24 - 30, the following abbreviations were used:

Sc = Sertoli cells
Sg = spermatogonia
1^o = primary spermatocytes
2^o = secondary spermatocytes
St = spermatids
S = spermatozoa
Cd = cellular debris

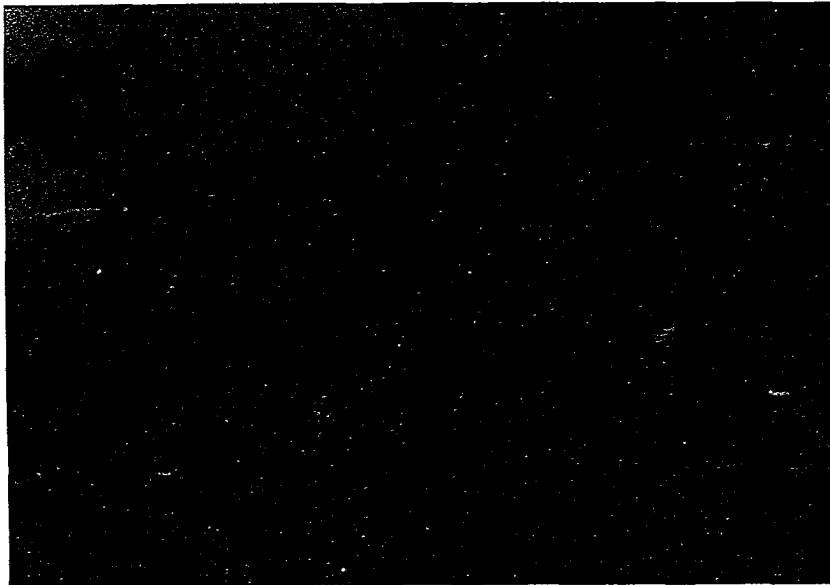


Figure 24. Seminiferous tubule in April showing spermatogonia, primary spermatocytes, and Sertoli cells (760 X).



Figure 25. Seminiferous tubules in May showing spermatogonia, primary spermatocytes, Sertoli cells, and cellular debris (345 X).



Figure 26. Seminiferous tubule (center) in June showing secondary spermatocytes and spermatids (760 X).

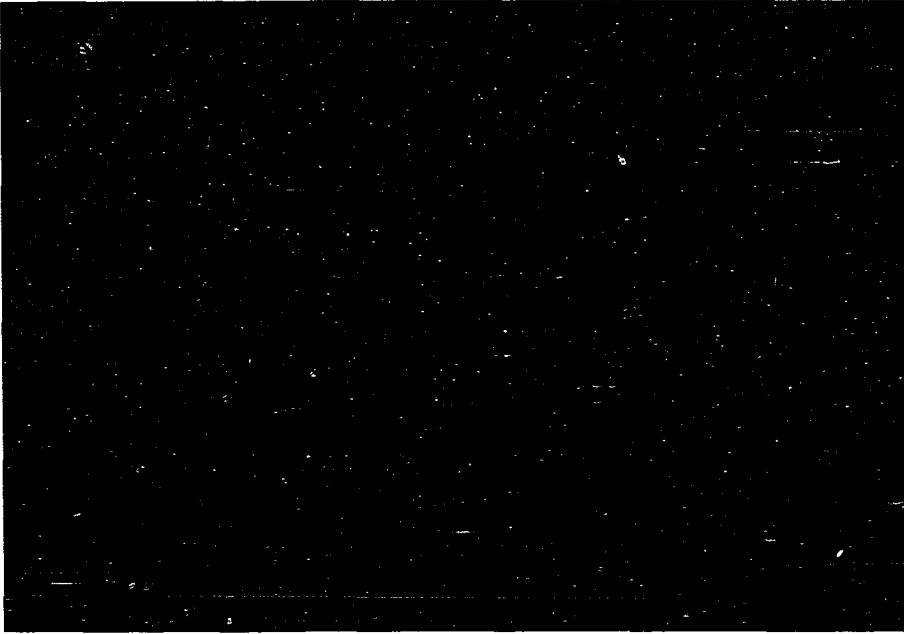


Figure 27. Seminiferous tubule (center) in July showing secondary spermatocytes, spermatids, and developing spermatozoa (760 X).

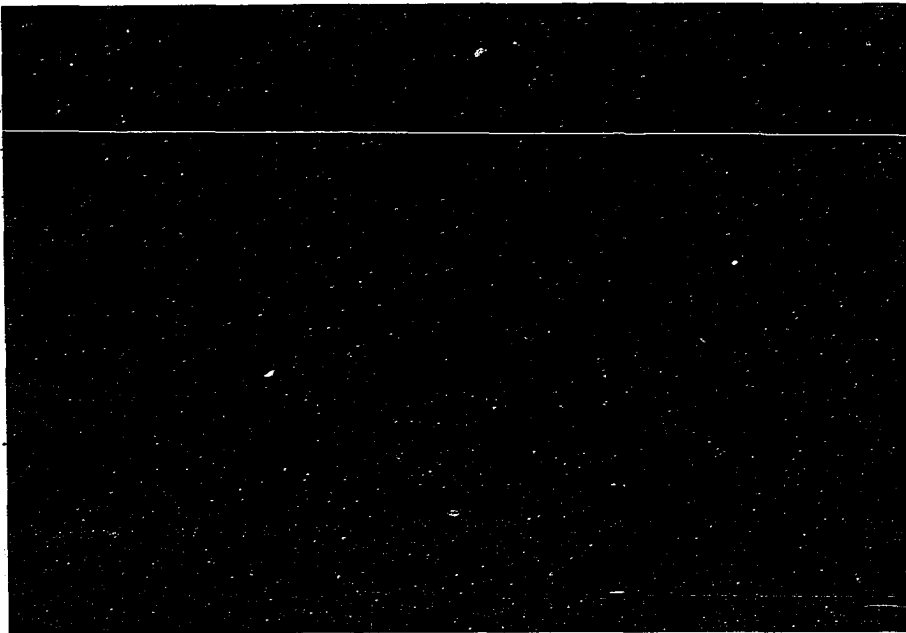


Figure 28. Seminiferous tubules in August showing secondary spermatocytes, spermatids, and spermatozoa (345 X).

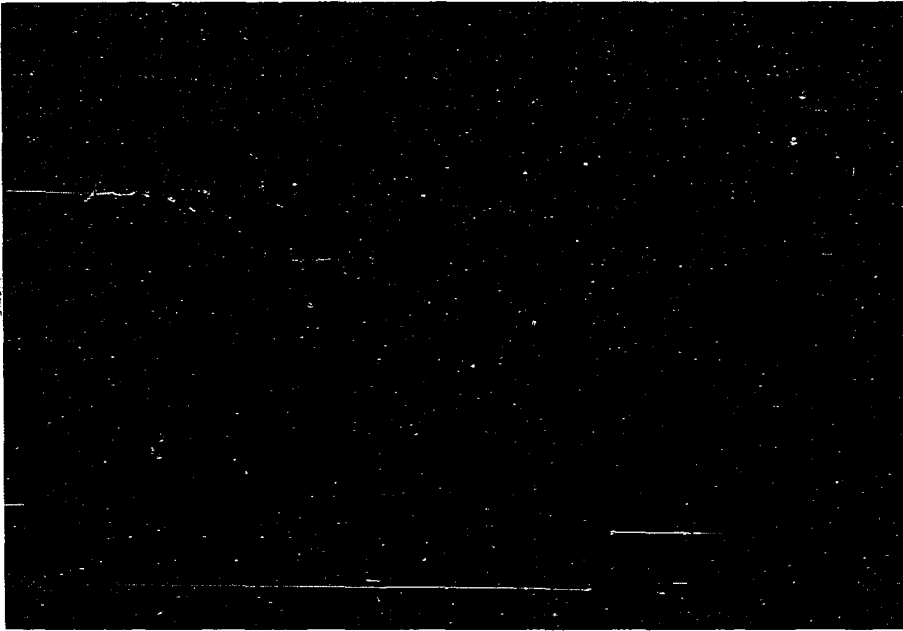


Figure 29. Seminiferous tubule in September showing spermatogonia, Sertoli cells, and cellular debris (760 X).

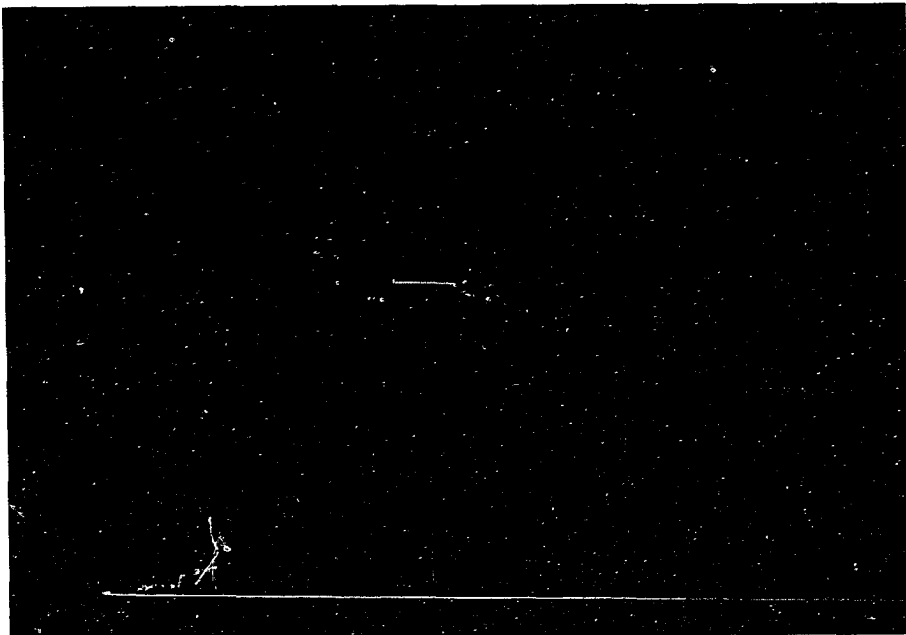


Figure 30. Seminiferous tubules in October showing spermatogonia, Sertoli cells, and some cellular debris (345 X).

B. Females

The reproductive tracts of 124 V. v. pulchra were studied. The ovaries, with accompanying follicles, and oviducts were examined. Both ovaries were examined grossly to give an accurate measure of potential litter size. However, histological preparations were made on the right only. One might expect microscopic identifications in either oviduct would be the same; however, since most species of snakes have more follicles in the right ovary (Fox and Dessauer, 1962; Tinkle, 1957) and thus, more eggs would enter the right oviduct (Clark, 1964), the right oviduct was preferred.

The ovaries are elongate, saccular structures located at the level of the ostium of the oviduct, and generally extend posteriorly to the level of the kidneys. The right ovary was located in all cases craniad to the left and was significantly longer ($t = 15.4$; $df = 113$; $p < .001$) and had more follicles ($t = 14.8$; $df = 113$; $p < .001$) than the left. Nine snakes appeared to have no ovaries (5 neonates and 4 first-year snakes).

Ovarian follicles were measured across their long axis following the methods of Betz (1963), Kofron (1979), and Pisani and Bothner (1970) to the nearest 0.1 mm ($n = 2169$). Four groups representing 3 age classes were observed (Table 20). Primary (Group I) follicles were in the smallest class and were spherical, translucent, and measured 0.1mm to 1.9mm. Secondary follicles (Group II) were opaque, turgid, medium-sized (2.0mm to 3.9mm), and white. Tertiary follicles (Group III) were off-white to dull yellow (Color code in Smithe, 1975

- cream), turgid, and ellipsoidal in shape. They ranged from 4.0mm to 5.9mm in length. Graffian follicles (Group IV) were enlarged follicles (6.0mm to 18.2mm) and yellow. These follicles rupture at lengths of 16mm or more.

| Group (Follicle Type) | Length (mm) | Number of Follicles | Percent of Total Follicles |
|--------------------------|-------------|---------------------------|----------------------------------|
| I | 0.1 to 1.9 | 1339 | 61.7% |
| II | 2.0 to 3.9 | 547 | 25.2% |
| III | 4.0 to 5.9 | 188 | 8.7% |
| IV | 6.0 plus | 95 | 4.4% |

Table 20. Types of ovarian follicles and their frequencies. Total number of follicles measured was 2169 from 115 snakes.

Follicular maturation for female V. v. pulchra of different ages (years equate with active seasons) is shown in Figure 31. This diagram demonstrates each follicle group (I to IV) and when they appear in different sized females. Primary follicles first appeared in the snakes' first active year; secondary follicles in the fall of their second year; and tertiary follicles in the fall of their third year. Graffian follicles (Group IV) were first observed in the spring of the fourth year. Not all females; however, formed Graffian follicles in the spring of their fourth year. Only 5 of 9 of those snakes entering the spring of their fourth year had either tertiary follicles or Graffian follicles in April and May. The four snakes that did not show tertiary or Graffian follicles in April or May of their fourth year were 200mm or less (preserved) while those that did were 200mm or

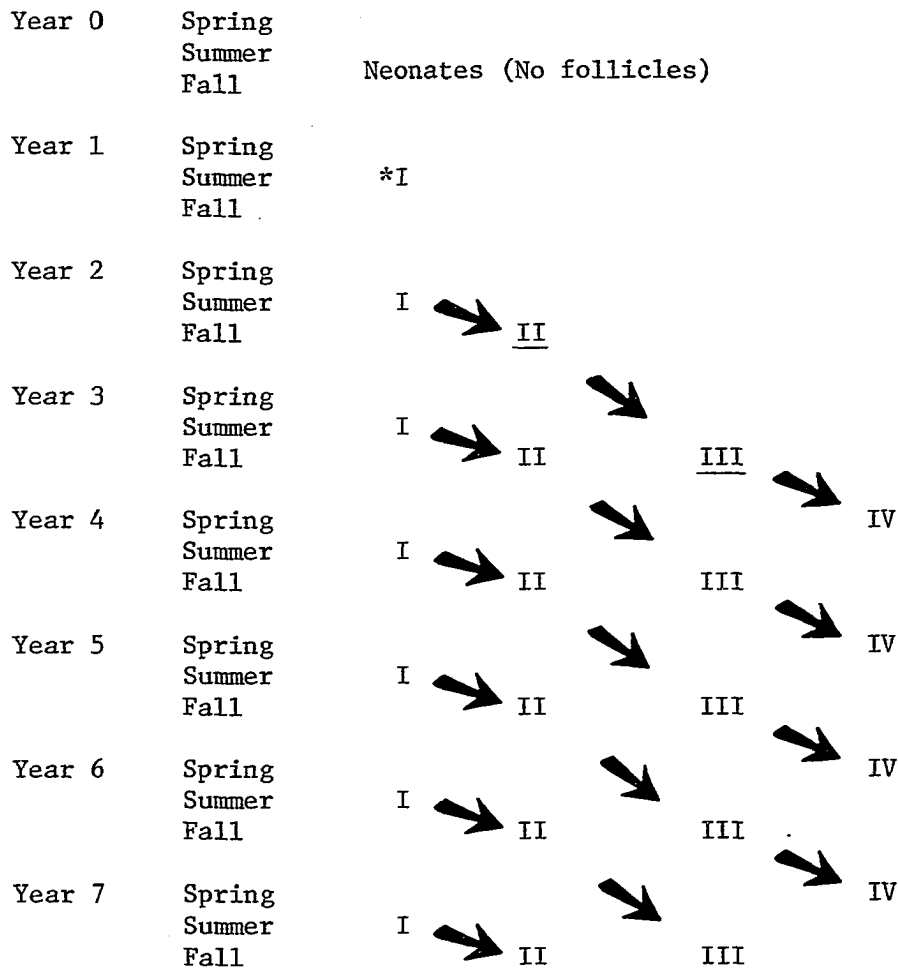


Figure 31. A diagram of the sequence of follicular maturation in V. v. pulchra. Roman numerals refer to follicle size groups and arrows denote when one group gives rise to the next. * indicates 1 of 5 snakes examined showed these follicles while underlining represents their earliest appearance.

more in snout-vent length (preserved). It appears that size (greater than 200mm) and the presence of well developed tertiary follicles in April of the fourth year are the most important criteria for determining time of first ovulation. Those specimens that didn't ovulate in the spring of the fourth year do so in the spring of the fifth.

Those that didn't ovulate (200mm or less) demonstrated no spermatozoa in their oviducts while 3 of the 5 snakes that presumably did ovulate (200mm or more) had spermatozoa. The one snake that didn't show spermatozoa was collected in early April. This suggests that those snakes entering the spring of their fourth year with enlarged tertiary or Graffian follicles get mated.

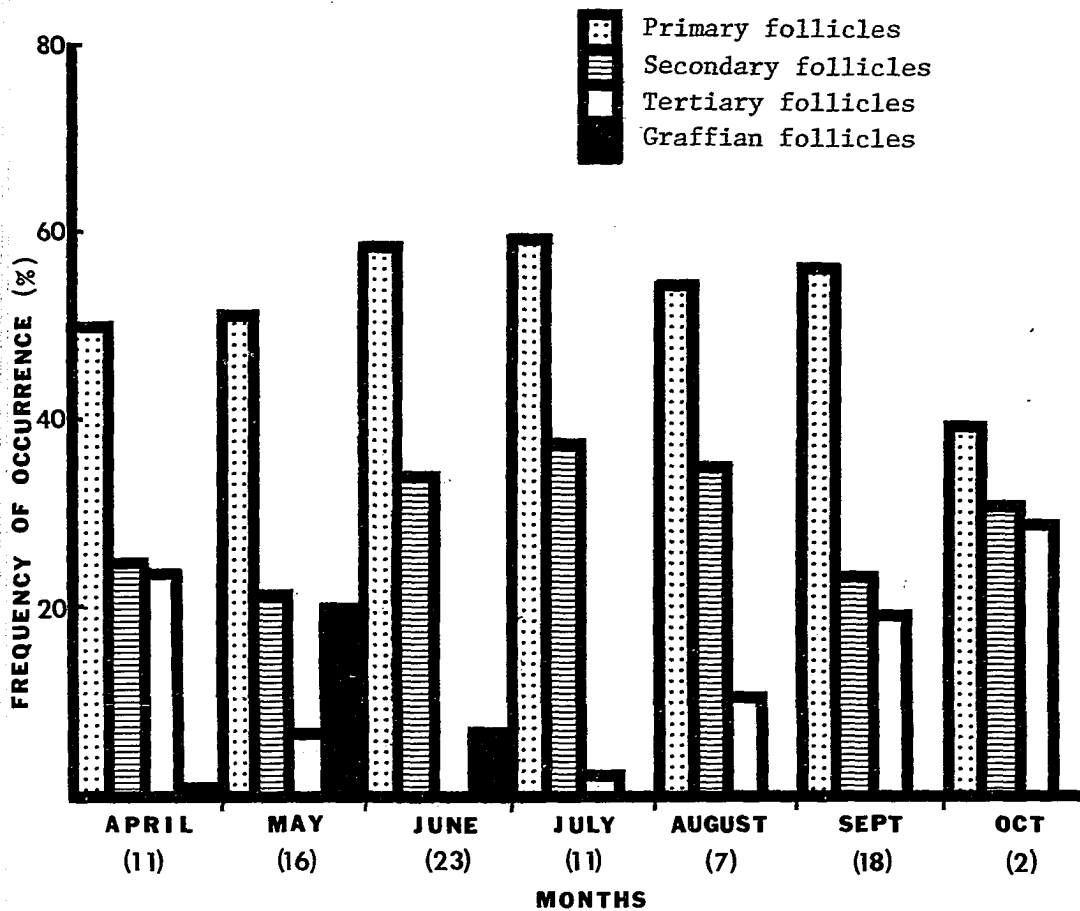


Figure 32. Frequency of occurrence (%) for each type follicle for 88 mature *V. v. pulchra*. Frequency was derived by dividing the number of follicles per group by the total number of follicles for that month. Numbers in parentheses represent snakes examined per month.

Figure 32, using mature snakes' (200mm or greater), shows that primary follicles give rise to secondary follicles in the fall; secondary follicles give rise to tertiary follicles in late summer to fall; and tertiary follicles give rise to Graffian follicles in late April, May, or early June.

Ovulation was determined by examining the ovaries for Graffian follicles and the oviducts for eggs. One specimen (TC - 134) on 2 May showed 8 oviducal eggs with follicular cells (most likely from the corona radiata of the Graffian follicle) around them in the lumen of the right oviduct. Figure 33 shows one such egg from TC - 134. Graffian follicles were found from 30 April through to 7 June. One specimen (TC - 306) collected on 7 June had enlarged Graffian follicles averaging 14.6mm in length. This snake would certainly ovulate soon. Ovulation extends from the first week in May to mid-June. Fertilization follows ovulation.

When an egg is released from an ovary, it usually but not necessarily enters the oviduct on the same side of the body (Mayew, 1966). This was shown in 25.0% of the gravid female V. v. pulchra I examined. These females had more corpora lutea than embryos in the oviduct on the same side and more embryos and fewer corpora lutea on the opposite side. In these snakes, the total number of corpora lutea and embryo's were equal. Extrauterine migration is demonstrated.

Corpora lutea were found after ovulation during May to mid-September. They appeared as yellow, compressed bodies. These glands shrank from approximately 4mm in length in May and June to 2mm

by mid-September. From mid-September on they appeared only as small orange-brown patches in the ovarian stroma. Two hundred and forty-eight corpora lutea were measured.

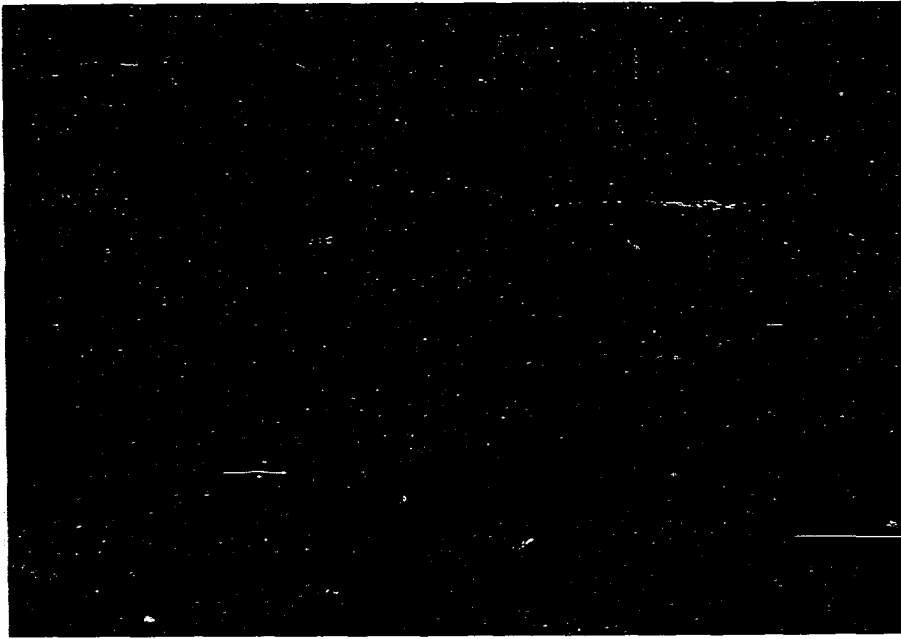


Figure 33. Photograph of an oviducal egg with follicular cells around it (345 X). This snake (TC - 134) was collected on 2 May 1980.

