To the Graduate Council:

I am submitting herewith a dissertation written by Leroy M. Scudder entitled "Food Consumption and Growth in Three Species of Water Snakes of the Genus Nerodia (Colubridae)." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology.

Gordon M. Burghardt
Gordon M. Burghardt, Major Professor

We have read this dissertation
and recommend its acceptance:

John C. Dittmacher

Ted Bonk

John T. Smith

Accepted for the Council:

Lou Minkel
The Graduate School

# FOOD CONSUMPTION AND GROWTH IN THREE SPECIES OF WATER SNAKES OF THE GENUS *NERODIA* (COLUBRIDAE)

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Leroy M. Scudder

December 1983

DEDICATION

To my mother, Cordelia J. Scudder,

who was always there when I needed a hand

and whose ideals taught me patience and sincerity.

ACKNOWLEDGMENTS

I should like to gratefully acknowledge the assistance of all those individuals that aided in the completion of this project and contributed to my well-being while completing my graduate studies.

Dr. Gordon M. Burghardt, who directed my graduate studies, not only provided the physical space to house over 120 snakes, but has shaped an ongoing research program that has the latitude to allow his students to explore a multitude of subjects with a variety of species. This atmosphere encouraged my exploration of growth. His words of encouragement during the final stages of this project helped me maintain my composure in a very anxiety provoking situation.

I should also like to acknowledge the contributions of the members of my dissertation committee. Dr. Arthur C. Echternacht organized the field trip during which the majority of the snakes in this study were obtained. He also contributed a litter of *Nerodia fasciata confluens* to the study. Dr. Neil Greenberg made me aware of the physiological aspects of digestion that provided a solid background for the study of growth. Dr. John Smith graciously consented to step outside of his field of expertise to serve on my committee. He also performed the caloric analyses of the food and feces. I am very grateful to these individuals for critically reviewing the manuscript.

Assistance in the collection of data was provided by Mary Pope, Gene Sapp, Jim Birckhead, Greg Johnson, and Hannah Frank.

Bob Jones assisted in the collection of specimens, and Bob Muenchen assisted in computer analysis.

The friendship and comaraderie of many individuals has been very important to me during this work. Paul Weldon's knowledge of and love for 50's Rock and Roll provided many an entertaining evening. The friendship of Jim Thompson, Tony DiMatteo, Märie Turner, and Julia Wade served on many occasions to lift my spirits. Arthur "Bud" Fields's love of volleyball, and the encouragement of the directors and members of the New Repertory Dance Company of The University of Tennessee allowed me to grow in directions that I once believed were beyond my abilities. The time spent with these people and in the activities that they loved are a valued part of my education.

Finally, I would like to thank Marilla Davis, whose support in a number of ways kept me from becoming my own worst enemy.

# PREFACE

'The best thing for disturbances of the spirit,' replied Merlyn, beginning to puff and blow, 'is to learn. That is the only thing that never fails. You may grow old and trembling in your anatomies, you may lie awake at night listening to the disorder of your veins, you may miss your only love and lose your moneys to a monster, you may see the world about you devastated by evil lunatics, or know your honor trampled in the sewers of baser minds. There is only one thing for it then--to learn. Learn why the world wags and what wags it. That is the only thing which the poor mind can never exhaust, never alienate, never be tortured by, never fear or distrust, and never dream of regretting. Learning is the thing for you. Look at what a lot of things there are to learn--pure science, the only purity there is. You can learn astronomy in a lifetime, natural history in three, literature in six. And then, after you have exhausted a milliard lifetimes in biology and medicine and theo-criticism and geography and history and economics, why, you can start to make a cartwheel out of the appropriate wood, or spend fifty years learning to begin to learn to beat your adversary at fencing. After that you can start again on mathematics, until it is time to learn to plow.'

from T. H. White's

*The Sword in the Stone*,

Chapter 21.

A bee settling on a flower has stung a child. And the child is afraid of bees and declares that bees exist to sting people. A poet admires the bee sucking from the chalice of a flower and says it exists to suck the fragrance of flowers. A beekeeper, seeing the bee collect pollen from flowers and carry it to the hive, says that it exists to gather honey. Another beekeeper who has studied the life of the hive more closely says that the bee gathers pollen dust to feed the young bees and rear a queen, and that it exists to perpetuate its race. A botanist notices that the bee flying with the pollen of a male flower to a pistil fertilizes the latter, and sees in this the purpose of the bee's existence. Another, observing the migration of plants, notices that the

bee helps in this work, and may say that in this lies the purpose of the bee. But the ultimate purpose of the bee is not exhausted by the first, the second, or any of the processes the human mind can discern. The higher the human intellect rises in the discovery of these purposes, the more obvious it becomes that the ultimate purpose is beyond our comprehension.