Parturition was found to extend from 16 August to 20 September with the majority of young delivered in the last week of August or the first week of September (Figure 34). Using the earliest and latest dates for ovulation and parturition, an approximate time for gestation would be 15 weeks (105 days).

Litter size was evaluated by using the following criteria:

(1) number of corpora lutea per female; (2) number of embryos per female; and (3) number of young born to each female in the lab.

Thirty-four gravid females bore litters in the lab averaging

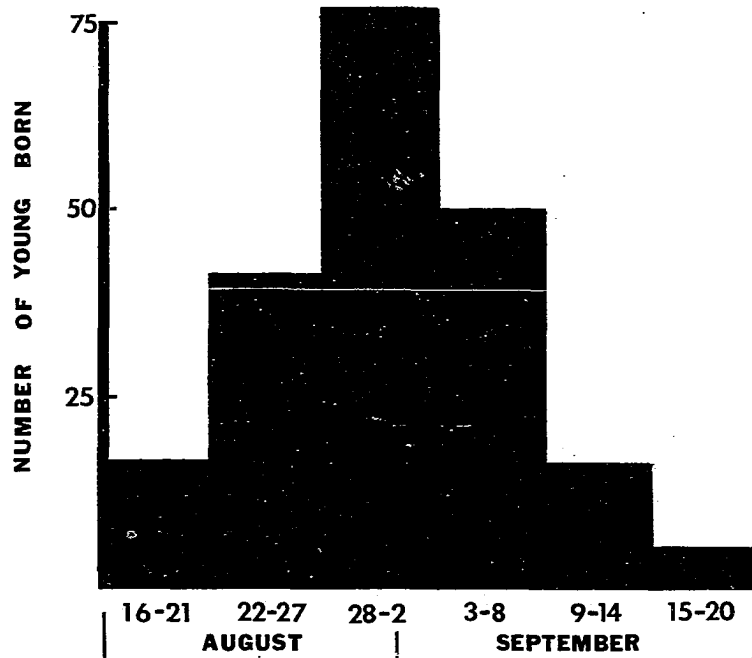


Figure 34. Number of young born to 34 females in the lab plotted in 5 day periods for August and September. The total number of young born was 205.

6.0 \pm 1.8 young per litter. Two hundred and five young were observed. Ninety-nine were females and 104 were males. This yields a sex ratio of 1:1. The number of corpora lutea per female was 6.9 \pm 1.6 while the number of embryos per female was 6.5 \pm 1.3. Using an F-test (one way analysis of variance), no difference was found between the number of corpora lutea in the ovaries, the number of embryos in the oviducts, or the number of young born to each female in the lab. Litters may range anywhere from 2 to 11 young. The right oviduct averaged more embryos than the left ($t = 5.4$; $df = 52$; $p < .001$) and more corpora lutea ($t = 4.9$; $df = 68$; $p < .001$). Table 21 compares the number of

corpora lutea per ovary and the number of embryos per oviduct. The neonates born in the lab averaged 40.6% of the total length of their mothers.

| | EMBRYOS (n = 27) | CORPORA LUTEA (n = 35) |
|---------|------------------|------------------------|
| Left | | |
| Mean±SD | 2.5±0.9 | 2.8±1.1 |
| Right | | |
| Mean±SD | 4.0±1.0 | 4.1±1.2 |

Table 21. Comparison of the number of embryos per oviduct and number of corpora lutea per ovary. SD equals one standard deviation unit.

Sexual maturity in female V. v. pulchra was determined using three criteria. They are: (1) those females that gave birth to litters in the lab; (2) those females that had oviducal eggs, embryos, or corpora lutea (Clark, 1964); and (3) those females that had spermatozoa in the oviducts (Clark, 1964). These three criteria were plotted against snout-vent length to determine sexual maturity (Figure 35). It was found that females began to reach sexual maturity in the spring of their fourth year (= active season) when a snout-vent length of 200mm to 212mm (preserved) or 214mm to 227mm (live) was achieved.

C. Mating

Mating was observed in the field on two occasions. The days were 3 April 1980 and 18 May 1981. Observations at this time and also in the fall showed sexually mature males and females under the same rocks. This association was not found during the summer months (Table 22). Such an association in the spring and fall suggest

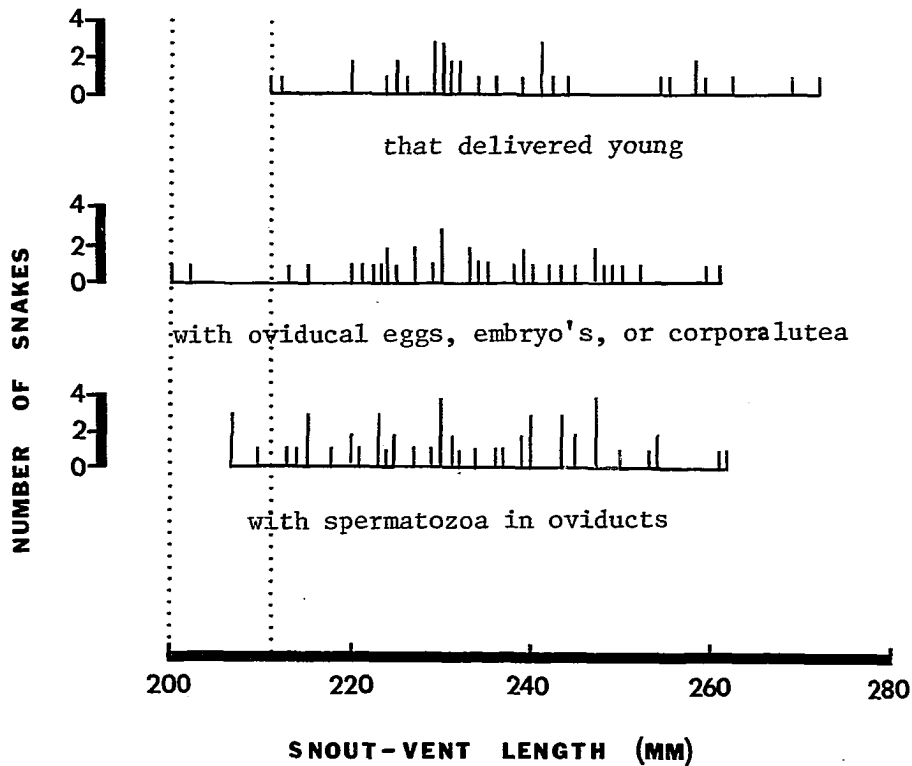


Figure 35. Presence of sperm in the oviduct, oviductal eggs, embryo's, corpora lutea, and young in relation to snout-vent length in female *V. v. pulchra*. The area included between the dotted lines denotes the snout-vent length (preserved) range for onset of sexual maturity in female *V. v. pulchra*.

reproductive behavior. Thus, 15 adult females were also inspected in the fall of 1981 (6 September to 24 September) for motile sperm. This was accomplished by flushing the cloaca with Amphibian Ringer Solution and immediately examining the slides in the field. Results for smears are shown in Table 23. The data show either no sperm or else very small, non-motile sperm from 6 September up through to 13 September. Motile sperm was first observed on 10 September. From 10 September to the last day of inspection (24 September), the number of snakes

demonstrating motile sperm increased dramatically. Thus, Virginia valeriae pulchra has both a spring and fall mating period.

OBSERVED UNDER THE SAME ROCK

| Months | Sexually Mature Male with Female | Immatures | Adult Females | Adult Males | Adult with Young |
|-----------|-------------------------------------|-----------|------------------|----------------|------------------------|
| April | 3 | | | | |
| May | 6 | 1 | 1 | | |
| June | 1 | | | 1 | |
| July | | 1 | | | |
| August | | | 1 | | |
| September | 7 | | | | 1 |

Table 22. The number of times V. v. pulchra was found with another V. v. pulchra under the same rock. N = 23 observations.

| Date | No sperm | Non-motile sperm | Motile sperm |
|--------------|----------|------------------|--------------|
| 6 September | 2 | 1 | |
| 7 September | 2 | | |
| 10 September | 1 | | 1 |
| 13 September | | 2 | 1 |
| 20 September | | | 3 |
| 24 September | | | 2 |

Table 23. Presence and condition of sperm in 15 females in September of 1981 demonstrated by cloacal smears.

Histological examination of the oviducts showed that sperm was found in the oviducts throughout the year. However, the condition of these sperm rapidly deteriorated (they became shrivelled) during the summer (Figure 36) as compared with sperm seen in the spring (Figure 37) and subsequent fall (Figure 38). Spermatozoa were observed in the seminal receptacles from April to the first week in June (Figure 39 - 6 May 1980) and again in late September to early October (Figure 40 - 20 September 1980). Sperm introduced into the females in the fall were presumably retained in the oviducts until the following spring.

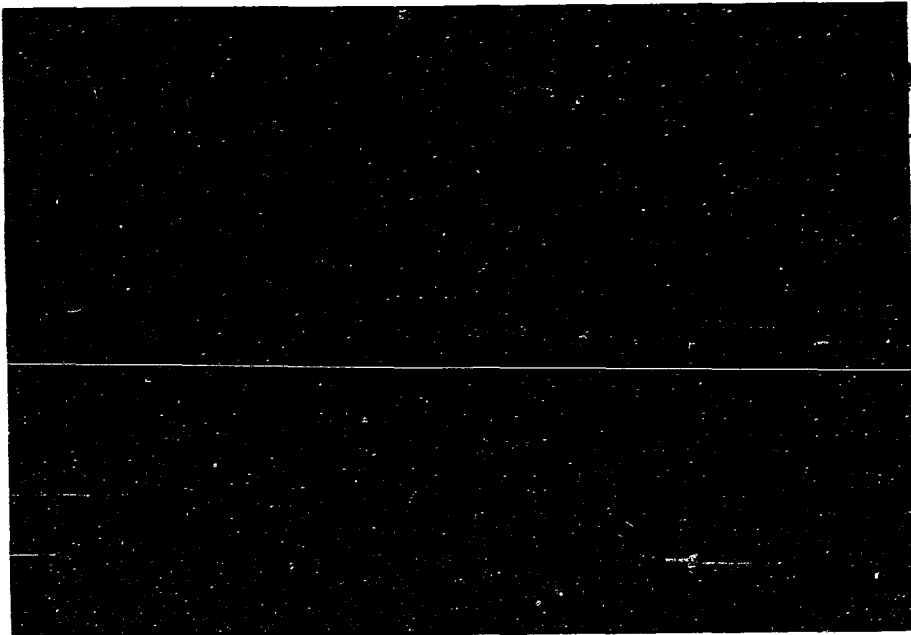


Figure 36. Spermatozoa in lumen of oviduct in July (172 X). Notice shrivelled condition.

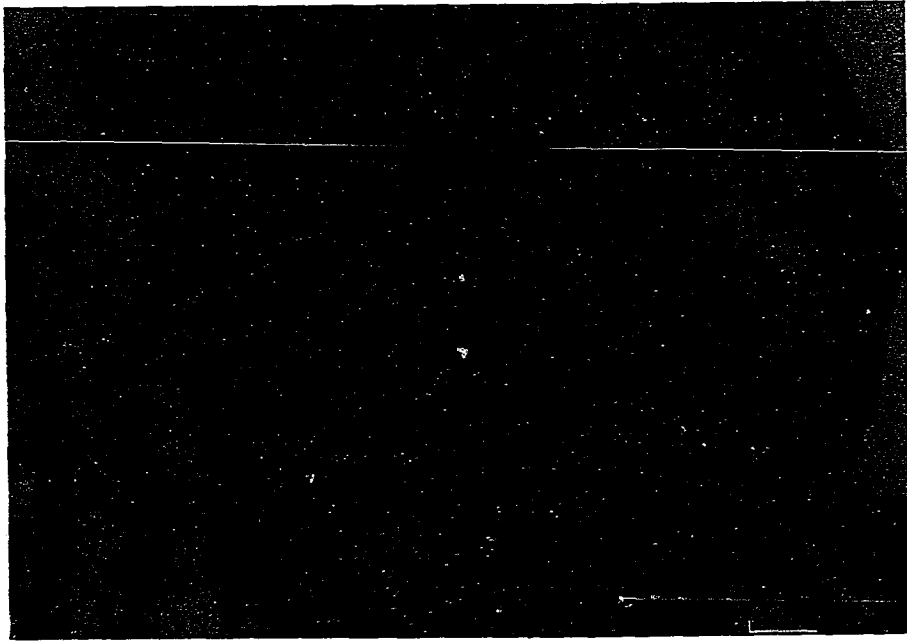


Figure 37. Spermatozoa aligned along wall of oviduct in April (345 X). Notice size of spermatozoa in comparison with Figure 36.

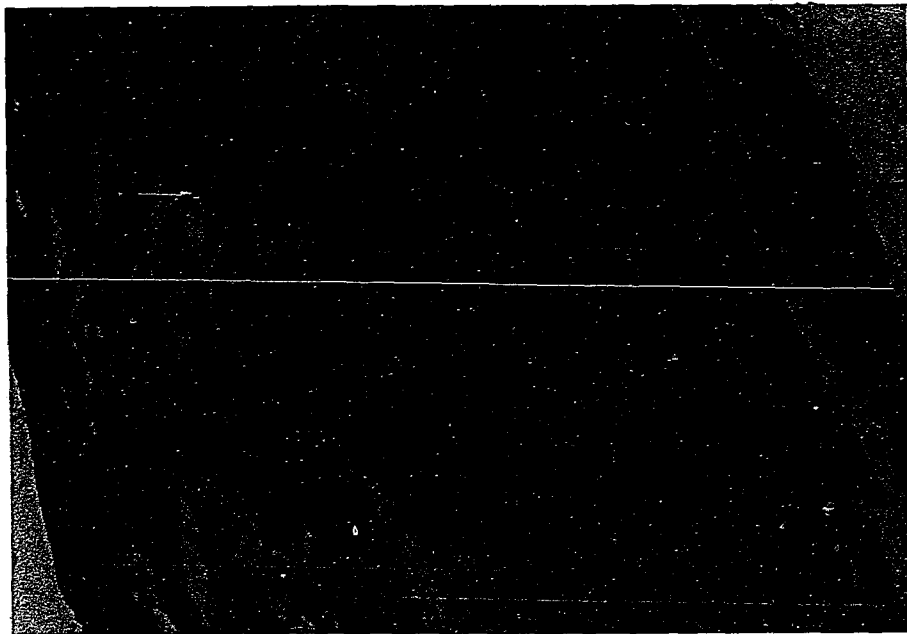


Figure 38. Spermatozoa aligned along wall of oviduct in October (172 X). Notice size of spermatozoa in comparison with Figure 36.

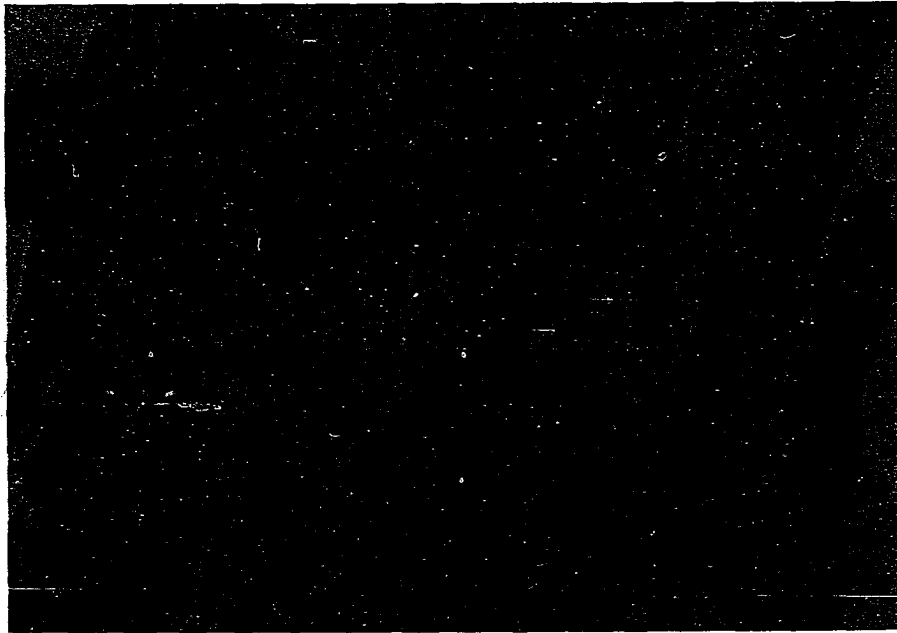


Figure 39. Spermatozoa in lumen of oviduct in May (172 X). Two seminal receptacles (far left) are shown with spermatozoa.



Figure 40. Spermatozoa in lumen of oviduct in September (172 X). Seminal receptacles are shown with spermatozoa.

D. Fat Bodies

In the process of dissecting the specimens, abdominal fat bodies were removed and weighed. The weight of each specimen was determined and from this, the percent fat per gram of body weight was calculated (Hahn and Tinkle, 1965; Goldberg and Bezy, 1974). Sexually mature males ($n = 85$) and females ($n = 51$) were studied per month for abdominal fat bodies (%/gm-body wt., Figure 41). Females showed more fat than males in the spring and possibly in the fall but only 1 fall female and male were examined. This is presumably due to the males' greater energy expenditure while actively searching for mates at these times. Fat bodies of females shrank dramatically from May to August because at this time females were gravid and the developing embryos were using up most of the fatty tissue. Gravid females fed infrequently during the gestation period, especially during their last month (see Diet section). It was found that when embryonic weights increased, abdominal fat bodies decreased ($r = -0.691$; $df=18$; $p<.001$).

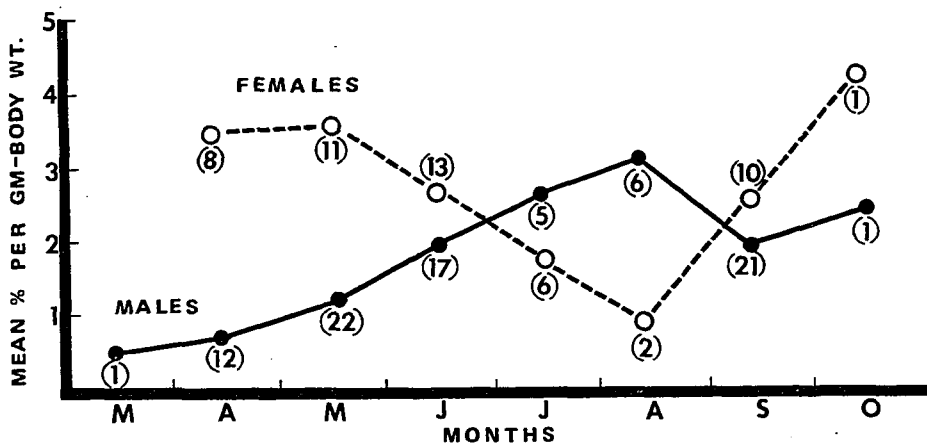


Figure 41. Mean comparison for abdominal fat bodies (Mean % per gm-body wt.) for sexually mature males ($n = 85$) and females ($n = 51$). Numbers in parentheses represent specimens examined per month.

Population Structure

A. Age Distribution

V. v. pulchra from northwestern Pennsylvania could be separated into age classes by the snout-vent length method of Bradford (1973). Four hundred and seventy-two specimens were measured in this study. This snout-vent length method of aging lost its accuracy in female specimens over 7 years old and in males over six.

Tables 24 and 25 show the sample size, mean, and standard deviation of snout-vent lengths for 218 males and 254 females. Sexes were plotted separately since sexual dimorphism in snout-vent lengths was previously noted (See Morphology section). Table 24 shows female age classes and Table 25; male age classes.

Age distributions for V. v. pulchra as shown in Figure 42. This figure demonstrates that (1) females greater than 4 years old are found in greater numbers than males for the same age; and (2) immatures were less often found in the field than were adults.

B. Growth Rate

The estimated growth rate for male and female V. v. pulchra was found by calculating the mean snout-vent length per age class and connecting the means. This method can only estimate growth in V. v. pulchra since mark-recapture techniques were not employed in this study. Figure 43 shows the males and females growing at the same rate from birth through the third year (or third active season). Thereafter, females grew at a greater rate than did males. Males

FEMALE AGE CLASSES

| Months | Neonates Born | 1st Year | 2nd Year | 3rd Year | 4th Year | 5th Year | 6th Year | 7th Year |
|------------------|------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| April | | | | | | | | |
| Sample Size | | 2 | 2 | 4 | 5 | 1 | 5 | 2 |
| Mean | | 122.5 | 155.5 | 173.3 | 214.2 | 236.0 | 252.8 | 276.0 |
| Std. Dev. | | 10.6 | 9.2 | 4.7 | 8.9 | | 5.1 | 2.8 |
| May | | | | | | | | |
| Sample Size | | 5 | | 6 | 8 | 9 | 9 | |
| Mean | | 115.2 | | 191.2 | 216.0 | 239.0 | 260.3 | |
| Std. Dev. | | 4.3 | | 5.2 | 8.3 | 6.0 | 7.2 | |
| June | | | | | | | | |
| Sample Size | | 2 | 1 | 3 | 6 | 15 | 12 | 3 |
| Mean | | 127.0 | 163.0 | 182.3 | 222.7 | 239.9 | 260.0 | 278.0 |
| Std. Dev. | | 9.9 | | 16.2 | 6.5 | 5.2 | 7.0 | 1.0 |
| July | | | | | | | | |
| Sample Size | | 5 | 2 | 5 | 5 | 11 | 9 | 1 |
| Mean | | 132.6 | 166.0 | 192.2 | 216.4 | 245.7 | 264.0 | 280.0 |
| Std. Dev. | | 9.4 | 1.4 | 11.3 | 5.8 | 3.6 | 5.7 | |
| August | | | | | | | | |
| Sample Size | 11 | | 3 | 4 | 6 | 13 | 12 | 1 |
| Mean | 94.7 | | 166.3 | 188.8 | 228.2 | 245.2 | 261.9 | 284.0 |
| Std. Dev. | 2.4 | | 3.5 | 10.5 | 4.0 | 6.7 | 6.8 | |
| September | | | | | | | | |
| Sample Size | 17 | | 1 | 2 | 7 | 20 | 6 | 3 |
| Mean | 90.0 | | 170.0 | 198.5 | 223.3 | 247.0 | 266.3 | 285.7 |
| Std. Dev. | 22.8 | | | 9.2 | 6.2 | 4.9 | 6.8 | 5.1 |
| October | | | | | | | | |
| Sample Size | 6 | | | | 3 | 2 | | |
| Mean | 94.7 | | | | 234.0 | 249.5 | | |
| Std. Dev. | 13.2 | | | | 1.7 | 6.4 | | |

Table 24. Average live snout-vent lengths (mm) per month for 254 female V. v. pulchra of varying ages. (Year increments pertain to active seasons.)

MALE AGE CLASSES

| Months | Neonates Born | 1st Year | 2nd Year | 3rd Year | 4th Year | 5th Year | 6th Year | 7th Year |
|------------------|------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| March | | | | | | | | |
| Sample Size | | | | | | 1 | | |
| Mean | | | | | | 217.0 | | |
| Std. Dev. | | | | | | | | |
| April | | | | | | | | |
| Sample Size | 7 | 2 | 8 | 5 | 3 | 1 | | |
| Mean | 106.1 | 147.0 | 184.2 | 203.2 | 215.3 | 229.0 | | |
| Std. Dev. | 6.6 | 4.2 | 8.0 | 5.6 | 0.6 | | | |
| May | | | | | | | | |
| Sample Size | 8 | 4 | 11 | 14 | 7 | 5 | | |
| Mean | 116.1 | 158.3 | 181.0 | 204.6 | 219.6 | 232.4 | | |
| Std. Dev. | 11.5 | 7.8 | 4.9 | 5.3 | 2.4 | 3.2 | | |
| June | | | | | | | | |
| Sample Size | 8 | 5 | 5 | 16 | 6 | | | |
| Mean | 120.9 | 158.2 | 190.6 | 206.9 | 222.5 | | | |
| Std. Dev. | 5.5 | 11.4 | 6.2 | 5.5 | 2.1 | | | |
| July | | | | | | | | |
| Sample Size | 3 | 2 | 8 | 9 | 4 | 2 | | |
| Mean | 138.3 | 163.0 | 191.4 | 207.4 | 221.5 | 233.0 | | |
| Std. Dev. | 2.9 | 2.8 | 6.5 | 5.3 | 3.7 | 4.2 | | |
| August | | | | | | | | |
| Sample Size | 4 | 1 | 3 | 4 | 7 | 1 | 1 | |
| Mean | 94.8 | 144.0 | 164.3 | 193.5 | 208.0 | 223.0 | 231.0 | |
| Std. Dev. | 2.6 | | 2.5 | 4.7 | 6.5 | | | |
| September | | | | | | | | |
| Sample Size | 8 | 1 | 9 | 5 | 12 | 5 | 1 | |
| Mean | 98.4 | 147.0 | 165.3 | 190.4 | 208.9 | 224.0 | 233.0 | |
| Std. Dev. | 6.4 | | 5.2 | 7.2 | 5.9 | 4.7 | | |
| October | | | | | | | | |
| Sample Size | 6 | | 2 | 2 | 1 | | 1 | |
| Mean | 93.2 | | 170.5 | 189.5 | 220.0 | | 237.0 | |
| Std. Dev. | 11.9 | | 2.1 | 0.7 | | | | |

Table 25. Average live snout-vent lengths (mm) for 218 male Virginia valeriae pulchra of varying ages. (Year increments pertain to active seasons.) Samples are grouped for each month of collecting.

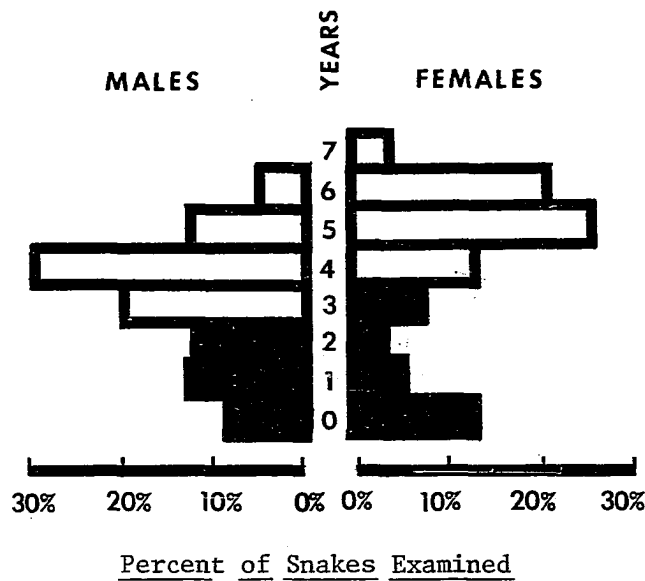


Figure 42. Age distribution for 218 male and 254 female Virginia valeriae pulchra. Frequency of occurrence for age classes (Years = Active Seasons) are in percent of the total number of males or females examined. Immatures are represented by shaded bars; adults by open bars.

lived beyond six years while females lived beyond seven years. Age classes beyond six years for males and seven years for females can not be recognized using the snout-vent length method because the growth rate is approaching zero. A sex ratio of 1:1 was found in this study.

Competitors, Predators, and Defense Mechanisms

A. Competitors

Interspecific and intraspecific competition among snakes may result from a lack of suitable shelter and diminished food reserves. Shelter in the form of fine sandstone rocks were used by Virginia

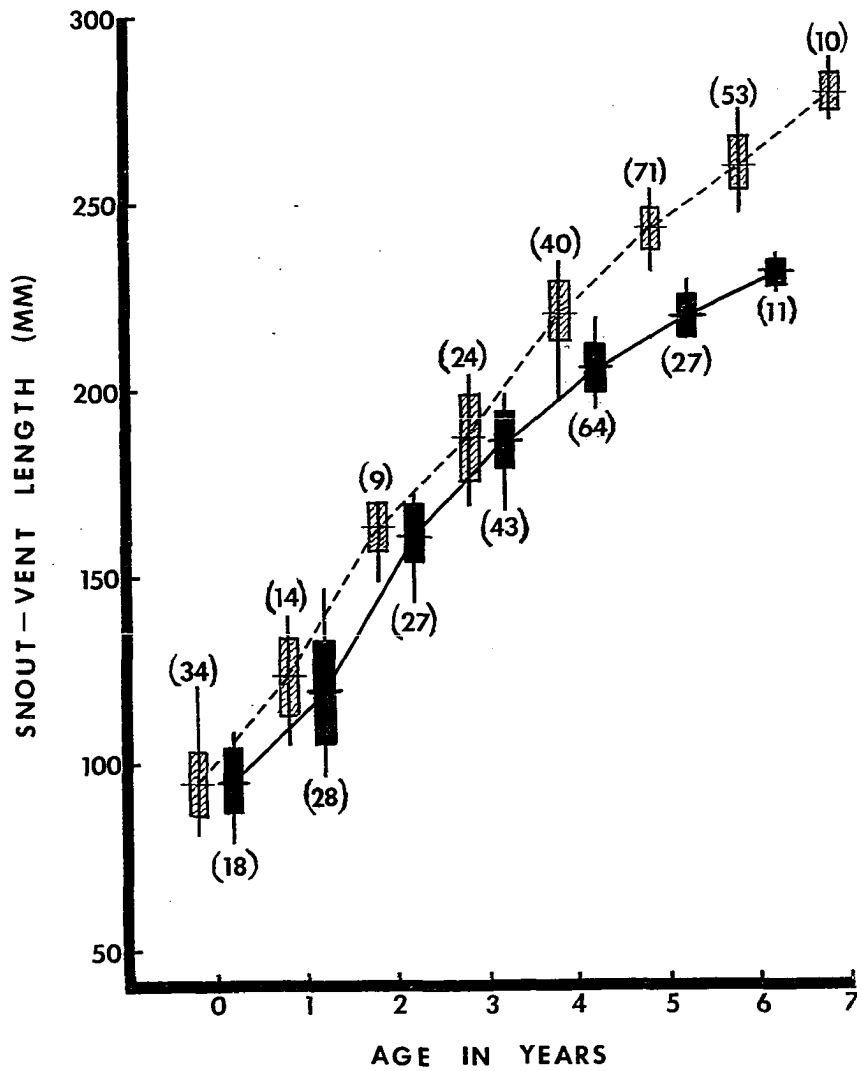


Figure 43. Snout-vent lengths (mm) for 218 male and 254 female in respects to age. Horizontal line = mean; vertical line = range; rectangle = \pm one standard deviation (Solid rectangles = males; hatched rectangles = females); numbers in parentheses = number of snakes measured. Estimated growth curves are shown for males (solid line) and females (dash line).

valeriae pulchra and other snakes in the immediate area. These rocks abound throughout the habitat and would not be limiting. Of 605 V. v. pulchra seen, only 60 (9.9%) were found under the same rock with other snake specimens of any type. If shelter were limiting, the frequency of finding V. v. pulchra with other snakes under the same rock should have been higher.

Food and its availability is of vital importance for any snake population. V. v. pulchra feeds solely on earthworms. Other snakes that feed on earthworms are Diadophis punctatus, Storeria occipito-maculata, Thamnophis brachystoma, Thamnophis sirtalis, and Storeria dekayi in their order of abundance in V. v. pulchra habitat. One would expect competition for this prey; however, prey as seemingly abundant as earthworms would seem unlikely to be limiting (Henderson, 1974).

B. Predators

V. v. pulchra was found in the laboratory to be preyed upon by the milksnake, Lampropeltis triangulum triangulum. The predator measured 450mm in snout-vent length and fed on four V. v. pulchra ranging in size from 100mm to 243mm in snout-vent length. An interesting predator-escape technique was demonstrated by three of the four V. v. pulchra observed. The smallest one (a neonate) did not demonstrate the following predator-escape technique. When the milksnake grasped the prey, the prey made only feeble attempts to escape. When the head of the prey was near disappearing into the mouth of the predator, the prey bit the inner lining of the predator's mouth and held on to this

area. This stopped any further advancement of the prey into the predator. After a minute or so, the predator began to gape and soon released its hold of the prey. This predator-escape technique was seen repeatedly even though the predator ultimately managed to consume all the snakes, although with considerable difficulty. In nature (not being confined by a cage), the prey might very well have escaped.

C. Defense Mechanisms

V. v. pulchra is a mild-mannered snake; however, on occasion three other types of negative behavior have been observed. The most common type is concealing its head in or under its coiled body. The second type, observed four times, was demonstrated by a motionless, belly-up posture. All observations were seen in the field and snakes were thought dead at that time; however, activity was immediately resumed upon touching the snake. One snake actually went limp in my hand but regained motion once placed on the ground. (Temperatures for these snakes were all within their normal activity range.) A third type of behavior was demonstrated only twice. This behavior was one of drawing back the lips, gaping, and exposing the teeth. The snake assumed a ribbon-flat posture in this display. Both snakes observed were gravid females. Even with this type of behavior, V. v. pulchra has never attempted to bite me.

DISCUSSION

Range

The geographic distribution for V. v. pulchra includes unglaciated areas on the Allegheny Plateau of western Pennsylvania, eastern West Virginia, and western Maryland. Its distribution is shown in Figure 1 along with the ranges for V. v. elegans and V. v. valeriae.

V. v. pulchra is one of two reptiles endemic to the northern Appalachian Plateau (Jopson, 1971). The other reptile is the coal skink Eumeces anthracinus. I have found both reptiles co-existing in the same habitat, while LeMay and Marsiglia (1952) reported Eumeces anthracinus in areas with "Virginia valeriae" in Swallow Falls State Park, Maryland. Since no V. v. pulchra have been recorded from the Swallow Falls State Park, quite probably the subspecies observed by LeMay and Marsiglia was V. v. pulchra (Cooper, 1958). Bothner and Moore (1964) and Lee (1973) found a similar association of Eumeces anthracinus and V. v. pulchra.

The current known ranges of V. v. pulchra and V. v. valeriae approach each other most closely along the Garrett County-Allegany County line in Maryland. They do not, however, appear to overlap one another in this area. Cooper (1958) considers V. v. pulchra as restricted to the Allegheny Plateau, Swallow Falls State Park and vicinity in Maryland, while the nearest V. v. valeriae recorded

(McCauley, 1945; Harris, 1969; 1975) in Maryland is 129 kilometers away in Big Pool, Washington County (R 1640 NHSM). This record is on the eastern edge of the Allegheny Ridge and Valley Province of the Appalachian Highlands Division (Fenneman, 1938; Thornbury, 1965). Another V. v. valeriae record has been reported by McCauley (1945) from Mineral County, West Virginia, which is across the Potomac River from Rawlings, Allegany County, Maryland. This Mineral County record is 53 kilometers from Swallow Falls State Park, Maryland. Three other V. v. valeriae specimens examined by me have come from Mineral County. They are CM 13893, CM 13826, and CM 9028. Specimen CM 9028 collected by Kephart on 22 September 1935 in Mineral County, West Virginia (3 miles SE of Keyser, E slope of Abram's Ridge) is but 32 kilometers from Swallow Falls State Park. These western records for V. v. valeriae are associated with the Potomac River drainage, whereas the V. v. pulchra records from Swallow Falls State Park vicinity are associated with the Youghiogheny River, a tributary of the Monongahela River. Cooper (1958) found no evidence of intergradation between these two forms in western Maryland. Considering the locality records for both forms, as well as differences in drainage systems occupied, topography, and climatological regimes such as temperature, precipitation, and length of growing season (Baker, 1936, Morey, 1931), the ranges for V. v. pulchra and V. v. valeriae are considered by me to be discontinuous along the Maryland-West Virginia border. However, V. v. pulchra specimen (CM 23795) collected in West Virginia: Hampshire County; near Romney by B. S. Kiser in July 1942, suggests an overlap

of the two forms. This specimen, the only known documented V. v. pulchra found within the range for V. v. valeriae, has a 17-17-17 dorsal scale formula with the dorsal scales weakly keeled throughout its body length. This dorsal scale formula (17-17-17) is characteristic of V. v. elegans, but is not altogether uncommon in V. v. pulchra. The nearest known record of V. v. elegans is approximately 682 kilometers away in the central portion of Kentucky. In 1981, Dr. Thomas K. Pauley collected 5 V. v. pulchra in the Spruce Knob Area of West Virginia (Quadrangles "Sinks of Gandy" and "Spruce Knob" - U.S. Coast and Geodetic Survey). With this discovery, it appears that specimen CM 23795 is an extension of this Spruce Knob population and that further collecting in this area, i.e., Spruce Knob to Romney, West Virginia may reveal intergrades between V. v. pulchra and V. v. valeriae. Also, Atkinson (1901) records a specimen of "Virginia valeriae" from Wilkinsburg, Allegheny County, Pennsylvania. I have examined this specimen (CM 4763) and have found it to be V. v. valeriae. Further collecting in this area of southwestern Pennsylvania is needed to explain this seemingly anomalous record.

Since 1928, over 400 preserved specimens of V. v. pulchra have been accumulated by others and myself. These comprise 60 specific locality records (Appendix II) which were used to determine the subspecies geographic distribution. The geographic distribution of V. v. pulchra is shown in Figure 2. Five specimens (CM 37285-6, CM 70610-11, CM 5010) from unspecified sites were not included in

Figure 2 due to insufficient locality data. Locality 14 is represented by a question mark since the specimen examined was released before verification was possible. The record is believed to be correct since Michael J. Kernan, the observer, has assisted the author in field excursions and has become quite familiar with V. v. pulchra and thus had sufficient insight to determine that the scales were "weakly keeled" and not smooth as in V. v. valeriae but unfortunately took no scale counts. The specific locality for this released snake was: Pennsylvania: Wharton Township, Markleysburg, 5 miles NE-E, near Lake Courage.

Since the geographic range for V. v. pulchra is discontinuous or spotty, I have divided the range into five areas. Area I is in the Pennsylvania counties of Potter, Cameron, Clinton, Elk, and Clearfield; Area II in Warren, Venango, and Forest counties. Area III is associated with Laurel Hill in the Pennsylvania counties of Westmoreland, Somerset, and Fayette. Area IV is on Laurel Ridge in Preston County, West Virginia (near the town of Terra Alta) and Garrett County, Maryland (Swallow Falls State Park). Area V, known as Spruce Knob, is in Randolph and Pendleton counties, West Virginia.

These 5 areas are within the unglaciated Allegheny Plateau Section (Fenneman, 1938), which is the middle portion of the Appalachian Plateau Province of the Appalachian Highlands Division (Thornbury, 1965). The hilltops of this mountainous section are broad and level, being supported by hard sandstones of the Pottsville and Pocono series (Abbe, 1902; Beck et al., 1975; Hennen and Reger, 1914; Hough and

Forbes, 1943). The climate is a continental type (Dailey, 1971) with winds primarily from the southwest (Beck et al., 1975). The valleys are V-shaped and their slopes are steep and rocky. Sand is the parent material of the existing soils (Baker, 1936). The forest consists mainly of the mixed mesophytic Beech-Birch-Maple-Hemlock type (Baker, 1936; Braun, 1950; Illick and Frontz, 1928). The summers are short and cool, while the winters are long and cold. The average growing season for the Allegheny Beech-Birch-Maple Region of western Pennsylvania, northeastern West Virginia, and western Maryland is 120-165 days (Morey, 1931).

The collecting sites for Virginia valeriae pulchra appear to be associated with major river drainages. Area I is associated with the headwater streams of the Susquehanna River; Area II, the Allegheny River, Tionesta Creek and the lower portion of the Clarion River; Area III, the Loyalhanna Creek; Area IV, the Youghiogheny and Cheat Rivers; and Area V, the Cheat, Potomac, and Greenbrier Rivers. Anderson (1965) and Christiansen (1973) found a similar riparian association for Virginia valeriae elegans in Missouri and Iowa respectively while McCauley (1945) implied a riparian association for Virginia valeriae valeriae along the Potomac drainage in Maryland.

Virginia valeriae pulchra occurs only in unglaciated areas. The author has searched extensively throughout northwestern Pennsylvania and southwestern New York State and has yet to find them in glaciated terrain. Area I lies south of the Wisconsin terminal moraine (Denny, 1956), while Area II abuts the Illinoisian terminal moraine

(Leverett, 1934; Shepps et al., 1959). Edgren and Ward (1952) has found two Virginia valeriae elegans in glaciated (Wisconsin) terrain. One specimen (RAE 1328) was found 15 miles north of the Wisconsin terminal moraine in Indiana (Pine Hills); the other specimen (UMMZ 101842) was found 10 miles north of the Wisconsin terminal moraine (Turkey Run State Park). Conant (1938) found one specimen (CSNH 2145) of Virginia valeriae valeriae approximately 37 miles within the Illinoisian drift, but outside the Wisconsin terminal moraine in Ohio. All other records for Virginia valeriae elegans and Virginia valeriae valeriae have come from unglaciated areas. All museum localities and published material on Virginia valeriae pulchra show it to be an unglaciated form. It is possible, however, that Virginia valeriae pulchra may enter glaciated areas in time, as have Virginia valeriae elegans and Virginia valeriae valeriae.

Virginia valeriae pulchra is found in areas where loamy sand to clay type soils exist. Area I contains primarily Leetonia channery loamy sand and Dekalb channery loam with 30-60 percent slopes (Goodman, 1958); Area II, Ernest very stony silt loam, 8-25 percent slopes overlain with Gilpin very stony silt loam, 25-60 percent slopes and Hazelton very stony loam, 25-80 percent slopes (Cerutti, 1971); and Area III, Gilpin-Wharton-Ernest associations or DeKalb-Hazelton-Cookport associations in Fayette County localities (Kopas, 1973) and primarily on Hazelton-Gilpin soil associations for Westmoreland-Somerset County localities (Beck et al., 1975). Baker (1936) describes Areas IV and V as being rough and stony lands. The author sampled one site in Area IV

where a gravid female V. v. pulchra was collected. The surface soil sample showed it to be sandy clay in texture (Johnson, 1975). The majority of snakes (85.3%) have been found on loamy sand to sandy loam type soils. Sandy-loam type soils appear to be an important factor in their distribution.

The range for V. v. pulchra as shown in Figure 2 is disjunct and includes 5 populations. Henceforth, Area I will be designated the Sizerville Population; Area II, the Warren Population; and Areas III, IV, and V as the Southern Pennsylvania-Maryland-West Virginia Population. Areas III, IV, and V have been combined since only a few specimens are available from each area. I have collected only a single specimen from Area IV and none from III and V.

Figure 2 depicts the north-south as well as the east-west separations in the distribution of V. v. pulchra in western Pennsylvania. The east-west disjunction in northwestern Pennsylvania is attributed to the cooler temperatures and shorter growing season while the north-south disjunction is attributed to a greatly decreased availability of suitable rock cover. Bleakney in 1958 developed the Environmental Tolerance Index for use in such cases where temperature may be the limiting factor. The Environmental Tolerance Index for V. v. pulchra in western Pennsylvania ranged from 8.1 to 9.9 (Mean = 9.1) while the east-west hiatus demonstrated a range of 5.9 to 7.5. I have found little suitable rock cover in collecting in the north-south hiatus. Flat, fine sandstone rocks where V. v. pulchra has been found in the north are scarce in this hiatus.

Areas in this north-south hiatus where fine sandstone rocks were observed, demonstrated fine shale slopes with dense herbaceous cover, and very little grass. These slopes are relatively unstable. Clay soils are very common in this north-south hiatus (O'Neill, 1965). Christiansen (1973) considered the range for V. v. elegans in Iowa to be limited by an absence, over a large geographic area, of a combination of loose stones on the surface, timber, and flowing streams in the southernmost localities. Temperature and growing season may be the limiting factors for the northernmost localities.

Habitat

V. v. pulchra resides in a highly dissected and wooded topography. Collecting sites in northwestern Pennsylvania along the Allegheny High Plateau demonstrate that V. v. pulchra may be found in the valleys or near the summit of these hills. Dr. Thomas K. Pauley (per. com.) has collected five V. v. pulchra in West Virginia on top of Spruce Knob which is approximately 1,463 meters above sea level. V. v. pulchra is a montane form (Richmond, 1954) while V. v. valeriae prefers lowlands (Netting, 1965). Little topographic information is available for V. v. elegans; however, the majority of reports locate them in hilly regions (Anderson, 1965; Christiansen, 1973; Dowling, 1957; Edgren and Ward, 1952).

The slope of the habitat of V. v. pulchra is flat to moderate. These gentle slopes are considered relatively stable as regards to

rock placement. The exposure of these slopes to the sun appears to be a matter of availability rather than selection. Only the north facing slope is avoided. There would be no direct sunlight here. Clark (1970) found a similar avoidance for Carphophis vermis (Kennicott) in Kansas.

All habitats I studied for V. v. pulchra were no further than 250 meters from permanent surface water. Anderson (1965) and Christiansen (1973) report a similar riparian correlation for V. v. elegans while McCauley (1945) suggested such a correlation for V. v. valeriae. This relationship, at least for V. v. pulchra, may be due to the fact that just about all of the roads in the region achieve the summit of the plateau by following the courses of the smaller brooks. It is here along the cleared sides of these roads that most V. v. pulchra are encountered.

The soil in V. v. pulchra habitat ranged from clay to loamy sand with the majority of the soil samples being of the loamy type (84.4%). Sand appears to be an important constituent of these soils and was found in appreciable amounts (50% or more) in 62 of 64 soil samples. Loamy sand to sandy clay loam soils are light to medium in weight and well to moderately drained. They are well to moderately aerated, dry to moist, and show high to moderate evaporation (Lyon and Buchman, 1943). These authors reported that sandy soils have their frost lines closer to the surface than clay soils. The colloidal

property of the clay component of these soils allows underground tunnels to persist, and facilitates the enlargement of these tunnels by fossorial or semi-fossorial vertebrates (earthworms or ants). Through manipulation of the head and/or body (Gans, 1974) vertebrate animals may secure and mold these pre-existing tunnels to their liking. Also, other environmental factors being equal, spring emergence would probably appear sooner in sandy or loamy soils than in clay soils. The undersides of rocks positioned on such soils would have a high relative humidity since their evaporation rate is high.