All that is accessible to man is the relation of the life of the bee to other manifestations of life. . . .

from Leo Tolstoy's

*War and Peace*,

First Epilogue.

## ABSTRACT

Several factors that can have an influence on the rate of growth were investigated in the water snake genus *Nerodia*. The study centered around the question of how these snakes attain the different adult body sizes that can be discerned between the sexes and between species. The three species used to investigate this question were *Nerodia fasciata confluens*, *N. c. cyclopion*, and *N. r. rhombifera*. In addition to the question of attainment of adult body size, the effect of different feeding regimens on growth, and the amount of individual variation in growth among members of the same litter were investigated. The Bertalanffy, logistic-by-length, and logistic-by-mass growth models were also tested against one another using growth data from *N. fasciata* to ascertain which model was the best predictor of the pattern of growth in this species. Both linear and non-linear regression models were used in the analysis of sexual, species, and individual variation in growth. Linear regression models were used in the analysis of the variation in growth due to the feeding regimen.

Changes in the feeding regimen had a more pronounced effect on the females than on the males. For increases in weight, the larger the meal size, the larger the increase in weight per gram of food consumed. For increases in length, the intermediate meal size was more effective in promoting growth on a per gram of food consumed basis than the large or small meal sizes. These conditions resulted

in significant differences in the weight per unit length among snakes in the different meal size groups.

In general terms, females initially grew more rapidly than conspecific males in all three species, and showed a more gradual decline in the growth rate with time. This pattern resulted in the females attaining a larger adult size than the males. The relationships of the patterns of growth for males and females could be modified by changes in the feeding regimen.

Although *N. fasciata* attains the smallest adult size of the three species, it initially grew more rapidly than *N. cyclopion* and *N. rhombifera*. The latter two species, however, showed a more gradual decline in the growth rate with time than the former species. As a result, *N. cyclopion* and *N. rhombifera* eventually were growing at a more rapid rate per gram of food consumed than *N. fasciata*. Significant individual variation in the rate of increase in length and weight per gram of food consumed was evident in all the litters for every species.

The results of this investigation are discussed in relation to natural selection for certain growth patterns under varying conditions in natural populations. Questions are presented that could lead to further research into the forces shaping the pattern of growth in natural populations of snakes.

TABLE OF CONTENTS


| CHAPTER | | PAGE |
|---|---|---|
| 1. | INTRODUCTION . . . . . | 1 |
| | Growth, Body Size, and the Niche | 1 |
| | Factors Influencing Body Size and Growth | 3 |
| | Dietary Efficiency | 7 |
| | Growth Models and Growth in Reptiles | 11 |
| | Growth in Snakes | 18 |
| | Niche Separation in *Nerodia* | 20 |
| | Experimental Rationale | 23 |
| 2. | GENERAL PROCEDURES . . . . . | 25 |
| | Subjects and Housing | 25 |
| | Weighing and Measuring | 25 |
| | Feeding | 26 |
| | Dietary Analysis | 27 |
| 3. | GROWTH MODELS AND GROWTH IN *NERODIA* . . . . . | 29 |
| | Introduction | 29 |
| | Materials and Methods | 29 |
| | Results | 32 |
| | Discussion | 48 |
| 4. | GROWTH PATTERNS IN *NERODIA* . . . . . | 52 |
| | Introduction | 52 |
| | Materials and Methods | 53 |
| | Data Analysis | 55 |
| | Results | 56 |
| | Sexual Variation in Growth | 73 |
| | Species Variation in Growth | 114 |
| | Dietary Assimilation Efficiency | 135 |
| | Discussion | 139 |
| 5. | INDIVIDUAL VARIATION IN GROWTH . . . . . | 143 |
| | Introduction | 143 |
| | Individual Variation in *N. fasciata* | 143 |
| | Discussion | 160 |

CHAPTER PAGE

6. GENERAL DISCUSSION . . . . . 162

Introduction 162
Growth Studies in the Literature 162
Growth Rates 164
Problems for Future Research 167

LITERATURE CITED . . . . . 170

APPENDIX. COMPARISON OF INDIVIDUAL GROWTH PARAMETERS . . . 176

VITA . . . . . 234

LIST OF TABLES


| TABLE | | PAGE |
|---|---|---|
| 1. | Caloric Assimilation Efficiencies in Reptiles . . . . . | 9 |
| 2. | Some Ecological Parameters of Four Species of *Nerodia* . . . . . | 22 |
| 3. | $r^2$ Values and Estimates of Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) at Birth for *Nerodia fasciata* from Shelby County, Tennessee Using the Bertalanffy Growth Model . . . . . | 35 |
| 4. | Comparisons of Growth Models on Data for *Nerodia fasciata* from Shelby County, Tennessee . . . . . | 42 |
| 5. | Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) by Meal Size for Two Species of *Nerodia* from Lake County, Tennessee . . . . . | 57 |
| 6. | Comparisons of the Rate of Increase in Weight Per Unit Length (W/SVL) for *Nerodia fasciata* and *N. rhombifera* by Meal Size . . . . . | 69 |
| 7. | Summary of the Results of the Effect of the Feeding Regimen on the Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), Tail Length (TL), and Weight Per Unit Length (W/SVL) in Two Species of *Nerodia* from Lake County, Tennessee . . . . . | 71 |
| 8. | Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) by Sex for Three Species of *Nerodia* . . . . . | 74 |
| 9. | Estimates of the Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for *Nerodia fasciata* from Shelby County, Tennessee from the Bertalanffy Growth Model . . . . . | 85 |

TABLE PAGE

10. Estimates of Asymptotes and Growth Constant Values (r) for Total Length (L), Snout-Vent Length (SVL), and Tail Length from the Bertalanffy Growth Model for Three Species of *Nerodia* . . . . . 87

11. The Effect of Meal Size on the Proportion of the Increase in Total Length (L), Attributed to Snout-Vent Length (SVL) and Tail Length (TL) in *Nerodia fasciata* and *N. rhombifera* . . . . . 95

12. Estimates of Asymptotes for Weight (W) from the Bertalanffy Growth Model for Three Species of *Nerodia* . . . . . 106

13. Comparisons of the Rate of Increase in Weight Per Unit Length (W/SVL) by Sex for Three Species of *Nerodia* . . . . . 111

14. Summary of the Results of Sexual Variation in the Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), Tail Length (TL), and Weight Per Unit Length (W/SVL) in Three Species of *Nerodia* . . . . . 112

15. Summary of the Results of Sexual Variation in the Estimates of the Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) in Three Species of *Nerodia* . . . . . 113

16. Measurements at Birth for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL), and Adult L Measurements for Three Species of *Nerodia* . . . . . 115

17. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) by Species for Three Species from Lake County, Tennessee . . . . 116

18. Comparisons of the Rate of Increase in Weight Per Unit Length (W/SVL) by Species for Three Species of *Nerodia* . . . . . 132

TABLE PAGE

19. Summary of the Results of Species Variation in the Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), Tail Length (TL), and Weight Per Unit Length (W/SVL) in Three Species of *Nerodia* from Lake County, Tennessee . . . . . 136

20. Summary of the Results of Species Variation in the Estimates of the Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) in Three Species of *Nerodia* from Lake County, Tennessee Fed the Intermediate Meal Size . . . . . 137

21. Weight and Caloric Assimilation Efficiencies for Three Species of *Nerodia* . . . . . 138

22. Individual Variation in the Production-Ingestion (P-I) Ratios for Weight (W) in Male *Nerodia fasciata* from Shelby County, Tennessee . . . . . 148

23. Individual Variation in the Production-Ingestion (P-I) Ratios for Snout-Vent Length (SVL) in Male *Nerodia fasciata* from Shelby County, Tennessee . . . 149

24. Individual Variation in the Production-Ingestion (P-I) Ratios for Total Length (L) in Male *Nerodia fasciata* from Shelby County, Tennessee . . . 150

25. Individual Variation in the Production-Ingestion (P-I) Ratios for Tail Length (TL) in Male *Nerodia fasciata* from Shelby County, Tennessee . . . 151

26. Correlation of the Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) and the Weight of Food Consumed for *Nerodia fasciata* from Shelby County, Tennessee . . . . . 154

27. Correlation of the Production-Ingestion (P-I) Ratios for Weight (W) with the P-I Ratios for Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for *Nerodia fasciata* from Shelby County, Tennessee . . . . . 154

28. Individual Variation in the Rate of Increase in Weight Per Unit Length (W/SVL) in Male *Nerodia fasciata* from Shelby County, Tennessee . . . 155

TABLE PAGE

29. Individual Estimates of Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) from the Bertalanffy Growth Model for *Nerodia fasciata* from Shelby County, Tennessee . . 156

A-1. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia fasciata* from Shelby County, Tennessee . 177

A-2. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia fasciata* from Shelby County, Tennessee . . . . . 181

A-3. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia fasciata* from Lake County, Tennessee Fed the Large Meal Size . . . . . 185

A-4. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia fasciata* from Lake County, Tennessee Fed the Large Meal Size . . . . . 187

A-5. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size . . . . . 189

A-6. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size . . . . . 192

A-7. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia cyclopion* Fed the Intermediate Meal Size . . . . . 194

TABLE PAGE

A-8. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia cyclopion* Fed the Intermediate Meal Size . . . . . 197

A-9. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia rhombifera* Fed the Intermediate Meal Size . . . . . 200

A-10. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia rhombifera* Fed the Intermediate Meal Size . . . . . 203

A-11. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia fasciata* Fed the Small Meal Size . . . . 206

A-12. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia fasciata* Fed the Small Meal Size . . . 208