Little research has been done on the importance of rocks and their influence on poikilotherms (Gans, 1974). Almost all (96.8%) of the Virginia valeriae pulchra specimens collected from northwestern Pennsylvania were found secreted under fine sandstone rocks while 5 habitat descriptions from southwestern Pennsylvania along Laurel Hill report only 1 specimen found under a rock with the remaining 4 secreted under man-made items. The importance of these rocks has long been viewed by most collectors as convenient sites where snakes congregate to warm themselves as well as to escape predation. However, rocks serve a greater function. For burrowing and semi-fossorial forms, the rocks serve to keep open tunnels under them and to be a heat sink during the day (Gans, 1974). They also radiate heat energy into the ground and insulate these underground areas during twilight hours, thus allowing the ground to be a heat source at night. Rocks not only reduce predation, but also minimize desiccation by providing humid microhabitats. Without available rock cover, the poikilotherms

would be exposed to lower average daily temperatures within their preferred range and thus prolong the gestational period. Virginia valeriae pulchra has a relatively lengthy gestational period of 105 days (15 weeks). Any prolongation or shifting of this period would be detrimental to the young born in the fall since they would have little time available to store up fat reserves needed for hibernation. The first frost day of the fall in this area is anywhere from 30 September to 10 October (Morey, 1931). I have found suitable rock cover to be quite unavailable in the north-south hiatus (Figure 2), thus minimizing seasonal average temperatures for any snake in this area. This would limit their reproductive performance, population densities, and their range. There are many shale pieces in this north-south hiatus. Almost all are very thin and afford only minimal thermal protection.

Gravid female Virginia valeriae pulchra prefer larger rocks than the other population components. Large rocks were shown not to differ from smaller rocks in substrate temperature over the whole active season; however, thicker or more voluminous rocks will cool and heat more slowly than will thinner ones. This would afford more thermal stability to the substrate temperature and would allow the gravid females to remain in one site for longer periods of time. Clark (1970) found large female Carphophis vermis in Kansas to secrete themselves under larger rocks than smaller females. He attributed this phenomenon to a reduction in predation upon those snakes using larger rocks.

The typical habitat for Virginia valeriae pulchra consists of short, herbaceous, leaf-littered slopes covered with flat, fine

sandstone rocks near the forest edge. The area is open and may be a woodland clearing or a road side bank. Such areas are near forest streams. Other authors have found specimens in the following circumstances: under fine sandstone rocks ranging from gravel-sized pieces to chunks about 18 inches in length in an open clearing in timbered area (Bothner and Moore, 1964); under rocks (except one DOR) in timbered areas with dense undergrowth of ferns and bryophytes, or in a bog where ferns, sphagnum, and other mosses predominate (Cooper, 1958); in boggy area, with moss the predominating vegetation - bog is underlain with small pools and streams; stones and pieces of wood are abundant (LeMay and Marsiglia, 1952); in a pile of old hay used as garden mulch (Netting, 1965); preferred habitat appears to be grassy areas near or in forests - usually found under small rocks, boards or other cover and are often found after heavy rains (Richmond, 1954); under boards, rocks, and other debris (Swanson, 1952). Habitat information from the Carnegie Museum of Natural History collection for Virginia valeriae pulchra included: (1) on Old Epply farm under sheets of corrugated iron (CM 21625); coiled under a board with a Carphophis (CM 26133); under trash in well clearing in woods (CM 32204, CM 32205); in dried leaves near fallen log (CM 35624); under piece of carpet under apple tree (CM 5592); under rock (CM 61020); and under rock in dam overflow (CM 4886).

The habitat descriptions reported for Virginia valeriae pulchra, Virginia valeriae elegans, and Virginia valeriae valeriae (see Introduction for references) appear to be similar in type. They are

open areas near forests (preferably deciduous) strewn with rocks or other suitable cover. It is noteworthy to mention that habitat descriptions for Virginia valeriae valeriae include many instances whereby they have been plowed up in fields. This may imply a burrowing life style. Records for Virginia valeriae elegans and Virginia valeriae pulchra indicate them on the surface under suitable cover (usually rocks) rather than in the ground.

The most common snakes found with Virginia valeriae pulchra were Diadophis punctatus edwardsi and Storeria occipitomaculata. Adult Virginia valeriae pulchra were found with adult and immature Diadophis punctatus edwardsi and Storeria occipitomaculata while in no instance were immature Virginia valeriae pulchra found with adult (large) Diadophis punctatus edwardsi. Predation by Diadophis punctatus edwardsi is suggested. They were found with adult Storeria occipitomaculata. B. Bechtel in his 1942 field notes (Carnegie Museum) mentions finding one Virginia valeriae pulchra under a board with a Carphophis vermis. Christiansen (1973) has found Virginia valeriae elegans to reside in areas with ringneck and worm snakes while Bothner and Moore (1964) have found similar snake associates as shown in Table 1.

Ants and ant mounds are very common in Virginia valeriae pulchra habitat. Ants perform a task that Virginia valeriae pulchra is incapable of, i.e., making tunnels. Virginia valeriae pulchra have been observed in 15 instances to use vacant tunnels of Formica sp. Early in the spring, immature Virginia valeriae pulchra have been

found near the perimeter of and found retreating into Formica sp. mounds. Virginia valeriae pulchra has been found hibernating in Formica sp. mounds. Even though a definitive biological interaction has not been demonstrated between Formica and Virginia, one is strongly suggested. Grissell (1949) and Neill (1948) have published information on hibernacula for Virginia valeriae valeriae and Virginia striatula. They have been found under rocks, logs, debris, and near an excavated woodchuck burrow. Carpenter (1953) found 26 Thamnophis sirtalis, 15 Thamnophis butleri, 11 Thamnophis sauritus, 4 Nerodia sipedon, 2 Storeria dekayi, 2 Storeria occipitomaculata, and 1 Opheodrys vernalis hibernating in an ant mound in Michigan while Criddle (1937) found 8 Thamnophis radix, 101 Storeria occipitomaculata, and 148 Opheodrys vernalis in an ant mound, probably the genus Formica, in Manitoba, Canada. To this author's knowledge, this is the first record of any Virginia using Formica sp. mounds as hibernacula.

Color and Morphology

A. Color

Live specimens of Virginia valeriae pulchra may have a dorsum of reddish brown to dark gray (Conant, 1975), russet tan, suffused with pinkish orange towards the ventrals (Cooper, 1958), and reddish brown (Richmond, 1954). I have found that V. v. pulchra may vary in color from reddish brown through to a smoke gray with the majority (greater than 98%) of the living specimens demonstrating a brownish olive to fuscous brown dorsum suffused with a vinaceous pink color intensifying

towards the ventrals and including the ends of these. The venter for V. v. pulchra may be off white to grayish white or a yellow color (Cooper, 1958; Richmond, 1954). The author has found living specimens to display a cream through to greenish-sulfur color on the venter.

Live specimens of V. v. elegans may have a dorsal color of reddish to grayish brown (Conant, 1975), brick red shading to hay's russet or carrot red on the first 2 or 3 scale rows or hazel, cinnamon-brown, and verona brown with the 2 middorsal rows of scales tawny-olive (Wright and Wright, 1957), dark chestnut or grayish brown (Ditmars, 1936), light brown (Edgren and Ward, 1952), light olivaceous brown to pinkish orange (Hurter, 1911), reddish or gray brown (Anderson, 1965), reddish brown (Christiansen, 1973), and generally dark brown or dark gray with a Covington, Louisiana specimen demonstrating an argus-brown dorsum, grading towards a carrot red on the lower-most row of dorsal scales and on the ends of the ventrals (Blanchard, 1923). The color of the venter for live V. v. elegans may be immaculate white (Christiansen, 1973), dull yellowish white (Hurter, 1911), cream color or grayish white (Anderson, 1965), pale greenish-yellow (Edgren and Ward, 1952), or yellowish-white (Ditmars, 1936).

Live specimens of V. v. valeriae have been reported with a dorsal color of gray or light-brownish gray (Conant, 1975), benzo brown, deep brownish drab, mars brown, or light brownish drab (Wright and Wright, 1957), dark brown or gray (Blanchard, 1923), dark chestnut or grayish brown (Ditmars, 1936), gray or light grayish brown (Ditmars, 1936), gray or light grayish brown (McCauley, 1945), and gray or brown

(Conant, 1938). The only published report describing a pink color for V. v. valeriae is Wright and Wright (1957). They report that under the lens, the scales from an Auburn, Alabama specimen showed a light vinaceous-fawn color with the first row of scales, like the belly, a light vinaceous-fawn, pale vinaceous-fawn, pale grayish vinaceous, or pale vinaceous pink. Richmond (1954) has found the V. v. valeriae usually showed a gray dorsum. The color of the venter for live V. v. valeriae may be whitish (Blanchard, 1923; Conant, 1938; McCauley, 1945) or yellowish-white (Ditmars, 1936)

Color as a rule is a quite subjective character. It has been found that age (Myers, 1962), humidity (Porter, 1972), and temperature (Waring, 1963 citing Zoond and Eyre, 1934) influence color in reptiles. Pre-molt and molting conditions may also influence investigators' descriptions. Myers (1962) found the venter color for V. v. elegans specimens (Neonates: grayish-white; Adults: yellow-green) to be age related. Richmond (1954) found V. v. pulchra neonates to be gray in color. The author has examined 267 V. v. pulchra neonates and has found a superficial gray color prior to their first molt due to the loose epidermal layer. However, when this skin was peeled away a fuscous brown color was apparent.

The dorsal and venter colors for the three subspecies of Virginia valeriae do overlap; however, it would appear from the preceding descriptions that V. v. pulchra resembles the dorsal and ventral colors of V. v. elegans more so than it does V. v. valeriae. V. v. valeriae usually has a gray dorsum (Netting, 1965; Richmond, 1954)

while V. v. pulchra and V. v. elegans specimens usually have dorsum colors of brown. The middorsal stripe of V. v. elegans and that of V. v. pulchra are of the same color, whereas a dorsal stripe for V. v. valeriae has only been mentioned once (Blanchard, 1923) with no color description reported.

B. Size

V. v. pulchra is a small snake as are its two other subspecies. Preserved V. v. pulchra and V. v. elegans specimens may have maximum lengths greater than 300mm while V. v. valeriae specimens seldom reach 275mm. To my knowledge, the largest known V. v. pulchra specimen is 320mm (Richmond, 1954). The longest V. v. elegans reported by Wright and Wright (1957) was 320mm and the longest V. v. valeriae 279mm. All three specimens were females. Females attain greater lengths than males for all three forms. Conant (1938) reported the largest Ohio V. v. valeriae specimen to be 308mm; however, this measurement was probably taken live. Blanchard (1923) found V. v. elegans specimens to be longer in total length than V. v. valeriae. I have examined 22 V. v. elegans and 63 V. v. valeriae and have found none to exceed these measurements. It would appear then that V. v. pulchra and V. v. elegans attain similar maximum total lengths and are both, therefore, longer than V. v. valeriae specimens.

C. Body Proportions

V. v. pulchra (both sexes) had longer average tail lengths (expressed as a percentage of total length) than V. v. elegans and V. v. valeriae specimens. V. v. pulchra demonstrated a closer

affinity to V. v. elegans than to V. v. valeriae for this trait. For all three forms, a highly significant difference was demonstrated between males and females for tail length. Information published for V. v. pulchra tail lengths expressed as a percentage of total length include Cooper (1958), and Richmond (1954); V. v. elegans, Blanchard (1923), Bradford (1973), Edgren and Ward (1952), Pisani and Collins (1971), and Smith (1965); and V. v. valeriae, Blanchard (1923), McCauley (1945), and Pisani and Collins (1971). The results published in these reports are all within one standard error of the mean listed for the three forms in Table 7 with the exception of Smith (1965). He found a mean tail length expressed as a percentage of total length of 16.3% (n=12) for female V. v. elegans.

It is not uncommon for males to have longer tails than females for the hemipenes must occupy a certain minimum tail space. This results in sexual dimorphism, especially in short-tailed genera. Clark (1966) compared the tail lengths for 49 colubrid snakes using the coefficient of divergence (CD) method devised by Klauber (1943). Following this method, comparisons were made for the three subspecies of Virginia valeriae using both neonates and adults. The CD found for tail lengths expressed as a percentage of total length for the 3 subspecies of Virginia valeriae should correlate with their terrestrial or fossorial habits. Clark (1966) found a high CD to correlate with burrowing genera.

The distinction should be made here, I believe, between the terms subterranean and fossorial. I have used the term fossorial as

implying the animal's ability to construct its own tunnel. An example would be the amphisbaenids. Subterranean forms on the other hand are animals that live underground and use tunnels constructed by other animals, or utilize natural cavities beneath the surface. Many other authors use the term fossorial somewhat broadly and have applied it to those snakes that are actually subterranean, yet physically incapable of constructing their own underground passageways.

V. v. valeriae had the highest CD (31.6)—suggesting a greater degree of subterranean activity. V. v. elegans had a CD of 26.2 while V. v. pulchra had a CD of 23.3. Clark (1966), using data from Smith (1965), found that V. v. elegans had CD of 21.3. From this information, the three forms may be considered as subterranean, but V. v. pulchra and V. v. elegans appear to be slightly less adapted for this mode of life than V. v. valeriae. It is possible that the whole species Virginia valeriae is presently undergoing a transition to a more consistently subterranean existence. In colubrid snakes, the dividing line between secretive habits of life under logs or in leaf mold and true subterranean existence is not sharp (Schmidt and Inger, 1957). Schmidt and Inger found many snake taxa that appeared to be passing through a secretive stage before becoming more or less completely subterranean. This may be the case for Virginia valeriae. If this is true, V. v. valeriae should be the most secretive; V. v. elegans less secretive; while V. v. pulchra the least secretive of the three forms. The number of V. v. pulchra collected by this author in northwestern Pennsylvania seems to support the contention that V. v. pulchra is

found more often on the surface and is less subterranean than V. v. valeriae.

The shape of the head in burrowing snakes is functionally very significant (Gans, 1974). Fossorial snakes usually have blunt and rounded heads (Jackson and Reno, 1974). Comparisons for the head shape for the three forms of Virginia valeriae was determined by evaluating the head width expressed as percentage of snout-vent length. Results indicated no significant difference among the three forms for this trait. All three forms show a small head only slightly distinct from the neck.

D. Body Scales

Virginia valeriae pulchra exhibits a strong sexual dimorphism in the number of subcaudal scales and a lesser amount in the number of ventral scales. There is, in addition, an apparent sexual difference in dorsal scale counts for the Sizerville population.

Sexual dimorphism for ventral and subcaudal scales is common and the reasons quite obvious. Males have longer tails than females because the retracted hemipenes need a longer tail to house them. Females have more ventral scales than males because they need longer bodies to carry the eggs and young and are so equipped with more ventral scutes (Klauber, 1972). Scale row reductions may vary ontogenetically with temperature (Fox, 1948). Gadow (1920) found the number of ventral scales corresponded in number to the number of vertebrae.

I have found that V. v. valeriae males have fewer ventral

scales than do males of V. v. elegans or V. v. pulchra, yet the females for these three forms showed no difference. The question arises as to why there is such a dissimilarity. Male V. v. valeriae are smaller in size than the other two forms and this reduction in size probably equates with a reduction in scale number. Klauber (1972) found the number of ventral scales to decrease with a reduction in size in rattlesnakes. Therefore, one can postulate why the males are different, yet why don't the females show the same trend? The reason may be the need of suitable body size with an accompanying ventral scale number to accommodate the developing young.

The number of subcaudal scales (both sexes) was greater for V. v. pulchra specimens than for either V. v. elegans or V. v. valeriae specimens. V. v. pulchra specimens showed a closer affinity with V. v. elegans than V. v. valeriae specimens for this trait. This affinity correlates with tail length expressed as a percent of total length for the three forms. V. v. pulchra has a longer tail, thus more subcaudal scales than V. v. elegans which has a longer tail and more subcaudal scales than V. v. valeriae specimens. As tail length decreases so too does the number of subcaudal scales (Klauber, 1972). The above correlation agrees well with the CD results for tail lengths expressed as a percentage of total length for the three forms.

The dorsal scale count for V. v. pulchra is typically 15-17-17, but other combinations have been demonstrated. These variations from the normal arrangement for V. v. pulchra (Table 2) will, therefore, overlap both the typical dorsal scale counts for V. v. elegans (17-17-

17) and V. v. valeriae (15-15-15). A higher percent of specimens of V. v. pulchra varied from the normal arrangement (20.2%) than did either V. v. elegans (4.8%) or V. v. valeriae (6.3%).

Atypical dorsal scale counts were found in all three V. v. pulchra populations. The males of the Sizerville population showed a significantly greater amount of variability from the normal 15-17-17 arrangement than did all the other specimens. These atypical counts for the Sizerville males were primarily found in the posterior region of the body. Dowling (1967) remarks that "row reductions for most colubrids tend to occur just behind the head, in the 3rd quarter just behind the pylorus, and in the fourth quarter." These reductions in V. v. pulchra may be temperature related for Fox (1948) and Osgood (1978) found that neonates exposed to cooler temperatures during development had significantly fewer scale rows (especially at the posterior end of the body), supralabials, ventrals, subcaudals, and postoculars than those whose mothers had been kept warmer during gestation. Fox emphasized though that his experiment did not prove that the geographic variation of scale characters is without a genetic basis. Klauber (1941) found humidity to affect dorsal scale counts in rattlesnakes. Male Virginia striatula show a decrease in the number of posterior scale rows like the Sizerville male V. v. pulchra population. Such a decrease in scale rows would reduce the proportional amount of skin to scales and thereby decrease the elasticity of the body wall (Clark, 1964). Clark suggested that this genetic tendency was not observed in females because elasticity in the body wall near

the anus would presumably aid in birth of the young and thus a selection against a decrease in posterior scales might be expected in the females.

E. Degree of Keeling in the Dorsal Scales

The scales for the three subspecies of Virginia valeriae may be keeled or smooth. The majority (84.9%) of V. v. pulchra specimens possessed weakly keeled anterior dorsal scales while all midbody and posterior dorsal scales were heavily keeled. The majority (85.7%) of V. v. elegans specimens had smooth anterior dorsal scales while the midbody and posterior dorsal scales were heavily keeled. All V. v. valeriae specimens had smooth anterior and midbody dorsal scales, but the posterior dorsal scales were keeled in 33.3% of the specimens. (When keeled dorsal scales are present, the ridges are more evident on the middorsal rows than on the lateral rows and are absent on rows one and two.)

A continuum can be constructed for keeled scales among the three forms of Virginia valeriae. V. v. pulchra is at one end with the majority of the specimens showing dorsal scales keeled throughout the three body regions. Some V. v. pulchra (15.1%) demonstrated smooth scales in the anterior region. V. v. elegans is positioned next in this continuum with all specimens demonstrating keeled scales in the midbody and posterior regions. Some V. v. elegans (14.3%) demonstrated keeled scales in the anterior region. V. v. valeriae is at the opposite end of this continuum with all specimens demonstrating smooth dorsal scales from

the anterior and midbody regions while some V. v. valeriae specimens (33.3%) demonstrated keeled scales for the posterior region. The keeled scales observed for V. v. pulchra and V. v. elegans specimens in the anterior region are weakly keeled or less ridged than those dorsal scales for the other two regions. The keeled scales in the posterior region for V. v. valeriae are also weakly keeled.

It appears that the evolutionary trend in Virginia valeriae may be a gradual trend away from keeled scales toward smooth ones. This trend begins in the anterior region of the body as shown by V. v. pulchra (15.1% smooth scales), V. v. elegans (85.7% smooth scales) and V. v. valeriae (95.2% smooth scales). This tendency continues caudally with V. v. valeriae being farthest along in this feature (66.7% smooth posterior scales). Whereas V. v. elegans has 14.3% smooth and V. v. pulchra has none (all are keeled). Keeled scales are considered more primitive than smooth scales in the genus Virginia (Richmond, 1954). Smooth scales are more specialized and would tend to streamline the snake's body facilitating subterranean locomotion (Jackson and Reno, 1975). For these reasons, V. v. pulchra is considered to be less specialized (less subterranean) than V. v. elegans which in turn, is less specialized (less subterranean) than V. v. valeriae. This dorsal scale modification is believed to be operative in all three subspecies with V. v. valeriae showing a greater advancement in this condition than the other two forms.

The surface area of a snake creates friction on the sides of a burrow and this adds to the work load of the snake (Schmidt and Inger,

1957). Any protrusions, such as keels, along the body would increase friction and the energy expended through subterranean passageways. This problem according to Schmidt and Inger (1957) has favored the development of smooth scales, cylindrical bodies, and low numbers of scale rows. A diminution in total size would also be advantageous. Jackson and Reno (1975) suggested Virginia striatula was a non-fossorial snake on the basis of its keeled scale and protruding eyes.

Morphologically, V. v. pulchra and V. v. elegans demonstrated greater total lengths, greater tail lengths expressed as a percent of total length, more keeled dorsal scales, and more dorsal scale rows than V. v. valeriae. V. v. valeriae demonstrates more subterranean traits than did V. v. pulchra or V. v. elegans. This author considers both V. v. pulchra and V. v. elegans as less adapted to subterranean existence than V. v. valeriae. Burrowing experiments for V. v. pulchra in the laboratory showed no indication that they have the ability to tunnel through even soft mulch much less through silt-loam soils, but were found to use pre-existing tunnels.

F. Head Scutes

The head scales for the three subspecies of Virginia valeriae showed some variability. The supralabial and infralabial scales usually numbered 6; however, 5 and 7 scales were not uncommon especially in the infralabials for V. v. pulchra. V. v. elegans and V. v. valeriae showed less variability from the normal number of 6 infralabial scales than did V. v. pulchra specimens. The low sample number for V. v. elegans and V. v. valeriae may be the reason.

Postocular scale counts for the three forms of Virginia valeriae usually showed two per side; however, 1 or 3 scales were not uncommon. Pisani and Collins (1971) found a tendency in V. v. valeriae to carry 3 postocular scales more so than did V. v. elegans. Klauber (1943) found a bilateral correlation in scale peculiarities or postocular contacts; any condition existing on one side of the head is much more likely to be duplicated on the other side than if its occurrence there were based purely on chance

One of the two or three postocular scales is usually in contact with the anterior temporal scale for the three forms of Virginia valeriae. V. v. pulchra specimens showed the least departure from this norm of postocular-temporal contact while V. v. elegans and V. v. valeriae specimens demonstrated a great percent of individuals with the two scales separated. This separation has been correlated with a decrease in size of the head which forces rearrangements, and eliminations of the scutes (Blanchard, 1923). Blanchard continues the argument that a dorso-ventral flattening would decrease the space between the parietals and upper labials until eventually they would come in contact with each other. A compaction of the head is associated with a burrowing existence. Gans (1974) has shown the effect of external forces on the various evolved head shapes in amphisbaenids. Since V. v. pulchra shows this trait less than the other two forms, it is considered to be less subterranean than the other two forms. V. v. valeriae has been ploughed from the ground (Carnegie Museum Notes: McCauley, 1945; Wright and Wright, 1957), but not V. v.

pulchra and V. v. elegans.

I believe that the Virginia valeriae Rassenkreis is presently undergoing morphological specializations for a subterranean existence. Such specializations would be: a diminution in size (Blanchard, 1923), a reduction in tail length expressed as percentage of total length (Clark, 1966), a reduction in dorsal scale rows (Schmidt and Inger, 1957), smooth scales (Jackson and Reno, 1975), and a separation in the temporal-postocular scales (Blanchard, 1923). Table 26 depicts the three subspecies of Virginia valeriae and their relationship with each other for the above traits. Using these characters, V. v. valeriae is the most specialized of the three forms while V. v. pulchra is the least.

ADAPTATIONS TO SUBTERRANEAN EXISTENCE


| Character |  | | |
|-----------------------------|--|----------------------|----------|
| | Least | More | Most |
| Size (Total Length) | | *pulchra *elegans | valeriae |
| Tail as % of Total Length | pulchra | elegans | valeriae |
| Dorsal Scale Number | elegans | pulchra | valeriae |
| Keeling (Dorsal Scales) | pulchra | elegans | valeriae |
| Temporal-Postocular Contact | pulchra | elegans | valeriae |

Table 26. Comparison of the three subspecies of Virginia valeriae for adaptations to a subterranean existence. *Denotes the same average size.

It would appear, following Richmond (1954), that V. v. valeriae split off at a very early time from a parent form that had keeled

scales arranged in 17 or more rows, and spread east and north along the coastal plain and Piedmont, while the prototype of V. v. elegans spread north and east in the interior until it reached western Pennsylvania prior to the Wisconsin glaciation and then became separated into two populations by the time of the Wisconsin ice sheet, and that the montane population (V. v. pulchra) in the east persisted throughout the glacial period in or near its present range. V. v. valeriae is the most specialized for subterranean life while V. v. pulchra is the least specialized and presumably has modified the ancestral characteristics the least. Brown (1904) considered the origin of the genus Virginia to be in the Austroriparian district of the Atlantic subregion.

Diet

In this study, V. v. pulchra was found to feed exclusively on earthworms in the field. Clark (1964) found only earthworms in 63 of 170 stomachs examined for Virginia striatula while Bradford (1973) found V. v. elegans and Virginia striatula in the lab to feed only on earthworms even though other prey was offered. Prey items reported for Virginia striatula were: earthworms, beetles, ants, sow bugs, mollusks, small anurans, and young lizards (Anderson, 1965; Bradford, 1973; Clark, 1964; Diani, 1974; Wright and Wright, 1957). V. v. elegans is known to eat earthworms, soft-bodied insects, insect larvae, and cutworms (Anderson, 1965; Bradford, 1973; Wright and Wright, 1957); and V. v. valeriae consumes earthworms, insect larvae, insects, and snails (Conant, 1938; Hamilton and Pollack, 1956; Wright

and Wright, 1957).

Earthworms are plentiful in V. v. pulchra habitat and it is not likely that they limit the densities or distribution of this snake. V. v. pulchra has often been observed to share its habitat with Diadophis punctatus edwardsi, Storeria occipitomaculata, Thamnophis brachystoma, and Thamnophis sirtalis. Of these four forms only Thamnophis brachystoma is known to feed, as does V. v. pulchra, exclusively on earthworms (Wozniak and Bothner, 1966). The other forms seek other items of fare as well, thus reducing competition.

Clark (1970) found no earthworm parts in 65 stomachs examined for Carphophis vermis for July and August. August especially showed a decrease in earthworm parts found in the stomachs for male and female V. v. pulchra. No earthworms were found in V. v. pulchra stomachs in August and only one specimen contained an identifiable earthworm in July samples. These results suggest that the digestion rate for V. v. pulchra is faster for the warmer months (July and August) and slower for the cooler periods (Spring and Fall) of the active season. For this reason, earthworms were more speedily digested in July and August.

The digestion rate for reptiles takes place with the greatest rapidity at temperatures close to the thermal preferendum, but may slow down near the highest temperatures tolerated (Gans, 1978). Henderson (1970) found digestion rates for Diadophis punctatus arnyi were greater at higher temperatures while little or no digestion occurred below 10 to 15.5°C (Benedict, 1932; Leuth, 1941). Henderson also found that digestion rates for Diadophis punctatus arnyi were

dependent upon age and the amount of food consumed; younger snakes appeared to digest food faster than older snakes. This did not appear to be the case for young V. v. pulchra.

The stomach contents of twenty-two young V. v. pulchra (less than 150mm body length) were studied. Eleven had empty stomachs while the remainder had either UFM or earthworms present. However, these young were collected during the cooler periods of the active season.

Thus, identification of earthworms to species ingested by V. v. pulchra was difficult for the characters used to identify Lumbricids are found in the anterior region (Reynolds, 1977). This region includes the area from the prostomium to and including the clitellum. Since the head was swallowed first, digestion was advanced in this area and obliterated key characters. Clark (1970) and Wozniak (1965) discussed similar problems for Carphophis vermis and Thamnophis brachystoma respectively.

Gravid females were observed to feed less often than the non-gravid ones. This was especially noted for the month of August which, for most specimens, is the last month of gestation. The gravid females were found to be responsible for the dissimilarity observed in male and female feeding frequencies for August. Fox (1948) maintained that gravid female Thamnophis elegans atratus fed less often than males and non-gravid females, especially in the last month of gestation.

Earthworms found in the stomachs of V. v. pulchra were of various sizes. Netting (1950) found that V. v. pulchra would eat

different sized earthworms offered to them as long as they were smaller than the snake. No particular species of earthworm appeared to be favored by V. v. pulchra and size alone appeared to dictate the species consumed. Hamilton (1951) found this to be true for Thamnophis sirtalis in New York State.

In V. v. pulchra, feeding frequency appears to be adventitious and to a certain extent dependent upon rainfall. Rainfall would draw earthworms to the surface whereupon V. v. pulchra would feed upon them. Richmond (1954) found V. v. pulchra easier to collect as the soil surface becomes moist from precipitation. This may correlate with the movement of the earthworms toward the surface.

V. v. pulchra fed readily on earthworms in the lab. Small Aporrectodea sp. and Octolasion sp. were given to these captive snakes weekly and room temperatures were kept around 25°C. Leuth (1941) suggested 25° as the optimum temperature to feed small snakes.

Feeding observations demonstrated that when one snake seized an earthworm, usually near the clitellum, the snake would straighten its body and devour the worm in a folded position if it were a small worm. If the worm were larger, the snake would reposition its hold near the head of the earthworm and devour it head first. The feeding activity appeared to incite other snakes to seize the same worm with both snakes devouring and tugging from each end. When the head of the two snakes met, a violent thrashing followed until the worm was drawn from one snake's mouth or was broken. It was not uncommon to find more than two snakes in a confrontation for the same worm.

In the process of swallowing the earthworm, mucus accumulated around the mouth. Soil particles adhered to these mucus-laden areas. When the worm was completely swallowed, the snake would drag or push its head in a tilted fashion along the substrate to rid the labials of this accumulated debris.

In one instance, I observed a neonate female (111 mm in total length) feeding on a small-white worm (most likely Octolasion tyrteum) while a sub-adult female (205 mm in total length) seized the other end of the worm. The larger female then swallowed the worm as well as the attached neonate. The following day, this larger female was killed and upon injecting it with 10% Buffered formalin, the now dead neonate was regurgitated. Stomach analyses for both individuals demonstrated that the small-white worm was within the neonate which in turn was within the larger female. I separated many other snakes that were about to be swallowed in this same manner. Such competitive feeding probably occurs infrequently in nature; however, dry seasons may cause such competition when earthworms are less available.

Thermal Preference, Moisture Selection, and Burrowing Activity

A. Thermal Preference

Thermal considerations are of utmost importance for any ectotherm; indeed, temperature controls all aspects of a reptiles' biology (Bogert, 1959; Brattstrom, 1965; Fry, 1967; Kitchell, 1969; Stewart, 1965; Wilhoft and Anderson, 1960).

Reptilian thermoregulation has received a considerable amount of attention since the pioneer publication of Cowles and Bogert in 1944.

Since then, many thermal studies, especially on lizards, have been published. Brattstrom (1965) and Kozubowski (1980) provide excellent reviews on the available literature. Even though much information has been compiled for snakes, the thermal ecology of V. v. pulchra was unknown.

Snakes may either be heliotherms or thigmotherms. Heliotherms thermoregulate by basking while thigmotherms acquire their heat by conduction from the medium in or on which they live (Brattstrom, 1965). This medium may be air, water, soil, or rock. Heliotherms have the highest body temperatures (Fitch, 1956) and show a higher temperature than that of the substrate. Thigmotherms, on the other hand, have lower body temperatures than heliotherms (Fitch, 1965) with their body temperature coinciding with those of the substrate. The body temperature (T_b) for V. v. pulchra showed no significant difference from that of the substrate (T_s). Therefore, V. v. pulchra is considered a thigmotherm. This is not surprising since almost all the snakes were found under rocks. Only on one occasion did I see this snake lying in the open. On 10 June 1980, at 1330 E.D.T., a gravid female was seen lying ribbon flat amidst some leaves. The day was windy and it had been raining off and on for the past 4 hours. An air temperature of 8.8°C had been recorded at 1230 E.D.T.

V. v. pulchra thermoregulated mainly by use of rocks warmed by the sun. Figure 14 with accompanying Table 16 suggests that when air and substrate (beneath rock) temperatures are suboptimal and higher rock temperatures are available, V. v. pulchra will position its body in contact with the underside of the rock, thus utilizing this

"heat" source. When the underside of the rock reaches too high a temperature, the snake lowers itself from contact with the rock and either lies ribbon-flat under, but not touching, the rock or retires into the ground through available tunnels, crevices, and burrows. Fitch (1956; 1975) found that Diadophis punctatus may maintain temperatures well above those of both the air and soil by this method. Such behavior provides for preferred temperatures without exposing these snakes to possible predation as would basking. This also avoids the cooling effect of any surface winds.

Gravid female V. v. pulchra were found to have higher body temperatures during August than did the males. This tendency has also been found for Agkistrodon contortrix (Fitch, 1960), Thamnophis sirtalis and Thamnophis ordinoides (Stewart, 1965). Fitch (1961) and Fox et al. (1961) showed that delayed parturition and abnormal young resulted when gravid copperheads and gartersnakes were kept at suboptimal temperatures. Blanchard and Blanchard (1940a) estimated that an increase of one degree Fahrenheit in average temperature brings the birth date for gartersnakes four and one half days earlier. The advantage to this would be the shortening of the gestation period with subsequent earlier parturition dates. This is especially significant for populations living within temperature zones where summers are short and cool.

Lower body temperatures were found in male V. v. pulchra in August. Kozubowski (1980) showed a similar August drop for male Thamnophis sirtalis while a drop in July was observed for male Thamnophis brachystoma. In this study and that of Kozubowski, both the males and

females had higher temperatures available to them. Why then did the males opt for lower body temperatures? In August, spermatogenesis is near completion and cessation of the spermatogenic cycle is soon to commence. Fox (1954) found a correlation between retardation of the spermatogenic cycle and lower environmental temperatures for male Thamnophis sirtalis and Thamnophis elegans in California. In Anolis carolinensis, Licht (1971) found that the onset and rate of regression is slightly retarded by high temperatures, whereas low temperatures accelerate the termination of spermatogenesis and initiate regression (Licht, 1972 citing Fischer, 1968). The biological advantage of lower male temperatures in August would be the prolongation of sperm viability prior to fall mating. This has been suggested for Thamnophis sirtalis sirtalis (Rahn, 1940).

The field ecritic temperature for V. v. pulchra was $23.8 \pm 4.5^{\circ}\text{C}$ with a range of 8.6°C to 33.0°C . This was found to be very close to that of Thamnophis sirtalis sirtalis yet less than that for Thamnophis brachystoma. Both species of Thamnophis were studied close to the range of V. v. pulchra. The ecritic temperature for Thamnophis sirtalis sirtalis (n=178) was $23.7 \pm 4.8^{\circ}\text{C}$ with an range of 7.0°C to 34.9°C while Thamnophis brachystoma (n=301) demonstrated an ecritic temperature of $26.2 \pm 4.2^{\circ}\text{C}$ with a range of 6.8°C to 34.4°C (Kozubowski, 1980). Kozubowski's study area (Olean, New York) was but 50 to 70 miles from the Sizerville and Warren areas studied in this manuscript (Figure 2).

It is worthy of mention that all snakes found in the field appeared in a health state. Kluger D.H. (1975) and M.J. Kluger (1978) found that ectotherms, when infected with the bacterium (Aeromonas

hydrophila), selected higher temperatures (at least in a thermal gradient). Survival rates were greater for these animals than for infected ones that didn't seek higher temperatures.

B. Moisture selection.

V. v. pulchra was found to be very resistant to desiccation. Adult V. v. pulchra (both sexes combined) averaged 2.9 ± 0.9 mgs of water lost per gram body weight per hour at less than 10% relative humidity, while subadults averaged 4.8 ± 1.2 . Subadult V. v. pulchra were less resistant to non-cloacal water loss than adults. This may be explained by the difference in the surface:mass ratio between these two groups. Subadults have more area per unit mass than do adults, thus their exposure is greater and consequently give up more water to the environment. The majority of these subadults were born the previous summer (15 August to 13 September). Elick and Sealander (1972) suggested that higher desiccation rates for young would limit their dispersal prior to the onset of cooler autumn weather. Bellairs (1970) and Woods (1973) suggested a greater amount of water loss during ecdysis and young would shed more frequently than adults.

The amount of non-cloacal water loss in V. v. pulchra (both subadults and adults) agrees well with results for V. v. elegans (Table 27). Table 27 shows the desiccation rates for young and adult V. v. pulchra and V. v. elegans, Carphophis vermis, Diadophis punctatus, and Tantilla gracilis. Table 28 depicts the percent soil moisture selected by the above five species. All data included in Tables 27 and 28 have come from Elick and Sealander (1972) with the exception of my data for V. v. pulchra.

| Species | Non-Cloacal Water Loss | | | |
|----------------------------------|------------------------|----|----------|-------------|
| | Adults | N | Mean±SD | Range |
| <u>Virginia valeriae elegans</u> | | 13 | 2.6±0.24 | 1.7 to 4.5 |
| <u>Virginia valeriae pulchra</u> | | 24 | 2.9±0.90 | 1.1 to 4.4 |
| <u>Carphophis vermis</u> | | 24 | 4.3±0.25 | 2.3 to 6.7 |
| <u>Diadophis punctatus</u> | | 28 | 4.7±0.33 | 2.1 to 10.1 |
| <u>Tantilla gracilis</u> | | 10 | 7.3±1.02 | 3.4 to 12.0 |
| | Young | | | |
| <u>Virginia valeriae elegans</u> | | 3 | 6.4±1.67 | 3.2 to 8.7 |
| <u>Virginia valeriae pulchra</u> | | 15 | 4.8±1.20 | 2.8 to 7.3 |
| <u>Carphophis vermis</u> | | 8 | 7.7±0.70 | 4.3 to 11.2 |
| <u>Diadophis punctatus</u> | | 5 | 7.9±1.09 | 5.1 to 11.4 |
| <u>Tantilla gracilis</u> | | 2 | 5.7±0.16 | 5.5 to 5.8 |

Table 27. Milligrams of non-cloacal water lost per gram body weight per hour for young and adult Virginia valeriae elegans, Virginia valeriae pulchra, Carphophis vermis, Diadophis punctatus, and Tantilla gracilis. All results have come from Elick and Sealander (1972) except for Virginia valeriae pulchra. N = sample size; SD = ± one standard deviation unit.

| Species | Percent Soil Moisture | | |
|----------------------------------|-----------------------|------|--------------|
| | N | Mean | Range |
| <u>Virginia valeriae elegans</u> | 15 | *9.5 | 4.3 to 14.6 |
| <u>Virginia valeriae pulchra</u> | 76 | 10.6 | 3.2 to 30.3 |
| <u>Carphophis vermis</u> | 20 | 20.4 | 15.9 to 42.1 |
| <u>Diadophis punctatus</u> | 21 | 19.6 | 4.3 to 26.6 |
| <u>Tantilla gracilis</u> | 2 | 26.4 | 23.2 to 29.6 |

Table 28. The percent soil moisture found for collecting sites for Virginia valeriae elegans, Virginia valeriae pulchra, Carphophis vermis, Diadophis punctatus, and Tantilla gracilis. All data except Virginia valeriae pulchra have come from Elick and Sealander (1972). N = sample size; * indicates median (per. com., Gerald E. Elick).

Desiccation rates and soil moisture preferences indicate that Virginia valeriae pulchra prefers drier habitats and loses less water to the environment than do Diadophis punctatus, Carphophis vermis, and Tantilla gracilis. No differences were observed between Virginia

valeriae pulchra and V. v. elegans for these two measurements. Elick and Sealander (1972) found that "lethal" desiccation rates for V. v. elegans, Storeria occipitomaculata and Storeria dekayi were not significantly different. It appears then that V. v. pulchra would not differ from either of the Storeria species for lethal desiccation rates.

C. Burrowing Activity

Clark (1967) found that burrowing snakes prefer wetter soils than non-burrowers and a definite correlation between habitat selection and the ability to resist desiccation has been found by Bentley and Schmidt-Nielsen (1966), Bogert and Cowles (1947), Elick and Sealander (1972), Krakauer et al. (1968), Noble and Mason (1932), and Prange and Schmidt-Nielsen (1969). Therefore, from the data presented for V. v. pulchra, a non-burrowing existence is indicated; the burrowing experiments in the laboratory reinforce this view.

Time of Appearance

The active season for V. v. pulchra in northwestern Pennsylvania is from late March to late October. Their apparent abundance in the spring may be attributed to warmer surface temperatures and the availability of earthworms on or near the surface. In spring, optimum moisture and temperature regimes exist for a breakdown of leaf litter from the previous fall. This would favor a concentration of earthworms on the surface (Clark, 1970). Spring mating (Klauber, 1972), winter food deprivation (Klimstra, 1958) and rising water table

(Gans, 1974) would also increase the snakes' availability on the surface at this time. Clark (1964) and Pisani and Collins (1971) found a greater occurrence in the spring for Virginia striatula and V. v. elegans respectively than for any other time of the year. Klimstra (1958) observed the same trend for other colubrids in Iowa.

The male:female ratio of V. v. pulchra found near the surface under rocks throughout the active season only differed in August. In August, the gravid females showed a higher availability on the surface than males (both immature and mature) and immature females. It has previously been shown that these gravid females feed less, prefer higher temperatures than the males, and are near completion of their gestational period. These gravid females are then more obvious in August than the other population components because they are seeking higher temperatures thus reducing the number of days until parturition (Fitch, 1960, 1961; Steward, 1965).

The summer decline found for V. v. pulchra is due to elevated substrate temperatures (above animal's voluntary maximum) and also to dry soil conditions. These high substrate temperatures would inhibit earthworm movements to the surface. Also, surface layers in the summer would be sub-optimal for earthworms, for the ground tends to dry out in the summer and nutrient levels on the surface would not be what they were in the spring (Clark, 1970). Rainfall then would moisten and cool the ground, thus attracting both earthworms and snakes to the surface. The author has found the occurrence of V. v. pulchra to decrease with the number of days following a rain. Richmond (1954)

found that the monthly trapping success for Virginia striatula was positively correlated with cumulative rainfall for that month plus the two preceding months. Loveridge (1927) considered the heat of June in Massachusetts an important factor in snake activity and believed that the daily high should fall between 80° to 96°F (26.7°C to 35.6°C) and not below 76°F (24.4°C). Seibert and Hagan (1947) suggested that optimum adjustment occurred between 50°F to 86°F (10°C to 30°C) and snakes retreated underground beyond these limits. Klimstra (1958) showed a direct correlation between increasing monthly air temperatures and reduced availability of snakes on the Eldon Research area, David County, Iowa. Clark (1964) suggested that heat and lack of moisture during the summer were more limiting to the activity of Virginia striatula in Texas than during the winter.

Hibernation for V. v. pulchra begins around mid-October and lasts until mid to late March (approximately 5 months). Emergence from and retirement into hibernation result from thermal overturns. In the spring, a thermal gradient with higher temperatures towards the ground surface would attract snakes upward; in the fall, cooler air temperatures with higher ground temperatures would attract snakes downward.

In this study, four V. v. pulchra were found hibernating in an abandoned Formica exsectoides mound at depths of 40 to 50 centimeters from the ground surface or 80 to 90 centimeters from the top of the mound. In this mound, V. v. pulchra were found hibernating in ant tunnels in the subsoil near the water table with Diadophis punctatus edwardsi and Thamnophis brachystoma. The advantage for hibernating

in such mounds would be access to available tunnels deep enough to protect the snakes from lethal surface temperatures. Carpenter (1953) and Criddle (1937) found other colubrids to use ant mounds as hibernacula (see Habitat Section).

V. v. pulchra is a diurnal animal. Field observations as well as 24-hour studies indicate that V. v. pulchra is most available on the surface under rocks from 1200 to 2100 hours E.D.T. with maximum availability from 1500 to 1800 hours. Seven 24-hour studies were conducted to determine if bias in times of collecting per day were involved. No such bias was found because both studies showed the mid-afternoon and early evening hours as the best time to collect this snake. The only other references on activity patterns for this genus came from Bradford (1973) and Clark (1964). Both men studied Virginia striatula in Texas. Bradford found a nocturnal or at least crepuscular pattern while Clark found a crepuscular or diurnal activity pattern. The discrepancy in activity patterns between V. v. pulchra and Virginia striatula was probably due to the differences in climate for these two forms. Virginia striatula was studied in Texas; V. v. pulchra was studied in northwestern Pennsylvania. Brattstrom (1965) found that many diurnal snakes became crepuscular and/or nocturnal as hot seasons began. This may account for why Virginia striatula was found more often in late evening--twilight hours while V. v. pulchra was most abundant on the surface during mid-afternoon to early evening hours.

The daily occurrence times for V. v. pulchra on the surface under

rocks depends upon the temperature difference between the substrate and ground temperatures. The author found that within the snakes' limits of thermal tolerance, when the substrate temperatures were above ground temperatures more snakes were found per hour on the surface. However, when ground temperatures were greater than substrate temperatures, snakes were not found on the surface and were using the ground as a heat source.

The average daily distances of movement for V. v. pulchra appear to be small. In this study, the mark-recapture method was used. I feel that telemetric methods would be of greater value. Such methods would reduce handling, identify individual specimens and their locations (in or out of the ground), and permit daily, seasonal, and yearly surveillance. Bradford (1973) and Clark and Fleet (1976) used the radioactive labeling method and found a low vagility for Virginia striatula in Texas.

Reproductive Biology

Much information is available on the reproductive biology of reptiles. Reproductive cycles were discussed by Aldridge (1969; 1975; 1979), Aldridge and Metter (1973), Betz (1963), Clark (1970), Fitch (1975), Goldberg and Bezy (1974), Hahn (1964), Jackson and Franz (1981), Kofron (1979), Mahew (1966), Nilson (1980), Pisani and Bothner (1970), Rahn (1942), Srivastava and Thapliyal (1965), Trauth (1979), and Wilhoft (1963). Mating was studied by Aleksiuik and Gregory (1974), Blanchard and Blanchard (1942), Crews (1980), Kubie et al. (1978a, 1978b), Pisani (1976), Trapido (1940), and reproductive

physiology by Aleksjuk and Stewart (1971), Cieslak (1945), Crews (1979), Hahn and Tinkle (1965), Licht (1971; 1972), Licht and Gorman (1970), and Lofts (1972). Crews (1979), Fox (1977), and Fitch (1970) present excellent reviews of the literature available on this topic. However, the reproductive biology of Virginia has received scant attention. Bradford (1973) studied Virginia striatula and V. v. elegans while Clark (1964) and Clark and Fleet (1976) reported information on Virginia striatula alone. Reproductive information on V. v. valeriae and V. v. pulchra, other than parturition data, is lacking. The reproductive patterns for V. v. pulchra are next discussed and comparisons with its congenetics are made.