A-13. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia rhombifera* Fed the Small Meal Size . . . 209

A-14. Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia rhombifera* Fed the Small Meal Size . . 211

A-15. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia fasciata* from Shelby County, Tennessee . . . . . 214

A-16. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia fasciata* from Shelby County, Tennessee . . . . . 216

TABLE PAGE

A-17. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia fasciata* from Lake County, Tennessee Fed the Large Meal Size . . . . . 217

A-18. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia fasciata* from Lake County, Tennessee Fed the Large Meal Size . . . . . 218

A-19. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size . . . . . 219

A-20. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size . . . . . 220

A-21. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia cyclopion* Fed the Intermediate Meal Size . . . . . 221

A-22. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia cyclopion* Fed the Intermediate Meal Size . . 222

A-23. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia rhombifera* Fed the Intermediate Meal Size . . . . . 223

A-24. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia rhombifera* Fed the Intermediate Meal Size . . 224

A-25. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia fasciata* from Lake County, Tennessee Fed the Small Meal Size . . . . . 225

A-26. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia fasciata* from Lake County, Tennessee Fed the Small Meal Size . . . . . 226

A-27. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia rhombifera* Fed the Small Meal Size . . . . . 227

TABLE PAGE

A-28. Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia rhombifera* Fed the Small Meal Size . . . . . 228

A-29. Estimates of the Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Three Species of *Nerodia* from Lake County, Tennessee from the Bertalanffy Growth Model . . . . 229

LIST OF FIGURES


| FIGURE | | PAGE |
|---|---|---|
| 1. | Equations and Growth Curves for the Bertalanffy Growth Model. A. Equation and Growth Curve for Length. B. Equation and Growth Curve for Weight . . . | 13 |
| 2. | Equations and Growth Curves for the Logistic Growth Model. A. Equation and Growth Curve for Size (Length or Weight). B. Equation and Growth Curve for Length When Growth is Logistic-by-Mass. C. Equation and Growth Curve for Weight When Growth is Logistic-by-Length . . . . . | 15 |
| 3. | The Linear Growth Model Fitted to the Weight (W) and Total Length (L) Data for Male *Nerodia fasciata* from Shelby County, Tennessee. A. The Data for Weight as a Function of Food Consumed. B. The Data for Total Length as a Function of Food Consumed . . . . . | 33 |
| 4. | The Linear Growth Model Fitted to the Snout-Vent Length (SVL) and Tail Length (TL) Data for Male *Nerodia fasciata* from Shelby County, Tennessee. A. The Data for Snout-Vent Length as a Function of Food Consumed. B. The Data for Tail Length as a Function of Food Consumed . . . . . | 34 |
| 5. | Growth Models Fitted to the Data for Weight (W) as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee . . . . . | 37 |
| 6. | Growth Models Fitted to the Data for Weight (W) as a Function of Time for Male *Nerodia fasciata* from Shelby County, Tennessee . . . . . | 38 |
| 7. | Growth Models Fitted to the Data for Snout-Vent Length (SVL) as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee . . | 39 |
| 8. | Growth Models Fitted to the Data for Snout-Vent Length (SVL) as a Function of Time for Male *Nerodia fasciata* from Shelby County, Tennessee . . . . . | 40 |
| 9. | Simulated Growth Curves for Snout-Vent Length (SVL) Using the Bertalanffy Growth Model . . . . . | 45 |

FIGURE PAGE

10. Simulated Growth Curves for Weight (W) Using the Bertalanffy Growth Model . . . . . 46

11. Effect of the Feeding Regimen on Growth in Length in Male *Nerodia fasciata* from Lake County, Tennessee. A. The Effect on Total Length (L). B. The Effect on Snout-Vent Length (SVL). C. The Effect on Tail Length (TL). Data Represent the First 10 Months of Growth . . . . . 60

12. Effect of the Feeding Regimen on Growth in Length in Female *Nerodia fasciata* from Lake County, Tennessee. A. The Effect on Total Length (L). B. The Effect on Snout-Vent Length (SVL). C. The Effect on Tail Length (TL). Data Represent the First Eight Months of Growth . . . . . 62

13. Effect of the Feeding Regimen on Growth in Length in Male *Nerodia rhombifera*. A. The Effect on Total Length (L). B. The Effect on Snout-Vent Length (SVL). C. The Effect on Tail Length (TL). Data Represent the First 10 Months of Growth . . . . . 63

14. Effect of the Feeding Regimen on Growth in Length in Female *Nerodia rhombifera*. A. The Effect on Total Length (L). B. The Effect on Snout-Vent Length (SVL). C. The Effect on Tail Length (TL). Data Represent the First 10 Months of Growth . . . . . 64

15. Effect of the Feeding Regimen on Growth in Weight (W) in *Nerodia fasciata* from Lake County, Tennessee. A. The Effect in Males. B. The Effect in Females. Data for Males Represent the First 10 Months of Growth. Data for Females Represent the First Eight Months of Growth . . . . . 66

16. Effect of the Feeding Regimen on Growth in Weight (W) in *Nerodia rhombifera*. A. The Effect in Males. B. The Effect in Females. Data Represent the First 10 Months of Growth . . . . . 67

17. Effect of the Feeding Regimen on the Rate of Increase in Weight Per Unit Length (W/SVL) for *Nerodia fasciata* from Lake County, Tennessee. A. The Effect in Males. B. The Effect in Females. Data for Males Represent the First 10 Months of Growth. Data for Females Represent the First Eight Months of Growth. The Numbers in Parentheses are Snout-Vent Length (SVL) . . . . . 70

FIGURE PAGE

18. Sexual Variation in Growth in Length in *Nerodia fasciata* from Shelby County, Tennessee. A. Variation in Total Length (L). B. Variation in Snout-Vent Length (SVL). C. Variation in Tail Length (TL) . . . . . 79

19. Sexual Variation in Growth in Total Length (L) in Snakes of the Genus *Nerodia* from Lake County, Tennessee. A. *N. fasciata* Large Meal Size. B. *N. fasciata* Intermediate Meal Size. C. *N. fasciata* Small Meal Size. D. *N. cyclopion* Intermediate Meal Size. E. *N. rhombifera* Intermediate Meal Size. F. *N. rhombifera* Small Meal Size . . . . . 80

20. Sexual Variation in Growth in Snout-Vent Length (SVL) in Snakes of the Genus *Nerodia* from Lake County, Tennessee. A. *N. fasciata* Large Meal Size. B. *N. fasciata* Intermediate Meal Size. C. *N. fasciata* Small Meal Size. D. *N. cyclopion* Intermediate Meal Size. E. *N. rhombifera* Intermediate Meal Size. F. *N. rhombifera* Small Meal Size . . . . . 81

21. Sexual Variation in Growth in Tail Length (TL) in Snakes of the Genus *Nerodia* from Lake County, Tennessee. A. *N. fasciata* Large Meal Size. B. *N. fasciata* Intermediate Meal Size. C. *N. fasciata* Small Meal Size. D. *N. cyclopion* Intermediate Meal Size. E. *N. rhombifera* Intermediate Meal Size. F. *N. rhombifera* Small Meal Size . . . . . 83

22. Sexual Variation in Growth in Total Length (L) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines . . . . . 90

23. Sexual Variation in Growth in Snout-Vent Length (SVL) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines . 91

24. Sexual Variation in Growth in Tail Length (TL) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines . . . . . 92

25. The Relationship Between Snout-Vent Length (SVL) and Total Length (L) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines . . . . . 94

FIGURE PAGE

26. The Relationship Between Tail Length (TL) and Total Length (L) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines . . . . . 98

27. The Relationship Between Snout-Vent Length (SVL) and Total Length (L) and Tail Length (TL) and Total Length in *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size. A. SVL and L. B. TL and L . . . . . 99

28. The Relationship Between Snout-Vent Length (SVL) and Total Length (L) and Tail Length (TL) and Total Length in *Nerodia cyclopion* Fed the Intermediate Meal Size. A. SVL and L. B. TL and L . . . . . 100

29. The Relationship Between Snout-Vent Length (SVL) and Total Length (L) and Tail Length (TL) and Total Length in *Nerodia rhombifera* Fed the Intermediate Meal Size. A. SVL and L. B. TL and L . . . . . 101

30. Sexual Variation in Growth in Weight (W) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines . . . . . 102

31. Sexual Variation in Growth in Weight (W) in Snakes of the Genus *Nerodia* from Lake County, Tennessee. A. *N. fasciata* Large Meal Size. B. *N. fasciata* Intermediate Meal Size. C. *N. fasciata* Small Meal Size. D. *N. cyclopion* Intermediate Meal Size. E. *N. rhombifera* Intermediate Meal Size. F. *N. rhombifera* Small Meal Size . . . . . 103

32. Sexual Variation in Growth in Weight (W) in *Nerodia fasciata* from Shelby County, Tennessee. Data Represent Four Years of Growth. A. The Data. B. The Regression Lines . . . . . 105

33. Sexual Variation in Weight Per Unit Length (W/SVL) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines . . . . . 107

FIGURE PAGE

34. Sexual Variation in Growth in Weight Per Unit Length (W/SVL) for *Nerodia fasciata* from Lake County, Tennessee. A. Large Meal Size. B. Intermediate Meal Size. C. Small Meal Size . . . 108