Sexual maturity was attained at an earlier age in male V. v. pulchra than in females. Bradford (1973) and Clark (1964) showed the same trend for Virginia striatula. Male V. v. pulchra began reaching sexual maturity in the fall of their second year (24 months from birth) when snout-vent lengths of 147-157mm (preserved) were achieved. Male Virginia striatula and V. v. elegans reached sexual maturity at 142mm (Clark, 1964). According to Bradford (1973), a snout-vent length of 142mm places these males in the late summer-fall of their second year.

Female V. v. pulchra began reaching sexual maturity in the spring of their fourth year (44 months from birth) when snout-vent lengths of 200mm to 211mm were observed. Virginia striatula reached sexual maturity at a snout-vent length of 177mm (Bradford, 1973) or 182mm (Clark, 1964). According to Bradford (1973), these females are in the spring of their fourth year.

The seasonal development of the testes was examined in V. v. pulchra. Seminiferous tubular diameters and testicular enlargement were at a maximum in July. Bradford (1973) found the testes of Virginia striatula in Missouri to be largest in August. Clark (1964) reported this condition in Texas in September or October. Testes were largest in July for V. v. elegans in Missouri (Bradford, 1973). Seminiferous tubules reached maximum size in July and August for Virginia striatula and V. v. elegans.

V. v. pulchra is a temperate zone snake that shows a pre- and post-copulatory pattern of gametogenesis, similar to the pattern found in Thamnophis sirtalis parietalis (Crews and Barstka, 1982). Female V. v. pulchra are ovoviviparous.

The spermatogenic cycle for V. v. pulchra is very similar to those of Virginia striatula and V. v. elegans (Bradford, 1973), and differs from them in only two minor points. They are: (1) the Sertoli syncytium is more prominent in the spring for V. v. pulchra than for the other two forms, and (2) the predominance of primary and secondary spermatocytes appear to persist longer in V. v. pulchra than in either Virginia striatula or V. v. elegans. Other than these two differences, V. v. pulchra, V. v. elegans, and Virginia striatula agree well as to the appearance and predominance of different cell types in the seminiferous tubule at various times of year. These differences probably represent an adjustment to climate.

Four size groups of ovarian follicles representing three age classes in V. v. pulchra were found. Kofron (1979) found similar sized groups of follicles for Storeria dekayi, and Pisani and Bothner (1970)

for Thamnophis brachystoma and Thamnophis sirtalis. Description of follicles agrees with Betz (1963). The percentage of females immature in the spring of their fourth year agrees with that of Clark (1970).

Corpora lutea were found throughout the gestation period. Rahn (1938; 1939) identified these structures in the genus Virginia; however, their persistence throughout the gestation period has not previously been reported. Bragdon (1952) contends that as a general rule, live-bearing squamates, such as V. v. pulchra, retain corpora lutea throughout pregnancy. Whether or not corpora lutea are essential for the maintenance of gestation in V. v. pulchra is unclear (Fox, 1977). Clausen (1940) and other authorities believe that it is more important in the early stages of gestation. Ovarectomies performed early in gestation elicit resorption of embryos; during the middle of the gestation period it causes the embryos to be born dead. At late gestation, the operation has no effect and parturition is normal (Fox, 1977). In V. v. pulchra, corpora lutea regress rapidly after parturition.

V. v. pulchra ovulates in May or early June as does Virginia striatula in Texas (Clark, 1964). The gestation period for V. v. pulchra extends from 3 May (earliest known date of ovulation) to 20 September (latest known date for parturition). Parturition dates have been recorded from 16 August to 20 September. Thus, the gestation period for V. v. pulchra averages about 15 weeks (105 days). Clark (1964) found the gestation period to extend for 10 weeks in Virginia striatula from Texas. The difference in times of gestation in these

two species is presumably determined by climate. V. v. pulchra were collected from northwestern Pennsylvania where cool, short summers are the rule while the Texas Virginia striatula were exposed to much warmer temperatures that would reduce the length of the gestation period (Bellairs, 1970). Gestation in Thamnophis sirtalis may vary from 87 days in an exceptionally hot summer to 116 days in an unusually cold one (Blanchard and Blanchard, 1940a). Summer temperatures for collecting sites of V. v. pulchra average 19.0°C (Morey, 1931). Such temperatures as these would certainly prolong embryonic development.

V. v. pulchra has one litter per year anywhere from 16 August to 20 September. Litters average 6.0±1.8 young with a range of 2 to 11. Parturition dates and litter sizes found in this study agree with those of Bothner and Moore (1964), Cooper (1958), Netting (1950), Pisani (1971), Richmond (1954), and Swanson (1952). An unusually large litter of 14 was reported by Pisani (1971); however, his average was 5.9 young for 6 litters. Clark (1964) found an average of 4.94 young per brood (Range 3-8) for Virginia striatula. Fitch (1970) reviewed litter sizes for Virginia striatula (n=17 litters) published by Carpenter (1958), Sabath and Worthington (1959), and Wright and Wright (1957). An average of 5.24 young per brood was found born anywhere from late June to mid-August. V. v. elegans showed similar size litters as Virginia striatula (Anderson, 1965; Christiansen, 1973; Keeler, 1956; Myers, 1962; Pisani and Collins, 1971; Smith, 1956, 1961; Wright and Wright, 1957). Less information is available for V. v. valeriae on litter size. McCauley (1945) reports 5 litters of

4, 6, 7, 7, 8 young for V. v. valeriae while Wilson and Friddle (1950) found one litter of 6. Groves (1961) reported on two litters of 14 and 11 young born on 10 August 1963 and 13 August 1960. Ditmars (1936), D.J. Walker (1963), and Wright and Wright (1957) found similar sized litters for V. v. valeriae. It would appear that all the forms of Virginia are rather consistent in number of young born per litter. The only difference appears in parturition dates. Those Virginia in northerly locations appear to give birth later in the season. A sex ratio of 1:1 (neonates) was found for V. v. pulchra as was Virginia striatula (Clark, 1964; Clark and Fleet, 1976).

Extrauterine migration of ova was observed in 25% of the gravid V. v. pulchra females examined. Legler (1958) reported that 57% of the Terepene ornata he examined showed extrauterine ova migration. Kofron (1979) found a frequency of 41.2% for Storeria dekayi. Betz (1963) found a similar disparity between the number of corpora lutea in the ovary on one side and the number of embryos in the uterus on the same side for Natrix rhombifera. He attributed such a phenomenon to extrauterine migration of ova to the contralateral uterus. The right oviduct showed more embryos than the left in V. v. pulchra. Clark (1964) found this to be true for Virginia striatula.

V. v. pulchra young are quite large at birth, averaging a total length of 40.6% that of their particular mother (n=205 young). Richmond (1954) found an average of 36.0% for 25 young. He found them to be relatively larger than Storeria dekayi or Storeria occipitomaculata young. Storeria dekayi gave birth to an average of

14.9 young per litter (Kofron, 1979) while Storeria occipitomaculata averaged 15.5 young per litter (Nelson, 1969). In general, the fewer young there were in a litter, the larger they were at birth (Fitch, 1970). Since Storeria dekayi and Storeria occipitomaculata give birth to more young than V. v. pulchra, one might expect them to be smaller. Thus, V. v. pulchra gives birth to fewer but larger young than Storeria dekayi or Storeria occipitomaculata.

Mating was found to occur for V. v. pulchra in the spring and fall. Mating pairs were found twice in the spring (3 April 1980 and 18 May 1981). One pair was discovered in leaf litter while the other was under a small, thin rock. In both cases the male's right hemipenis was inserted. Cloacal smears for the Fall of 1981 demonstrated motile sperm. According to Fitch (1960), this indicated recent mating.

Spermatozoa were also found in mature females in the summer; however, these sperm were in a shrivelled condition and represent spermatozoa that were carried over in the lumen from spring copulations.

Blanchard and Blanchard (1942) suggested that spermatozoa from spring copulations in Thamnophis sirtalis did not survive to the next spring while Fox (1956) showed they did not last through to parturition.

Rahn (1940) reported that sperm survival was temperature dependent. Lower temperatures promoted sperm survival while high temperatures reduced their survival. Hence, high summer temperatures may very well cause the shrivelled condition observed.

Fall mating is an interesting phenomenon. This is the first written report of it for the genus Virginia. It has also been found

in Thamnophis (Aleksiuk and Gregory, 1974; Blanchard and Blanchard, 1942; Fox, 1946) and Storeria (Trapido, 1940). In this study, sperm were seen to enter seminal receptacles in the fall. These receptacles were located in the distal third of the oviduct. Fox (1956) believed that these receptacles nourished, protected, and reduced sperm activity, thus enhancing sperm survival. Low temperatures in the winter further increased sperm survival. Whether or not V. v. pulchra maintained sperm viability and the capacity to fertilize in the following spring is unknown. The considerable investment of energy by the snakes for gametogenesis and mating activities would appear to mandate delayed fertilization; however, further investigations are necessary. The biological advantages for fall mating might be: (1) assurance of fertilization in the spring with or without a male present; (2) continuance of sparse populations (Fitch, 1960), and (3) colonization by the female of new areas in the absence of a mate.

Fat bodies were present in every V. v. pulchra examined. All temperate zone reptiles show them (Hahn and Tinkle, 1965). In the spring, fat bodies were larger in females than in males because in females fat from these bodies passes to the liver where it is processed to form yolk for the developing oocytes in the ovary (Bellairs, 1971). The gradual loss of fat bodies in females in the summer coincides with an increase in embryonic development. The females feed little during gestation and even less as gestation progresses. The incorporation of much of this fat then nourishes the female and embryos. After parturition, fat bodies increase with increased

feeding. In contrast, males showed a steady increase in fat body weight from May through August. In March, April and September, lower values were observed. These times correspond with spring and fall mating. The fat reserves of males may thus be reduced by energy demands during the breeding season (Fox, 1977; Jackson and Franz, 1981). Gregory (1971) found that food intake in male Thamnophis sirtalis parietalis does not occur during spring mating under natural conditions. Male V. v. pulchra showed only slight traces of fat in the spring and a sharp decrease in September from the August high. These observations agree with those of Gregory (1971) and suggest that feeding is inhibited during mating activities. Also, greater activity uses up the males' fat reserves (See diet section, Table 9).

Male V. v. pulchra, upon emerging from hibernation, show less fat reserves than do the females. Twelve males sampled in March and April averaged 0.7% fat per total body weight. Eight females sampled for the same period showed an average of 3.5%. It is believed this is due to the males entering hibernation with lower fat reserves than females. Once in a state of hibernation, the metabolic rate would presumably be equal. A single male (2.3% fat) and a single female (4.3% fat) were sampled for the previous October. This would suggest that the observed contention is correct; however, the sample number is too small to allow definitive comment.

Population Structure

Population studies of snakes are uncommon. Those studies available include information on Masticophis taeniatus taeniatus (Parker,

1976), Crotalus horridus horridus, Coluber constrictor flaviventris, Elaphe obsoleta obsoleta (Fitch, 1961, Stickel et al., 1980), Agkistrodon contortrix contortrix (Fitch, 1960), Thamnophis radix, Thamnophis sirtalis, Opheodrys vernalis (Siebert and Hagen, 1947), Diadophis punctatus edwardsi (Blanchard et al., 1979; Fitch, 1975), Carphophis vermis (Clark, 1970), Tantilla coronata (Semlitsch et al., 1981), and Virginia striatula (Bradford, 1973).

Snake populations are believed to fluctuate drastically (Fitch, 1961). Klimstra (1958) worked on several common snakes in Iowa and Illinois (Coluber, Elaphe, Heterodon, Nerodia, Thamnophis), and suggested that their populations actually are cyclic. Fitch (1961) contended that Klimstra's attempt to show that these changes constituted a cycle was unconvincing. Whether or not V. v. pulchra is cyclic is unknown. However, fluctuations from year to year most certainly do occur.

Population studies necessitate knowing the exact age of the animals collected. Two methods have been used to determine age in snakes. The first method is plotting snout-vent length against date collected (Bradford, 1973; Jackson and Franz, 1981; Quinn, 1979). When sufficient numbers of snakes are available, age classes are distinguishable by this method. This method is only effective when growth rate is significant, for, when growth rate approaches zero, as is the case with V. v. pulchra, when 6-7 years old, this method is useless. The second method is marking neonates and collecting them in later years and measuring their gain in length (Fitch, 1975). When enough

are recaptured and measured, age classes and growth rates can be determined. It is worthy of mention that if the marking technique involves tissue destruction it will adversely affect growth. Fitch (1975) found that marked animals failed to grow normally for about a month after processing. He also found that this stunting effect disappeared about four to six months after the injury was received.

In this study, the snout-vent length was plotted against dates collected. However, the mark-recapture method is strongly advised for any future studies on V. v. pulchra; this method would disclose, beyond a doubt, longevity in male and female V. v. pulchra which I tentatively set at six years for males and seven years for females using the snout-vent length method. Another more exact method devised by Peabody (1958) is counting annual growth rings in the ectopterygoid bone. This method is good for temperate snakes that hibernate, but is too destructive for a form as uncommon as V. v. pulchra.

Growth rates for male and female V. v. pulchra were similar from birth through the third year (=3rd active season). Thereafter, the females grew more than the males. Bradford (1973) found a similar trend in Virginia striatula.

In V. v. pulchra, females appear to live longer than males. Virginia striatula (Bradford, 1973), Agkistrodon contortrix contortrix (Fitch, 1961), and Elaphe obsoleta obsoleta (Stickel et al., 1980) show the same phenomenon. This is attributed to a higher mortality rate in males than females, and is probably due to the males more active life and wandering tendencies (Fitch, 1961). Since most food

is obtained by awaiting the approach of the prey rather than by active search (Fitch, 1961) the more active male V. v. pulchra would be more likely to encounter a predator.

Adult V. v. pulchra were found more often than immatures. This situation was also reported for Virginia striatula (Bradford, 1973), Agkistrodon contortrix contortrix (Fitch, 1960), and Thamnophis sirtalis, Carphophis amoenus, and Agkistrodon contortrix (Aldridge, 1969). This may be due to the fact that juveniles move less than adults (Semlitsch et al., 1981) and/or spend more time in concealment.

The sex ratio for V. v. pulchra was essentially 1:1 (218 males: 254 females). Virginia striatula (Bradford, 1973) showed a similar 1:1 sex ratio as did Storeria occipitomaculata (Blanchard, 1937). Most other studies show a predominance of males (Fitch, 1960, 1975; Gregory, 1974; Parker, 1976; Semlitsch et al., 1981). The higher ratio of males to females found in the above studies may be due to a bias in sampling. Fitch (1975) believes that such a bias could arise from the fact that sexually mature males are more active than mature females or immatures of either sex, causing these males to be found more often. Time of collecting during the active season would influence a male-female ratio too (See Period of Occurrence).

Competitors, Predators, and Defense Mechanisms

Shelter is not considered a limiting factor for V. v. pulchra, yet food may be, especially during the dry summer. Henderson (1974) found snakes with similar food preferences in the same general habitat at the same time. Diadophis punctatus, Storeria occipitomaculata,

Storeria dekayi, Thamnophis brachystoma, and Thamnophis sirtalis, all feed on earthworms and are found in the same habitat with V. v. pulchra. Diadophis punctatus feeds on many different types of small terrestrial animals and is considered euryphagous (Fitch, 1975). Salamanders, worms, and small reptiles are their primary diet with Plethodon cinereus the preferred prey item (Blanchard et al., 1979). Storeria occipitomaculata and Storeria dekayi feed solely on slugs and earthworms (Hamilton and Pollack, 1956; Judd, 1954). Thamnophis sirtalis feeds primarily on earthworms and amphibians (Hamilton and Pollack, 1956; Wozniak and Bothner, 1966) and to a lesser extent on insects, fish, and snails (Hamilton, 1951). Thamnophis brachystoma feeds solely on earthworms (Wozniak and Bothner, 1966). V. v. pulchra, like Thamnophis brachystoma, feeds solely on earthworms. If any strong competition existed, it would be between these latter two snakes. The predominance of V. v. pulchra in small, isolated colonies suggests to this observer that their numbers reflect habitat specificity and possibly competition for food. Furthermore, larger snakes most likely would prey on all sizes of earthworms while smaller snakes would be restricted to the smaller ones. Henderson (1974) found snakes of the same size tend to have similar food preferences which would increase competition for this food source.

Predation is probably only minimal on V. v. pulchra. These snakes are very secretive. They are found under rocks and are rarely ever seen in the open. Even then, their color blends extremely well with the background colors of the rocks and leaf litter. Milksnakes have been shown to feed on V. v. pulchra, but are not common in V. v.

pulchra habitat (See Table 7). Diadophis punctatus edwardsi may feed on smaller V. v. pulchra (Gehlbach, 1974). He found that Diadophis punctatus arnyi and Diadophis punctatus regalis fed on small Virginia and Sonora. Christiansen (1973) found a V. v. elegans in the stomach of a D. P. arnyi. Potential predators of V. v. pulchra which have been documented for other small colubrids of equivalent size are chipmunks (Hamilton, 1939; McKeever, 1958), feral house cats (Fitch, 1960), opossums (Bradford, 1973; Fitch, 1960, 1975), skunks (Fitch, 1975), eastern mole (Fitch, 1960, 1975), and the red-tailed hawk (Conant, 1938; Fitch, 1960, 1975). The short-tailed shrew is also a potential predator. All of these animals have been seen in or near V. v. pulchra habitat and are potential predators. Many V. v. pulchra were collected with broken (incomplete) tails. The eastern mole, chipmunk, or short-tailed shrew could be responsible. Fitch (1975) found many Diadophis punctatus bore scars on their bodies, especially on their tails, that he interpreted as shrew bites.

The predator-escape technique observed in V. v. pulchra has also been documented for Virginia striatula (Kirk, 1972), who reported that Virginia striatula clamped its jaws over the predator's glottis. In this study, V. v. pulchra simply grabbed the lining of the mouth. Both behaviors produced the same results; that is, release of the prey. In nature, the prey probably would have escaped.

Defense postures for V. v. pulchra include protecting the head, death-feigning, and gaping of the mouth (exposing the teeth). Carpenter and Ferguson (1977) and Conant (1938) reported gaping for

Virginia valeriae while Keeler (1956) found "death-feigning" in V. v. elegans. Protecting the head is a common behavior found in many small snakes. The actual effectiveness of such behavior patterns remains to be evaluated.

SUMMARY

1. V. v. pulchra is confined to the unglaciated Allegheny Plateau of western Pennsylvania, eastern West Virginia, and western Maryland and shows a disjunct distribution within its range.
2. V. v. pulchra typically inhabits herbaceous, leaf-littered clearings bordered by wooded areas with flat, fine sandstone rocks. These clearings have gentle to moderate slopes and tend to be located near water on well-drained soils facing any direction except north.
3. A study of size, body proportions and scalations show V. v. pulchra to be the most primitive from the species' presumptive ancestral form. It is the least subterranean of the three subspecies and, in this, resembles V. v. elegans more closely than the more derived V. v. valeriae.
4. Dorsal scale counts for V. v. pulchra ranged from 17-17-17 to 15-15-15 with 15-17-17 the most common. These are usually keeled.
5. V. v. pulchra feeds solely on earthworms, with gravid females feeding less often than non-gravid ones.
6. V. v. pulchra is a thigmotherm with an ecritic temperature of $23.8 \pm 4.5^{\circ}\text{C}$.
7. In August, gravid (incubating) females prefer higher temperatures than do males.
8. V. v. pulchra moves for only short distances and thermoregulates more by vertical rather than horizontal movements.
9. V. v. pulchra is similar to V. v. elegans in resistance to desiccation. Immature V. v. pulchra have higher rates of non-cloacal water loss than do adults.
10. V. v. pulchra show diurnal activity patterns and are observed more in the spring and the fall than in summer.
11. Immature V. v. pulchra are less commonly encountered than are adults.
12. V. v. pulchra are most readily observed during or immediately after a rain.

13. Sexual maturity in male V. v. pulchra is reached in the fall of their second active season when a snout-vent length of 158 to 168mm is achieved.
14. Sexual maturity in female V. v. pulchra is reached in the spring of the fourth year when a live snout-vent length of 214 to 227mm is achieved.
15. Spermatogenesis reaches a peak in July.
16. V. v. pulchra mates both in the spring and fall.
17. Ovulation can occur anytime from the first week in May to mid-June.
18. Parturition extends from 16 August to 20 September; the gestation period lasting for approximately 105 days.
19. Litter size ranges from 2 to 11 with an average of 6.0 ± 1.8 .
20. Males appear to live 6 years or more while females live seven years or more.
21. Growth rates for both male and female V. v. pulchra are similar from birth through the third active season. Thereafter, females grow at a faster rate than males.
22. In the V. v. pulchra population, a sex ratio of 1:1 was found.
23. In the laboratory, the milksnake was found to prey on V. v. pulchra.
24. V. v. pulchra was observed using a defense technique of biting and holding on to the lining of the milksnakes' mouth.
25. Death feigning, hiding the head, and a threatening strike posture were other presumptive defense mechanisms observed.

LITERATURE CITED

- Abbe, C., Jr. 1902. The physiography of Garrett County. Md. Geol. Surv. 3:27-54.
- Aldridge, R. D. 1969. The reproductive cycle and some aspects of the ecology of the worm snake, Carphophis amoenus, in Missouri. Unpublished Master's Thesis, University of Missouri Library. Pp. 42.
- _____. 1975. Environmental control of spermatogenesis in the rattlesnake Crotalus viridis. Copeia 1975(3):493-496.
- _____. 1979. Seasonal spermatogenesis in sympatric Crotalus viridis and Arizona elegans in New Mexico. Journal of Herpetology 13(2):187-192.
- Aldridge, R. D. and D. E. Metter. 1973. The reproductive cycle of the western worm snake, Carphophis vermis, in Missouri. Copeia 1973(3):472-477.
- Aleksiuk, M. and P. T. Gregory. 1974. Regulation of seasonal mating behavior in Thamnophis sirtalis parietalis. Copeia 1974(3):681-688.
- Aleksiuk, M. and W. Stewart. 1971. Seasonal changes in the body composition of the garter snake (Thamnophis sirtalis parietalis) at northern latitudes. Ecology 52(3):485-490.
- Anderson, P. 1965. The Reptiles of Missouri. Univ. of Missouri Press, Columbia, Missouri. Pp. 330.
- Atkinson, D. A. 1901. Reptiles of Allegheny County, Pa. Annals of the Carnegie Museum 1:145-157.
- Baker, O. E. 1936. Atlas of American Agriculture: Physical basis including Land Relief, Climate, Soils, and Natural Vegetation. U. S. Dept. of Agric., U. S. Gov. Printing Office, Washington, D. C.
- Beck, M., G. Cannelos, J. Clark, W. Curry, and C. Loehr. 1975. The Laurel Hill Study. Ms. of Regional Planning, Grad. School of Fine Arts, University of Pennsylvania. Pp. 301.
- Bellairs, A. 1970. The Life of Reptiles. Volume II. Universe Books, New York City. Pp. 283-590.