35. Sexual Variation in Growth in Weight Per Unit Length (W/SVL) in *Nerodia rhombifera* and *N. cyclopion*. A. *N. rhombifera* Intermediate Meal Size. B. *N. rhombifera* Small Meal Size. C. *N. cyclopion* Intermediate Meal Size . . . . . 109

36. Variation in Growth in Total Length (L) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data for Males. B. The Regression Lines for Males. C. The Data for Females. D. The Regression Lines for Females . . . . 120

37. Variation in Growth in Snout-Vent Length (SVL) and Tail Length (TL) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. SVL for Males. B. SVL for Females. C. TL for Males. D. TL for Females . . . . . 121

38. Variation in Growth in Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Two Species of *Nerodia* Fed the Small Meal Size. A. L for Males. B. L for Females. C. SVL for Males. D. SVL for Females. E. TL for Males. F. TL for Females . . . . . 122

39. Growth Curves for Total Length (L) for Males of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines . 124

40. Growth Curves for Total Length (L) for Females of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines . 125

41. Growth Curves for Snout-Vent Length (SVL) and Tail Length (TL) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. SVL for Males. B. SVL for Females. C. TL for Males. D. TL for Females . . . . . 126

42. Variation in Growth in Weight (W) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data for Males. B. The Regression Lines for Males. C. The Data for Females. D. The Regression Lines for Females . . . . . 128

FIGURE PAGE

43. Growth Curves for Weight (W) for Males of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines . . . . 129

44. Growth Curves for Weight (W) for Females of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines . . . . . 130

45. Variation in Growth in Weight Per Unit Length (W/SVL) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines . . . . . 133

46. Variation in Growth in Weight Per Unit Length (W/SVL) for Females of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines . . . . . 134

47. Weight (W) and Snout-Vent Length (SVL) as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee. A. Weight. B. Snout-Vent Length. Data Represent 12 Months of Growth . . . . . 145

48. Individual Regression Lines for Weight (W) as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee . . . . . 146

49. Individual Regression Lines for Snout-Vent Length (SVL) as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee . . . . . 147

50. Production-Ingestion (P-I) Ratios as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee. A. P-I Ratios for Weight (W). B. P-I Ratios for Snout-Vent Length (SVL) . . . . . 152

# CHAPTER I

# INTRODUCTION

## *Growth, Body Size, and the Niche*

The demands of a particular lifestyle are very important in shaping the pattern of growth in a species. In some cases, the ability to grow rapidly can determine whether an individual lives or dies. Many birds have predictable seasonal migrations during which the young, as well as the old, must survive. Johnson and McFarlane (1967) postulated that Pacific Golden Plovers (*Pluvialis dominica fulva*) can fly 4000 km non-stop in 37 hours utilizing 18 g of fat for the required energy. They also suggest that only a plover containing at least 18 g of fat and weighing at least 150 g will attempt the 4000 km flight. Juveniles of this species must obviously grow at a rate that will ensure that they will meet these minimum requirements or they will either be left behind or die in transit.

The consequences of a slower growth rate are often less drastic than in the above example. Most notable among these less drastic effects are a delay in the onset of reproduction, and a consequent reduction in the potential number of offspring that can be produced. Many mammals do not breed unless they reach a minimum weight (Heaney 1978). Reptiles and amphibians likewise seem to reach sexual maturity after completion of a certain amount of growth rather than reaching a particular age (Porter 1972). Because reproduction is seasonal in most reptiles, slight delays in the age of maturation

may mean relatively long delays in the age at first reproduction. Short-lived species may not be able to reproduce at all if they do not reach sexual maturity by the breeding season following hatching or birth (Andrews 1982).

The rate of growth has other important consequences for a species. Many things may change as an animal grows larger and certainly changes in prey size and type are among the most important. Small rattlesnakes tend to eat lizards while larger individuals of the same species tend to eat rodents (Klauber 1956). Water snakes of the genus *Nerodia* tend to eat larger prey as they mature, and *N. erythrogaster* and *N. fasciata* change their feeding preferences from fish to frogs as the snakes exceed a snout-vent length of 50 cm. (Mushinsky et al. 1982). In all of these cases, the rate of growth will determine when these changes occur.

Overall body size and the size of various body parts have a very intimate relationship with other niche parameters of a species. Consider the classic evolutionary example of size changes in the Galapagos finches. From a common ancestor, the body size, and particularly the bill size, of these birds have changed apparently according to the size of the food items commonly consumed (Pianka 1974). Body size also has implications in relation to the size of shelter required, habitat preferences, and the number of potential predators. Insular bird populations have evolved longer bills and longer tarsometatarsi than their mainland counterparts in order to utilize a greater range of food sizes and a wider variety of perches respectively (Grant 1965). The lizard *Lacerta serpa* has

shortened legs and tail on islands apparently because of the reduced demand for locomotion due to the absence of predators. On islands with cliffs this shortening trend is somewhat reversed owing to an increased demand on climbing ability (Kramer 1951). Young animals are also prone to predation from sources that are not a threat to the larger adults. Potential predators on newborn water snakes include painted turtles, greenfrogs, bullfrogs, and grackles (Feaver 1977). Adult snakes are far too large to fall victim to these predators, and thus the rate of growth will determine the length of time that an individual will be susceptible to certain predators. In addition, while body size and other niche parameters have an intimate relationship, it should be remembered that any evolutionary change in body size or proportions necessitates a change in the growth pattern of that species.

*Factors Influencing Body Size and Growth*

Adult body size is a very complex biological parameter and there are many factors that can have an effect on it. Two generalizations that have a bearing on body size are Bergmann's rule and Allen's rule. Bergmann's rule states that in species of warm-blooded vertebrates, races from cooler climates tend to be larger than races of the same species living in warmer climates. Allen's rule states that protruding body parts of warm-blooded animals are shorter in cooler climates than in warmer ones. These generalizations are not unalterable laws, but are purely a means for describing the parallelism between morphological variation and features of the

physical environment (Mayr 1970). Numerous other variables such as inter- and intraspecific competition, predation pressure, various physiological and physical factors, and resource availability, may alter any geographic trend in body size and proportions.

Bergmann's and Allen's rules, as their definitions indicate, are generally only applicable to warm-blooded animals. There are, however, some cold-blooded animals that follow the same body size trends. Ray (1960) found that 13 of the 17 species he examined followed Bergmann's rule, and seven of 10 examined for changes in their extremities followed Allen's rule. These species included forms as diverse as a moneran (*Chlamydomonas*), a nematode (*Cephalobus*), fruit flies (*Drosophila*), spiders (*Padosa*), and amphibians (*Rana sylvatica* and *Bufo boreas*). Honey bees (*Apis mellifera*) in Russia also follow Bergmann's rule (Alpatov 1929). The reverse of Bergmann's rule is also seen in cold-blooded animals. The average adult size of the carabid beetle *Dicaelus purpuratus* increases from north to south in eastern North America (Park 1949), and the body size of lizards of the genus *Liolaemus* from Chile decreases with decreasing temperatures (Hellmich 1951). Other trends are also discernible in cold-blooded animals. For example, butterfly pupae (*Melitaea chalcedona*) are largest and heaviest in coastal southern Califronia where humidity is highest, and smallest and lightest in the Mojave Desert where humidity is the lowest (Hovanitz 1942). This finding illustrates the point that where factors other than temperature affect body size, the largest size will be reached in the

optimal portion of the species range, independently of temperature (Mayr 1970).

What constitutes the optimal portion of a species range? There are many factors that can contribute to the optimal conditions for a species. A great deal of the information concerning these factors and changes in body size and proportions comes from studies of island populations. The body size of solitary species of the lizard genus *Anolis* on Caribbean islands tends to be restricted to a narrow range (55-75 mm in males and 40-60 mm in females). On multi-species islands, most of the males fall into the 40-60 mm range. The increase in size of solitary species is apparently due to the lack of interspecific competition (Schoener 1969). Male *Anolis sagrei* on Abaco in the Caribbean do now show the increase in body size characteristic of solitary species even though the females do. It has been suggested by Lister (1975) that females can increase in size because they have less overlap in prey size with insectivorous warblers than do males. The body size of the iguanid lizard *Uta stansburiana* on islands in the Gulf of California also appears to be inversely proportional to the number of sympatric iguanid species (Soulé 1966). Intraspecific competition can favor large body size in males through male combat (Dunham et al. 1978 for lizards, Shine 1978 for snakes) or in females through increased fecundity (Semlitsch and Gibbons 1982 for snakes). Predation pressure, or lack of it, can cause body size changes in either direction depending on the species in question. Small animals that avoid predation primarily by escape to shelter would be expected to increase in size in the absence of

predation. Large animals that avoid predation by outrunning or physically overwhelming a predator could be expected to decrease in size in the absence of predators (Heaney 1978).

Physical and physiological factors in many cases tend to affect body size in a manner peculiar to the species in question. Bird body sizes are constrained by the necessity of flight and perching. Geckos are constrained by the clinging capacity of their toe pads. Rodents may also be constrained by the soil type since the diameter of their burrows may become large enough for them to collapse (Case 1978a). Larger animals will have relatively less heat loss in cold climates. In hot climates, intermediate sized animals can neither store heat to cut down on evaporative water loss (Taylor 1969) nor dissipate it as quickly as a small animal. Large mammals also have more efficient locomotion, but small mammals are able to climb vertically with little more energy than is required to move horizontally (Taylor et al. 1972) providing a distinct advantage in more hilly terrain.