- Bellairs, R. 1971. Developmental Processes in Higher Vertebrates. Logos Press Ltd., London.
- Benedict, F. G. 1932. The physiology of large reptiles. Publs. Carnegie Instn., No. 425. Pp. 1-539.
- Bentley, P. J. and K. Schmidt-Nielsen. 1966. Cutaneous water loss in reptiles. Science 151:1547-1549.
- Betz, T. W. 1963. The gross ovarian morphology of the Diamond-backed Water Snake, Natrix rhombifera, during the reproductive cycle. Copeia 1963(4):692-697.
- Blanchard, F. N. 1923. The snakes of the genus Virginia. Papers of The Michigan Academy of Science, Arts and Letters 3:343-365.
- _____. 1937. Data on the natural history of the Red-bellied Snake, Storeria occipito-maculata (Storer), in northern Michigan. Copeia 1937(3):151-162.
- Blanchard, F. N. and F. C. Blanchard. 1940a. Factors determining time of birth in the garter snake Thamnophis sirtalis sirtalis (Linnaeus). Papers of The Michigan Academy of Sciences, Arts and Letters 26:161-176.
- _____. 1942. Mating of the garter snake Thamnophis sirtalis (Linnaeus). Papers of the Michigan Academy of Sciences, Arts and Letters 27:215-234.
- Blanchard, F. N., M. R. Gilreath, and F. C. Blanchard. 1979. The Eastern Rigneck Snake (Diadophis punctatus edwardsi) in northern Michigan (Reptilia, Serpentina, Colubridae). Journal of Herpetology 13(4):377-402.
- Bleakney, J. 1958. A zoogeographical study of the amphibians and reptiles of eastern Canada. National Museum of Canada, Bulletin No. 155. Pp. 1-119.
- Bogert, C. M. 1959. How reptiles regulate their body temperature. Sci. Am. 200:105-120.
- Bogert, C. M. and R. B. Cowles. 1947. Moisture loss in relation to habitat selection in some Floridian reptiles. American Museum Novitates, No. 1358:1-34.
- Bothner, R. C. and T. R. Moore. 1964. A collection of Haldea valeriae pulchra from western Pennsylvania, with notes on some litters of their young. Copeia 1964(4):709-710.
- Bradford, J. 1973. Reproduction and ecology of two species of earth

- snakes: Virginia striatula and Virginia valeriae. Univ. of Missouri, Columbia, Ph.D. dissertation. Pp. 105.
- Bragdon, D. E. 1952. Corpus luteum formation and follicular atresia in the common garter snake - Thamnophis sirtalis. Jour. of Morphology 91:413-446.
- Brattstrom, B. H. 1965. Body temperatures of reptiles. Amer. Midl. Nat. 73(2): 376-422.
- Braun, E. L. 1950. Deciduous Forests of Eastern North America. The Blakiston Company, Philadelphia. Pp. 596.
- Brode, W. E. and P. Allison. 1958. Burrowing snakes of the panhandle counties of Mississippi. Herpetologica 14:37-40.
- Brown, A. E. 1904. Post glacial nearctic centers of dispersal for reptiles. Proceedings of the Academy of Natural Sciences of Philadelphia 56:464-474.
- Campbell, H. W. 1962. An extension of the range of Haldea valeriae in Florida. Copeia 1962(2):428-439.
- Carpenter, C. C. 1953. A study of the hibernacula and hibernating associations of snakes and amphibians in Michigan. Ecology 34 (1):74-80.
- _____. 1958. Reproduction, young, eggs and food of Oklahoma snakes. Herpetologica 14(2):113-115.
- Carpenter, C. C. and G. W. Ferguson. 1977. Variation and evolution of stereotyped behavior in reptiles, pp. 335-554. In Carl Gans and Donald Tinkle (eds.), Volume 7, Biology of Reptilia. Academic Press, New York.
- Cerutti, J. R. 1971. Warren County Pennsylvania Interim Soil Survey Report. Volumes I and II. U. S. Dept. of Agric., The Pennsylvania State University.
- Christiansen, J. L. 1973. The distribution and variation of the Western Earth Snake Virginia valeriae elegans (Kennicott) in Iowa. Proceedings Iowa Acad. Sci. 80(3):167-170.
- Chew, R. M. and A. E. Dammann. 1961. Evaporative water loss of small vertebrates, as measured with an infrared analyzer. Science 113: 384-385.
- Cieslak, E. S. 1945. Relations between the reproductive cycle and pituitary gland in the snake Thamnophis radix. Physiological Zoology 18:299-329.

- Clark, D. R. 1964. Reproduction and sexual dimorphism in a population of the rough earth snake, Virginia striatula (Linnaeus). Texas Journal of Science 16:265-295.
- _____. 1966. Notes on sexual dimorphism in tail length in American snakes. Transactions of the Kansas Academy of Science 69:226-232.
- _____. 1967. Experiments into selection of soil type, soil moisture level, and temperature by five species of small snake. Trans. Kansas Acad. Sci. 70(4):490-496.
- _____. 1970. Ecological study of the worm snake Carphophis vermis (Kennicott). Univ. of Kansas Publications Museum of Natural History 19(2):85-194.
- Clark, D. R. and R. R. Fleet. 1976. The rough earth snake (Virginia striatula): Ecology of Texas population. The Southwestern Naturalist 20(4):467-478.
- Clausen, H. J. 1940. Studies on the effect of ovariectomy and hypophysectomy on gestation in snakes. Endocrinology 27:700-704.
- Claussen, D. L. 1967. Studies of water loss in two species of lizards. Comp. Biochem. Physiol. 20:115-130.
- Cliburn, J. W. 1958. Notes on some snakes from Mississippi. The American Midland Naturalist 60(1):196-201.
- Conant, R. 1936. Virginia valeriae valeriae in Pennsylvania. Herpetologica 1(1):17.
- _____. 1938. The Reptiles of Ohio. The American Midland Naturalist 20(1):1-201.
- _____. 1975. A Field Guide to Reptiles and Amphibians of Eastern/Central North America. 2nd edition, Houghton Mifflin Company, Boston. Pp. 429.
- Cooper, J. E. 1948. Extension of the range of the eastern ground snake in Maryland. Maryland Naturalist 18(3):51-52.
- _____. 1958. The snake Haldea valeriae pulchra in Maryland. Herpetologica 14:121-122.
- Cowles, R. B. and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. 83:261-296.

- Crews, D. 1979. Endocrine Control of Reptilian Reproductive Behavior, pp. 167-222. In C. Berger (ed.), Endocrine Control of Sexual Behavior. Raven Press, New York.
- _____. 1980. Studies in Squamate Sexuality. *BioScience* 30(12): 835-838.
- Crews, D. and W. R. Garstka. 1982. The ecological physiology of a garter snake. *Scientific American* 1982 (Nov.):158-168.
- Criddle, S. 1937. Snakes from an ant hill. *Copeia* 1937(2):142.
- Dailey, P. W., Jr. 1971. Revised ed. "Climate of Pennsylvania." U. S. Dept. of Commerce, NOAA, Climatology of the U. S. No. 60-36. Washington: Government Printing Office.
- Dawson, W. R., V. H. Shoemaker, and P. Light. 1966. Evaporative water losses of some small Australian lizards. *Ecology* 47:589-594.
- Denny, C. S. 1956. Surficial Geology and Geomorphology of Potter County Pennsylvania. Geological Survey Professional Paper 288, U. S. Government Printing Office, Washington.
- Diani, A. R. 1974. A comparative study of the Ophidian digestive tract. Saint Louis University, Ph.D. dissertation. Pp. 256.
- Ditmars, R. L. 1936. The reptiles of North America. Doubleday, Doran and Co., Inc., Garden City, New York. Pp. 476.
- Dowling, H. G. 1957. Amphibians and reptiles in Arkansas. *Occ. Pap. Univ. Arkansas Mus.* 3:1-51.
- _____. 1967. Hemipenes and other characters in colubrid classification. *Herpetologica* 23(2):138-142.
- Downie, N. M. and R. W. Heath. 1970. Basic Statistical Methods. 3rd edition, Harper and Row Publishers, New York. Pp. 356.
- Edgren, R. A. and D. B. Ward. 1952. The western ground snake, Haldea valeriae elegans; in Indiana. Chicago Academy of Sciences, *Natural History Miscellanea* 95:1-3.
- Elick, G. E. and J. A. Sealander. 1972. Comparative water loss in relation to habitat selection in small colubrid snakes. *The American Midland Naturalist* 88(2):429-439.
- Fenneman, N. M. 1938. Physiography of Eastern United States. McGraw-Hill Book Co., Inc. Pp. 714.

- Ferguson, G. A. 1966. *Statistical Analysis in Psychology and Education*. 2nd edition, McGraw-Hill Book Co., New York. Pp. 446.
- Fischer, K. 1968. Untersuchungen zur Jahresperiodik der Fortpflanzung bei männlichen Ruineideeschsen (Lacerta sicula campestris, Betta). II. Einflüsse verschiedener Photoperioden und Temperaturen auf die Progressions - und die Regressionsphase. *Z. Vergl. Physiol.* 61:394-419.
- Fitch, H. S. 1956. *Temperature Responses of Free-living Amphibians and Reptiles of Northeastern Kansas*. University of Kansas Publications, 8(7):417-476.
- _____. 1960. *Autecology of the Copperhead*. University of Kansas Publications, Museum of Natural History 13:85-288.
- _____. 1960a. Criteria for determining sex and breeding maturity in snakes. *Herpetologica* 16:49-51.
- _____. 1961. Longevity and age-size groups in some common snakes. Pp. 396-414. In W. Frank Blair (ed.), *Vertebrate Speciation*. University of Texas Press, Austin.
- _____. 1965. *An Ecological Study of the Garter Snake, Thamnophis sirtalis*. University of Kansas Publications, Mus. Nat. Hist. 15:493-564.
- _____. 1970. *Reproductive Cycles of Lizards and Snakes*. Univ. of Kansas Museum of Natural History, Misc. Publ. No. 52. Pp. 1-247.
- _____. 1975. *A Demographic Study of the Ringneck Snake (Diadophis punctatus) in Kansas*. Univ. of Kansas Museum of Natural History, Misc. Publ. No. 62. Pp. 53.
- Fox, H. 1977. The urinogenital systems of reptiles, pp. 1-157. In Carl Gans and Thomas Parsons (eds.), *Biology of Reptilia*. Volume 6. Academic Press, New York. Pp. 505.
- Fox, W. 1948. Effect of temperature on development of scutellation in the garter snake, Thamnophis elegans atratus. *Copeia* 1948 (4):252-262.
- _____. 1954. Genetic and environmental variation in the timing of the reproductive cycles of male garter snakes. *J. Morph.* 95:415-450.
- Fox, W. 1956. Seminal vesicles of snakes. *Anat. Rec.* 124:519-539.
- Fox, W., C. Gordon, and H. Fox. 1961. Morphological effects of low

- temperatures during embryonic development of the garter snake, Thamnophis elegans. *Zoologica* 46:57-71.
- Fry, F. E. 1967. Responses of vertebrate poikilotherms to temperature, pp. 375-409. In A. H. Rose (ed.), *Thermobiology*. Academic Press, New York.
- Gadow, H. 1920. *Amphibia and Reptiles*. London, MacMillan and Co. Pp. 668.
- Gans, C. 1974. *Biomechanics*. J. B. Lippincott Company, Philadelphia, Pa. Pp. 261.
- _____. 1978. *Biology of Reptilia*, Volume 8. Academic Press, New York. Pp. 782.
- Gans, C., T. Krakauer and C. V. Paganelli. 1968. Water loss in snakes: interspecific and intraspecific variability. *Comp. Biochem. Physiol.* 27:747-761.
- Gehlbach, F. R. 1974. Evolutionary relations of southwestern ring-neck snakes (Diadophis punctatus). *Herpetologica* 30(2):140-148.
- Goldberg, S. R. and R. L. Bezy. 1974. Reproduction in the island night lizard, Xantusia riversiana. *Herpetologica* 30(4):350-360.
- Goodman, K. V. 1958. *Soil Survey of Potter County, Pennsylvania*. U. S. Dept. of Agriculture, Pa. Agricultural Experiment Station, Series 1953 (No. 2). Pp. 101.
- Gregory, P. T. 1971. Overwintering populations of the red-sided garter snake (Thamnophis sirtalis parietalis) at a northern latitude. M. Sc. Thesis, University of Manitoba, Winnipeg, Canada.
- _____. 1974. Patterns of spring emergence of the red-sided garter snake (Thamnophis sirtalis parietalis) in the Interlake region of Manitoba. *Can. J. Zool.* 52:1063-1069.
- Green, N. B. 1969. *Amphibians and Reptiles in West Virginia: Their Identification and Distribution*. Call Notes. Published by the Huntington Bird Club, Huntington, W. V., Marshall University, Dept. of Biological Sciences, Huntington, W. V.
- Grizzell, R. A., Jr. 1949. The hibernation site of three snakes and a salamander. *Copeia* 1949(3):231.
- Groves, F. 1961. Notes on two large broods of H. v. valeriae. (Baird and Girard) - *Herpetologica* 17:71.

- Hahn, W. E. 1964. Seasonal changes in testicular and epididymal histology and spermatogenic rate in the lizard Uta stansburiana stejnegeri. J. Morph. 115:447-460.
- Hahn, W. E. and V. W. Tinkle. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard Uta stansburiana. Journal of Experimental Zoology 158:79-86.
- Hamilton, W. J. 1939. American Mammals Their Lives, Habits, and Economic Relations. First Ed. McGraw-Hill Book Co., Inc., New York. Pp. 144.
- _____. 1951. The food and feeding behavior of the garter snake in New York State. The American Midland Naturalist 46:385-390.
- Hamilton, W. J. and J. A. Pollack. 1956. The food of some colubrid snakes from Fort Benning, Georgia. Ecology 37:519-526.
- Harris, H. S. Jr. 1969. Distributional Survey: Maryland and the District of Columbia. Bull. Md. Herp. Soc. 5(4):97-161.
- _____. 1975. Distributional Survey (Amphibia/Reptilia): Maryland and the District of Columbia. Bull. Md. Herp. Soc. 11(3):73-170.
- Henderson, R. W. 1970. Feeding behavior, digestion, and water requirements of Diadophis punctatus arnyi (Kennicott). Herpetologica 26(4):520-526.
- _____. 1974. Resource partitioning among the snakes of the University of Kansas Natural History Reservation: A preliminary analysis. Milwaukee Public Museum Contributions in Biology and Geology No. 1:1-11.
- Hennen, R. V. and D. B. Reger. 1914. Preston County, W. Va., Geol. Surv. County Reports, Morgantown, W. Va.
- Hough, A. F. and R. D. Forbes. 1943. The Ecology and Sylvics of Forest in the High Plateau of Pennsylvania. Ecological Monographs 13(1):299-320.
- Hurter, J. Sr. 1911. Herpetology of Missouri. Trans. Acad. Sci. St. Louis. 20:59-274.
- Illick, J. S. and L. Frontz. 1928. The Beech-Birch-Maple Forest Type in Pennsylvania. Bulletin of Pennsylvania, Department of Forests and Waters, 46:3-40.

- Jackson, D. R. and R. Franz. 1981. Ecology of the eastern coral snake (Micrurus fulvius) in northern Florida. *Herpetologica* 37(4):213-228.
- Jackson, M. K. and H. W. Reno. 1975. Comparative skin structure of some fossorial and sub-fossorial leptotyphlopoid and colubrid snakes. *Herpetologica* 31(3):350-359.
- Johnson, W. M. 1975. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. Agriculture Handbook No. 436. U. S. Soil Conservation Service, U. S. Dept. of Agriculture. Pp. 469-474.
- Jopson, G. M. 1971. The origin of the reptile fauna of the southern Appalachians, pp. 189-196. In Perry C. Hold (ed.), *The Distributional History of the biota of the southern Appalachians*. Part III: Vertebrates. Research Division Monograph 4, Virginia Polytechnic Institute and State University, Blacksburg, Va.
- Judd, W. W. 1954. Observations on the food of the little Brownsnake, Storeria dekayi, at London, Ontario. *Copeia*, 1954(1):62-64.
- Keeler, J. E. 1956. Some Observations on an Unusual Physiological Display of a Brood of Western Ground Snakes with Notes on Parturition (Abstract). *J. Ala. Acad. Sci.* 31:99.
- Kirk, V. M. 1972. An observation of a predator-escape technique practiced by a rough earth snake. *Bulletin Va. Herpet. Soc.* No. 69:1.
- Kitchell, J. F. 1969. Thermophilic and thermophobic responses of snakes in a thermal gradient. *Copeia* 1969(1):189-191.
- Klauber, L. M. 1943. Tail length differences in snakes with notes on sexual dimorphism and the coefficient of divergence. *Bull. Zool. Soc., San Diego* 1:1-60.
- _____. 1972. *Rattlesnakes: their habits, life histories, and influence on mankind*. 2nd ed., Berkeley, Published for the Zoological Society of San Diego by the Univ. of California Press. Pp. 1533 (2 volumes).
- Klimstra, W. D. 1958. Some observations on snake activities and populations. *Ecology* 39(2):232-239.
- Kluger, D. H. 1975. Fever and survival. *Science* 188:166-168.
- Kluger, M. J. 1978. The evolution and adaptive value of fever. *American Scientist* 66:38-43.

- Kofron, C. P. 1979. Female reproductive biology of the brown snake, Storeria dekayi, in Louisiana. *Copeia* 1979(3):463-466.
- Kopas, F. A. 1973. Soil Survey of Fayette County, Pennsylvania. U. S. Dept. of Agric., Soil Conservation Service, The Pennsylvania State University. Pp. 108.
- Kozubowski, M. M. 1980. The comparative thermal ecology of two species of Thamnophis (Reptilia; Serpentes) on the Allegheny High Plateau. Master's Thesis, St. Bonaventure University. Pp. 41.
- Krakauer, T. C., C. Gans, and C. V. Paganelli. 1968. Ecological correlation of water loss in burrowing reptiles. *Nature* 218 (May 18):659-660.
- Kubie, J. L., J. Cohen, and M. Halpern. 1978a. Shedding enhances the sexual attractiveness of oestradiol treated garter snakes and their untreated penmates. *Animal Behavior* 26:562-570.
- Kubie, J. L., A. Vagvolgi, and M. Halpern. 1978b. The roles of the vomeronasal and olfactory systems in the courtship behavior of male snakes. *J. Comp. Physiol. Psych.* 92:627-641.
- Lee, D. S. 1973. Creatures in distress. *Maryland Conservation* 49 (6):14-15; 18-20.
- Legler, J. M. 1958. Extra-uterine migration of ova in turtles. *Herpetologica* 14:49-52.
- Lemay, L. and G. Marsiglia. 1952. The coal skink, Eumeces anthracinus (Baird), in Maryland. *Copeia* 1952(3):193.
- Leuth, F. X. 1941. Effects of temperature on snakes. *Copeia* 1941: 125-132.
- Leverett, F. 1934. Glacial deposits outside the Wisconsin Terminal Moraine in Pennsylvania. Department of Internal Affairs, Topographic and Geologic Survey, Harrisburg, PA.
- Lewis, A. E. 1966. *Biostatistics*. Reinhold Publishing Corporation: New York. Pp. 227.
- Licht, P. 1971. Regulation of annual testis cycle by photoperiod and temperature in the lizard Anolis carolinensis. *Ecology* 52:240-252.

- Licht, P. 1972. Problems in experimentation on timing mechanisms for annual physiological cycles in reptiles, pp. 681-711. In F. E. South (ed.), *Hibernation and Hypothermia, Perspectives and Challenges*. Elsevier, Amsterdam.
- Licht, P. and G. C. Gorman. 1970. Reproductive and fat cycles in Caribbean Anolis lizards. *Univ. Calif. Publ. Zool.* 95:1-52.
- Lofts, B. 1972. The sertoli cell. *General and Comparative Endocrinology, Supplement* 3:636-648.
- Loveridge, A. 1927. On the seasonal incidence of 3 common species of Massachusetts snakes. *Antivenin Inst. Amer. Bull.* 1:54-58.
- Lyon, T. L. and H. O. Buckmann. 1943. *The Nature and Properties of Soils: A College Text of Edaphology*. 4th ed. The MacMillan Company, New York. Pp. 499.
- Marvin, C. F. 1941. Psychrometric tables for obtaining the vapor pressure, relative humidity, and temperature of the dew point. W. B. No. 235, U. S. Government Printing Office, Washington. Pp. 85.
- Mayew, W. W. 1966. Reproduction in the psammophilous lizard Uma scoparia. *Copeia* 1966(1):114-122.
- McCall, R. B. 1980. *Fundamental Statistics for Psychology*. 3rd ed. Harcourt Brace Jovanovich, Inc., New York. Pp. 420.
- McCauley, R. H. 1945. *The Reptiles of Maryland and the District of Columbia*. Free Press Printing Co., Burlington, Vt. Pp. 119-121.
- McCoy, C. J. 1965. Mountain earth snake in West Virginia. *The Redstart* 1965(Oct.):108.
- _____. 1980. Identification Guide to Pennsylvania Snakes. Educational Bulletin No. 1, Benedum Resource Project, Section of Education, Carnegie Museum of Natural History. Pp. 1-12.
- _____. 1982. *Amphibians and Reptiles in Pennsylvania: Checklist, Bibliography, and Atlas of Distribution*. Carnegie Museum of Natural History, Special Publication No. 6, Pittsburgh, Pa.
- McKeever, J. L. 1958. Chipmunk and garter snake. *Canadian Field Nat.* 72:170.
- Miller, W. D. 1916. Notes on New Jersey batrachians and reptiles. *Copeia* 1916:67-68.

- Minton, S., Jr. 1944. Introduction to the study of the reptiles of Indiana. *Amer. Mid. Nat.* 32(2):438-477.
- Morey, H. F. 1931. Climatological charts for the Allegheny Forest Region. *Monthly Weather Review*, U. W. Dept. of Agriculture, 59:18-28.
- Myers, C. W. 1957. Amphibians and reptiles of Washington State Park, Washington County, Missouri. *Trans. Kansas Acad. Sci.* 60:288-293.
- _____. 1962. Ontogenetic color variation of the snake Virginia valeriae. *Herpetologica* 18(4):273-274.
- Neill, W. T. 1948. Hibernation of amphibians and reptiles in Richmond County, Georgia. *Herpetologica* 4:107-112.
- Nelson, W. F. 1969. Notes on parturition and brood sizes in Storeria occipitomaculata. *Journal of the Tennessee Academy of Science* 44(1):20-21.
- Netting, M. G. 1950. The amphibians and reptiles of Pennsylvania. Pennsylvania Government's File. Pp. 29.
- _____. 1965. Snake christened by Carnegie Museum scientist now discovered at Powdermill Nature Reserve. *Carnegie Mus. Educ. release No.* 56:1-2.
- Nilson, G. 1980. Male reproductive cycle of the European adder, Vipera berus, and its relation to annual activity periods. *Copeia* 1980(4):729-737.
- Noble, G. K. and E. R. Mason. 1932. The relation of water regulation to habitat selection in reptiles. *Science* 76:545-546.
- O'Neill, J., Jr. 1965. Properties and uses of Pennsylvania shales and clays. Pa. Geol. Survey, Bulletin M51, 4th series, Harrisburg, Pa. Pp. 448.
- Osgood, D. W. 1978. Effects of temperature on the development of meristic characters in Natrix fasciatus. *Copeia* 1978(1):33-47.
- Parker, W. S. 1976. Population estimates, age structure, and denning habits of Whipsnakes, Masticophis t. taeniatus, in a northern Utah atriplex-sariobatus community. *Herpetologica* 32:53-57.
- Peters, J. A. 1964. Dictionary of Herpetology. 1st ed., Hafner Publishing Company, New York. Pp. 392.

- Pisani, G. R. 1967. The Annual Reproductive Cycle of Thamnophis brachystoma with Comparative Notes on the Cycle of Thamnophis sirtalis sirtalis. Master's Thesis. St. Bonaventure Univ. Pp. 57.
- _____. 1971. An unusually large litter of Virginia valeriae pulchra. Journal of Herpetology 5(3/4):207-208.
- _____. 1972. Remarks on the holotype of Virginia valeriae elegans (Kennicott). Herpetologica 28(4):348.
- _____. 1976. Comments on the courtship and mating mechanisms of Thamnophis (reptilia, serpentes, colubridae). J. Herpetology 10:139-142.
- Pisani, G. R. and R. C. Bothner. 1970. The annual reproductive cycle of Thamnophis brachystoma. Science Studies 26:15-34.
- Pisani, G. R. and J. T. Collins. 1971. The smooth earth snake, Virginia valeriae (Baird and Girard) in Kentucky (description). Transactions of the Kentucky Academy of Science Vol. 32($\frac{1}{2}$):16-25.
- Porter, K. R. 1972. Herpetology. W. B. Saunders Co., Toronto. Pp. 524.
- Prange, H. D. and K. Schmidt-Nielsen. 1969. Evaporative water loss in snakes. Comp. Biochem. Physiol. 28:973-975.
- Quinn, H. R. 1979. Reproduction and growth of the Texas coral snake (Micrurus fulvius tenere). Copeia 1979(3):453-463.
- Rahn, H. 1938. The corpus luteum of reptiles. Anat. Rec. 72:55.
- _____. 1939. Structure and function of placenta and corpus luteum in viviparous snakes. Proc. Soc. exp. Bio. 40:381-382.
- _____. 1940. Sperm viability in the uterus of the garter snake, Thamnophis. Copeia 1940(2):109-115.
- _____. 1942. The reproductive cycle of the prairie rattler. Copeia 1942(4):233-240.
- Reynolds, J. W. 1977. The earthworms (Lumbricidae and Sparganophilidae) of Ontario. Life Sci. Misc. Pub., R. Ont. Mus. Pp. 141.
- Richmond, N. D. 1954. The ground snake, Haldea valeriae, in Pennsylvania and West Virginia with description of new subspecies. Annals of the Carnegie Museum 33(Art. 15):251-260.

- Sabath, M. and R. Worthington. 1959. Eggs and young of certain Texas reptiles. *Herpetologica* 15:31-32.
- Schmidt, K. P. and D. D. Davis. 1941. Field Book of Snakes of the United States and Canada. G. P. Putnam's Sons, New York. Pp. 365.
- Schmidt, K. P. and R. F. Inger. 1957. Living Reptiles of the World. Hamish Hamilton, London. Pp. 287.
- Schmidt-Nielsen, K. and P. J. Bentley. 1966. Desert tortoise Gopherus agossizii: cutaneous water loss. *Science* 154:911.
- Schmidt-Nielsen, K. and W. R. Dawson. 1964. Terrestrial animals in dry heat: desert reptiles, pp. 476-680. In D. B. Dillet (ed.), *Adaptation to Environment. Handbook Physio. 4*, Amer. Physiol. Soc.
- Seibert, H. C. and C. W. Hagen, Jr. 1947. Studies on a population of snakes in Illinois. *Copeia* 1947(1):6-22.
- Semlitsch, R. D., K. L. Brown, and J. P. Caldwell. 1981. Habitat utilization, seasonal activity, and population size structure of the southeastern crowned snake Tantilla coronata. *Herpetologica* 37(1):40-46.
- Sheehan, D. C. and B. B. Hrapchak. 1980. Theory and Practice of Histotechnology. 2nd edition, The C. V. Mosby Company, St. Louis. Pp. 481.
- Shepps, V. C., G. W. White, J. B. Droste, and R. F. Sitler. 1959. Glacial geology of northwestern Pennsylvania. Pa. Geological Survey, 4th series, Bulletin G-32. Pp. 59.
- Smith, H. M. 1956. Handbook of Amphibians and Reptiles of Kansas. Univ. of Kansas Publ. Mus. Nat. Hist. Pp. 356.
- Smith, P. W. 1961. The amphibians and reptiles of Illinois. Illinois Natural History Survey Bulletin 28(Article 1):1-298.
- Smithe, F. B. 1975. Naturalists Color Guide. The American Museum of Natural History, New York. Pp. 229.
- Srivastava, P. C. and J. P. Thapliyal. 1965. The male sexual cycle of the chequered water snake, Natrix piscator. *Copeia* 1965(4): 410-415.
- Stewart, G. 1965. Thermal ecology of the garter snakes Thamnophis sirtalis concinnus (Hallowell) and Thamnophis ordinoides (Baird and Girard). *Herpetologica* 21: 81-102.

- Stickel, L. F., W. H. Stickel, and F. C. Schmid. 1980. Ecology of a Maryland population of black rat snakes (Elaphe o. obsoleta). The American Mid. Nat. 103(1):1-14.
- Swanson, P. L. 1952. The reptiles of Venango County, Pennsylvania. The American Midland Naturalist 47(1):161-182.
- Thornbury, W. D. 1965. Regional Geomorphology of the U. S. John Wiley and Sons, New York. Pp. 607.
- Trapido, H. 1940. Mating time and sperm viability in Storeria. Copeia 1940(2):107-109.
- Trauth, S. E. 1979. Testicular cycle and timing of reproduction in the collared lizard (Crotaphytus collaris) in Arkansas. Herpetologica 35(2):184-192.
- Walker, J. M. 1963. Amphibians and reptiles of Jackson Parish, Louisiana. Proc. La. Acad. Sci. 26:91-101.
- Walker, D. J. 1963. Notes on broods of Virginia valeriae valeriae (Baird and Girard) in Ohio. Journal of the Ohio Herpetological Society 4(½):54.
- Waring, H. 1963. Color Change Mechanisms of Cold-Blooded Vertebrates. Academic Press, New York. Pp. 266.
- Werler, J. E. and M. McCallion. 1951. Notes on a collection of reptiles and amphibians from Princess Anne County, Virginia. The American Midland Naturalist 45(1):245-252.
- Westing, A. H. 1961. Northerly range extension for the smooth earth snake, Virginia valeriae. Herpetologica 17(2):144.
- Wilhoft, D. C. 1963. Gonadal histology and seasonal changes in the tropical Australian lizard Leiolepisma rhombadalis. Journal of Morphology 113:185-204.
- Wilhoft, D. C. and J. D. Anderson. 1960. Effect of acclimation on the preferred body temperature of the lizard Sceloporus occidentalis. Science 131:610-611.
- Wilson, L. W. and S. B. Friddle. 1950. The Herpetology of Hardy Co., W. Va. The American Midland Naturalist 43(1):165-172.
- Woods, W. H. 1973. A comparative study of skin ultrastructure in three species of small colubrid snakes. Univ. of Arkansas, Ph.D. dissertation, Zoology. Pp. 46.

- Wozniak, E. M. 1965. Some ecological comparisons between Thamnophis brochystoma and Thamnophis sirtalis sirtalis on the Allegheny High Plateau. Master's Thesis, St. Bonaventure University. Pp. 48.
- Wozniak, E. M. and R. C. Bothner. 1966. Some ecological comparisons between Thamnophis brochystoma and T. sirtalis sirtalis on the Allegheny High Plateau (Abstract). J. Ohio Herpetol. Soc. 5:164-165.
- Wright, A. H. and A. A. Wright. 1957. Handbook of Snakes of the U. S. and Canada. Comstock Publishing Associates, Ithaca, New York. Pp. 1075. (2 Volumes).
- Zillig, L. D. 1958. The status of Haldea (Baird and Girard) and Virginia (Baird and Girard). Copeia 1958(2):152.
- Zoond, A. and J. Eyre. 1934. In H. Waring, Color Change Mechanisms of Cold-Blooded Vertebrates, 1963. Academic Press, New York. Pp. 266.

APPENDIX I

Sources of preserved specimens examined during this study.

A. Virginia valeriae pulchra

| | | | | |
|-------------|-------------|-------------|---------|--------|
| AMNH 108529 | CM 32145 | R 2254 NHSM | TC 40 | TC 108 |
| AMNH 108530 | CM 32146 | R 2256 NHSM | TC 41 | TC 109 |
| AMNH 108531 | CM 32204 | R 2257 NHSM | TC 42 | TC 110 |
| AMNH 108532 | CM 32206 | R 2258 NHSM | TC 43 | TC 112 |
| AMNH 108533 | CM 32206A | R 2272 NHSM | TC 44 | TC 117 |
| AMNH 108534 | CM 32206B | | TC 45 | TC 118 |
| AMNH 108535 | CM 32206C | TC 1 | TC 46 | TC 122 |
| AMNH 108536 | CM 32206D | TC 2 | TC 47 | TC 124 |
| AMNH 108537 | CM 32206E | TC 3 | TC 48 | TC 125 |
| AMNH 108538 | CM 32206F | TC 4 | TC 49 | TC 129 |
| AMNH 108539 | CM 32219 | TC 5 | TC 50 | TC 130 |
| AMNH 108540 | CM 32220A | TC 6 | TC 51 | TC 132 |
| AMNH 108541 | CM 32220B | TC 7 | TC 53 | TC 133 |
| AMNH 108542 | CM 32220C | TC 8 | TC 54 | TC 134 |
| AMNH 108543 | CM 32220D | TC 10 | TC 62 | TC 135 |
| AMNH 108544 | CM 32220E | TC 12 | TC 63 | TC 136 |
| AMNH 108545 | CM 32220F | TC 13 | TC 64 | TC 138 |
| AMNH 108546 | CM 32220G | TC 14 | TC 66 | TC 139 |
| AMNH 108547 | CM 32682 | TC 15 | TC 69 | TC 141 |
| AMNH 108548 | CM 40529 | TC 16 | TC 75 | TC 143 |
| AMNH 108549 | CM 43525 | TC 17 | TC 76 | TC 145 |
| AMNH 108550 | CM 43526 | TC 18 | TC 79 | TC 146 |
| AMNH 108551 | CM 43527 | TC 19 | TC 86 | TC 147 |
| AMNH 108552 | CM 64115 | TC 20 | TC 87 | TC 155 |
| | CM 64116 | TC 21 | TC 88 | TC 156 |
| CM 4886 | CM 64117 | TC 22 | TC 90 | TC 157 |
| CM 21625 | CM 64118 | TC 23 | TC 91 | TC 158 |
| CM 21939 | CM 64119 | TC 24 | TC 92 | TC 159 |
| CM 21940 | CM 64120 | TC 25 | TC 93 | TC 160 |
| CM 21941 | CM 64121 | TC 26 | TC 94 | TC 161 |
| CM 21942 | | TC 27 | TC 95 | TC 162 |
| CM 21943 | RS 340 HSH | TC 28 | TC 97 | TC 169 |
| CM 21944 | RS 341 HSH | TC 29 | TC 98 | TC 171 |
| CM 26133 | RS 342 HSH | TC 30 | TC 99 | TC 172 |
| CM 29200 | RS 348 HSH | TC 31 | TC 100 | TC 181 |
| CM 29382 | RS 349 HSH | TC 32 | TC 101A | TC 183 |
| CM 29384 | RS 350 HSH | TC 33 | TC 101B | TC 189 |
| CM 32137 | RS 351 HSH | TC 34 | TC 101C | TC 195 |
| CM 32140 | RS 526 HSH | TC 35 | TC 101 | TC 196 |
| CM 32141 | | TC 36 | TC 103 | TC 197 |
| CM 32142 | R 1670 NHSM | TC 37 | TC 105 | TC 202 |
| CM 32143 | R 1671 NHSM | TC 38 | TC 106 | TC 203 |
| CM 32144 | R 1672 NHSM | TC 39 | TC 107 | TC 204 |

| | | | | |
|--------|--------|--------|--------|-----------|
| TC 205 | TC 254 | TC 294 | TC 322 | TC 379 |
| TC 208 | TC 256 | TC 295 | TC 323 | TC 381 |
| TC 210 | TC 258 | TC 296 | TC 330 | TC 382 |
| TC 212 | TC 260 | TC 297 | TC 332 | TC 383 |
| TC 213 | TC 261 | TC 298 | TC 338 | TC 384 |
| TC 219 | TC 262 | TC 299 | TC 340 | TC 385 |
| TC 221 | TC 263 | TC 300 | TC 342 | TC 386 |
| TC 222 | TC 267 | TC 301 | TC 350 | TC 387 |
| TC 225 | TC 268 | TC 302 | TC 351 | TC 388 |
| TC 226 | TC 269 | TC 303 | TC 352 | TC 389 |
| TC 227 | TC 270 | TC 304 | TC 353 | TC 390 |
| TC 228 | TC 271 | TC 305 | TC 354 | TC 393 |
| TC 229 | TC 272 | TC 306 | TC 355 | TC 394 |
| TC 230 | TC 273 | TC 307 | TC 356 | TC 395 |
| TC 232 | TC 274 | TC 308 | TC 360 | TC 396 |
| TC 233 | TC 275 | TC 309 | TC 361 | TC 397 |
| TC 234 | TC 276 | TC 310 | TC 365 | TC 401 |
| TC 235 | TC 277 | TC 311 | TC 366 | TC 403 |
| TC 236 | TC 278 | TC 312 | TC 367 | TC 407 |
| TC 237 | TC 280 | TC 313 | TC 368 | |
| TC 240 | TC 281 | TC 314 | TC 369 | TKP 6801 |
| TC 241 | TC 284 | TC 315 | TC 370 | TKP 6803 |
| TC 244 | TC 287 | TC 316 | TC 372 | TKP 6804 |
| TC 245 | TC 288 | TC 317 | TC 373 | TKP 6805 |
| TC 247 | TC 289 | TC 318 | TC 374 | |
| TC 250 | TC 290 | TC 319 | TC 375 | WVBS 3961 |
| TC 251 | TC 291 | TC 320 | TC 376 | WVBS 4071 |
| TC 253 | TC 293 | TC 321 | TC 377 | WVBS 4455 |

B. Virginia valeriae valeriae

| | | | |
|----------|----------|-------------|-------------|
| CM 4763 | CM 26177 | CM 58699 | R 952 NHSM |
| CM 7193 | CM 26178 | CM 73647 | R 958 NHSM |
| CM 9028 | CM 27756 | | R 960 NHSM |
| CM 9529 | CM 27757 | RS 39 HSH | R 1394 NHSM |
| CM 9536 | CM 28710 | RS 115 HSH | R 1395 NHSM |
| CM 9654 | CM 38672 | RS 219 HSH | R 1496 NHSM |
| CM 9695 | CM 39613 | RS 230 HSH | R 1629 NHSM |
| CM 9696 | CM 40468 | RS 569 HSH | R 1640 NHSM |
| CM 9882 | CM 55708 | RS 957 HSH | R 1707 NHSM |
| CM 9883 | CM 56398 | RS 1197 HSH | R 2252 NHSM |
| CM 13826 | CM 56410 | | R 2270 NHSM |
| CM 13893 | CM 56411 | R 541 NHSM | R 2271 NHSM |
| CM 16770 | CM 58645 | R 679 NHSM | |
| CM 16771 | CM 58646 | R 718 NHSM | WVBS 1313 |
| CM 21681 | CM 58673 | R 731 NHSM | WVBS 1945 |
| CM 23794 | CM 58681 | R 779 NHSM | |
| CM 23795 | CM 58697 | R 851 NHSM | |

C. Virginia valeriae elegans

| | | | |
|---------|---------|----------|----------|
| CM 713 | CM 8301 | CM 9983 | CM 25159 |
| CM 714 | CM 8302 | CM 19811 | CM 25422 |
| CM 716 | CM 8303 | CM 19891 | CM 50070 |
| CM 717 | CM 8304 | CM 19908 | CM 58729 |
| CM 1072 | CM 8305 | CM 22832 | |
| CM 1073 | CM 9819 | CM 25076 | |

AMNH: American Museum of Natural History
(Curator - Richard G. Zweifel)

CM: Carnegie Museum of Natural History
(Curator - Clarence J. McCoy)

HSH: Private collection of Herbert S. Harris in the
Natural History Society of Maryland collection
(Curator - Herbert S. Harris)

NHSM: Natural History Society of Maryland
(Curator - Herbert S. Harris)

TC: Tom Cervone - personal collection housed in the
St. Bonaventure University Herp. collection
(Curator - Richard C. Bothner)

TKP: Thomas K. Pauley - personal collection housed at
Univ. of Pittsburgh (Bradford Campus)

WVBS: West Virginia Biological Survey at Marshall Univ.
(Curator - Mike E. Seidel)

APPENDIX II

Virginia valeriae pulchra has been recorded from the following localities. Abbreviations in parentheses (identified in Appendix I) indicate the institution holding the specimen(s) collected. SBU stands for St. Bonaventure University holdings; OSU, Ohio State University holdings.

A. Specific Records in Maryland

GARRETT COUNTY

- (1) Swallow Falls State Park (NHSM)
- (2) Swallow Falls State Park, Moss Fields (NHSM)
- (3) Swallow Falls State Park, saw dust pile near Moss Fields (HSH)
- (4) Swallow Falls State Park, at old saw mill off Maple Glade road, east of Moss Field (HSH)
- (5) Swallow Falls State Park, Maple Glade road (CM)
- (6) Snaggy Mountain road near Swallow Falls (CM, SBU)

B. Specific Records in Pennsylvania

CAMERON COUNTY

- (1) Portage Township, Emporium, 7.5 miles NE, on a east facing roadside bank along Rt. 155 approximately 200 yards S of the Potter-Cameron County line (SBU)
- (2) Shippen Township, Emporium, 2 miles NW (DOR) on Rt. 46 (SBU)
- (3) Gibson Township, Sinnamahoning, 1 mile NW, on a S facing fallow field along Rt. 120 (SBU)
- (4) Gibson Township, Driftwood, 6 miles SW, on a SE facing roadside bank along Mix Run, 1.7 miles NE of the junction of Red Run and Mix Run (SBU)
- (5) Gibson Township, Sinnamahoning, 3 miles S, on a S facing roadside bank, 1.7 miles S of Rt. 120 on Wykoff Run road (SBU)
- (6) Gibson Township, Hoover Farm, S of Sinnamahoning (CM)
- (7) Gibson Township, 4 miles S of Sinnamahoning (CM)
- (8) Gibson Township, Little Fork Draft at Mix Run (OSU)

CLEARFIELD COUNTY

- (1) One mile north of Hyde City (SBU)

CLINTON COUNTY

- (1) Keating (CM)

CLINTON COUNTY (Cont.)

- (2) Sproul Forest Plateau, S of Keating (CM)

ELK COUNTY

- (1) Bennezette Township, along Mix Run approximately 2 miles west of junction with Red Run, at path to state gamelands area gate(OSU)

FAYETTE COUNTY

- (1) Springfield Township, 3.5 miles E of Indian Head, Spook Hill (CM)
- (2) Wharton Township, Markleysburg, 5 miles NE-E, near Lake Courage (Specimen released by Mike Kernan)

FORREST COUNTY

- (1) Fryburg, 2.5 miles N (CM)
- (2) Near Cooksburg (CM)
- (3) Tionesta, 3 miles SW, west side of Allegheny River along US 62 (CM)
- (4) Kingsley Township, Kelletville, 2 to 2.5 miles NE, on a SW facing roadside bank along Route 666 (SBU)
- (5) Kingsley Township, Kelletville, 100 yards SW of the Kelletville Inn on a SE facing roadside bank along Route 666 (SBU)

POTTER COUNTY

- (1) Portage Township, Keating Summit, 3.5 miles S, on a SE facing roadside bank at the intersection of Colley Road and Route 155 (SBU)
- (2) Portage Township, Emporium, 8 miles NE, on a east facing roadside bank along Route 155 across from Sizerville State Park (SBU)
- (3) Keating Township, Keating Summit, 2.2 to 2.7 miles SE, on a S facing roadside bank along Route 607 (SBU)
- (4) Portage Township, Keating Summit, 3.5 miles S, on a SW facing field approximately 0.6 miles NE of Route 155 along Colley Road (SBU)
- (5) Portage Township, Keating Summit, 3.5 miles S-SE, on a SW facing roadside bank approximately 1.3 miles NE of Route 155 along Colley Road (SBU)
- (6) Portage Township, Emporium, 8.5 miles NE, on a E facing roadside bank along Route 155 approximately 0.5 miles N of Sizerville State Park (SBU)

SOMERSET COUNTY

- (1) Johnstown, 15 miles SW (CM)
- (2) Laurel Ridge, 4 miles N of Bakersville (CM)
- (3) Bigelow Heights, 0.5 miles S on the east side of Laurel Hill crest (CM)

VENANGO COUNTY

- (1) Oil City, 5 miles E near Ten Mile Bottom (CM)
- (2) Van, 4 miles N (CM)
- (3) Sadler's Corners, 1 mile NE (CM)

WARREN COUNTY

- (1) Dirt road under shale on uphill SE facing bank on cleared area N of Tidioutte, 10 miles S of Irvine and 200 yards W of the Allegheny River (SBU)
- (2) Warren, 9 miles SW along U.S. 62 (CM)
- (3) Warren, 9.5 miles SW (CM)
- (4) Warren, 10 miles SW (CM)
- (5) Irvin, 11 miles S-SW (CM)
- (6) Tidioutte, 5 miles N (CM)
- (7) Deerfield Township, Warren, 7.5 miles W-SW, on a east facing roadside bank approximately 3.7 miles S of Rt 27 on a dirt road along the west bank of the Allegheny River (SBU)
- (8) Deerfield Township, Tidioutte, 3 to 3.6 miles NE, on a S facing roadside bank along the west bank of the Allegheny River (SBU)
- (9) Pleasant Township, Warren, 8 miles SW, on a west facing roadside bank 3.9 to 4.1 miles S of Route 6 along U.S. 62 (SBU)
- (10) Pleasant Township, Warren, 8.5 miles SW, on a west facing roadside bank 4.5 miles S of Route 6 along Route 62, 100 yards N of the Pleasant-Watson Township line (SBU)
- (11) Watson Township, Warren, 12.5 miles SW, on a NW roadside bank 8.9 miles S of Route 6 along Route 62 (SBU)
- (12) Tidioutte, 11 miles N (AMNH)

WESTMORELAND COUNTY

- (1) Near Laughlintown, Old Epply farm, 1/2 way up west slope of Laurel Ridge, S. of Lincoln Highway (CM)
- (2) Near Waterford Boy Scout Camp (CM)
- (3) Powdermill Nature Reserve (CM)
- (4) Pine Flat, Top of Laurel Hill (CM)

C. Specific Records in West Virginia

PRESTON COUNTY

- (1) Terra Alta (CM)
- (2) Terra Alta Biological Station, W.V.U. (WVBS)
- (3) NE shore of Lake Terra Alta (WVBS)

PENDLETON COUNTY

- (1) Sinks of Gandy Quadrangle, 1.4 km S of Drill Hole, edge of Forest Road 103 on a SW facing slope (TKP)

RANDOLPH COUNTY

- (1) Grassy SW hillside between Forest Road 1 and parking lot above Spruce Knob Lake (WVBS)