While all of the factors discussed have some effect on body size, food resource availability seems to be of primary importance in determining body size. Case (1978a) supports the idea that an increase in the mean amount of available food should lead to an evolutionary increase in body size, and a decrease in the mean amount of available food should lead to an evolutionary decrease in body size. There does seem to be evidence to support this idea. In the absence of competitors, rodents on islands utilize a wider variety of food and therefore have evolved larger body sizes (Grant 1965). When

a population is food stressed, selection should favor individuals that breed at a small size leading to an evolutionary decrease in body size (Heaney 1978).

The above predictions based on the amount of available food are, of course, only generalizations and many exceptions can be found. Foxes on islands off the coast of California range in size according to the type and not the amount of food available. Large prey, such as rabbits and hares and large gallinaceous birds, are absent from these islands and the endemic foxes are smaller than their mainland counterparts (Case 1978a). Rodents are also scarce on these islands, but lizards are abundant. The rattlesnakes on these islands appear to be smaller in response to the size distribution of the available prey. Where the abundance of prey is reversed, the snakes are the same size of in one case larger on the island than on the mainland (Case 1978a).

While the majority of these examples are taken from island situations, the same trends can be applied to any population. The major problem with mainland populations is not in the trends themselves, but in delineating the boundaries of the influence of any set of factors. In any case, body size changes both ontogenetically and evolutionarily are real and any evolutionary change in body size or proportions requires a concomitant change in the growth pattern.

*Dietary Efficiency*

The above discussion has established that body size and consequently growth can be affected by a number of ecological parameters.

The immediate determinant of growth rate, however, is how efficiently the food consumed is utilized. Dietary efficiency is dependent upon many factors not the least of which are the type of foodstuff consumed and the type of organism consuming it. Cellulose and chitin appear to present the most problems in digestion, but several specializations in various groups of animals have evolved to deal with them. These specializations range from outright secretion of the necessary enzymes to the use of microorganisms in various ways for the production of the digestive enzymes (see Barnard 1973).

The changing composition of the dietary intake can also offer problems to dietary efficiency. The ability to respond to these changes has been demonstrated in a variety of taxa. Various mammals show an increase in the production of pancreatic amylase and protease with an increase in the starch and protein content respectively of the diet (Barnard 1973). Snails produce more amylase on a starch diet, and snail species that change from a herbivorous to an omnivorous diet show a decline in the amylase/protease ratio upon maturation reflecting the increase in protein and decrease in starch in the diet (Barnard 1973).

Differences in the assimilation efficiency between species probably reflect the differences in digestibility of the food consumed (Smith 1976). Among reptiles the assimilation efficiencies for insectivores and carnivores are higher than for herbivores (see Table 1). *Ctenosaura pectinata*, a large iguanid lizard, however, fed on a diet of sweet potatoes, which are low in crude fiber, had a digestive efficiency of 86.3% (Trockmorton 1973). Herbivorous

Table 1

Caloric Assimilation Efficiencies in Reptiles

| Species | Food | Assimilation Efficiency (%) | Reference |
|---|---|---|---|
| Carnivores (Snakes) | | | |
| *Elaphe guttata* | Mice | 88.9 | Smith 1976 |
| *Heterodon platyrhinos* | *Bufo terrestris* | 83.9 | Smith 1976 |
| *Nerodia erythrogaster* | Minnows | 78.5-81.7 | Gehrmann 1971 |
| Insectivores (Lizards) | | | |
| *Anolis carolinensis* | Crickets, grasshopper nymphs, mealworms | 69.9-72.2 | Kitchell and Windell 1972 |
| | *Tenebrio*--adult | 54.4 | Licht and Jones 1967 |
| | *Tenebrio*--larva | 89.3 | |
| | House crickets | 69.5 | |

Table 1 (Continued)

| Species | Food | Assimilation Efficiency (%) | Reference |
|---|---|---|---|
| *Lacerta vivipara* | *Tenevrio*--larva | 89.0 | Avery 1971 |
| *Sceloporus graciosus* | *Tenebrio*--larva | 83.0 | Mueller 1970 |
| *Sceloporus occidentalis* | *Tenebrio*--larva | 83.0 | Mueller 1970 |

reptiles do not seem to be as efficient at digestion as the herbivorous mammals. The herbivorous lizard *Dipsosaurus dorsalis* is only 50-55% efficient as compared to 71% for cattle and 64% for rabbits (Bennett and Dawson 1976). Dietary assimilation efficiency for reptiles appears to be independent of the level of food consumption (Gehrmann 1971, Kitchell and Windell 1972), but does show a decrease with age (Gehrmann 1971).

*Growth Models and Growth in Reptiles*

The information regarding the equations and the explanations of the symbols presented below for the growth models have been adapted from Dunham (1978), Schoener and Schoener (1978), and Andrews (1982). Two models have been commonly utilized to describe growth in reptiles. The Bertalanffy growth model is based on the idea that growth represents the difference between synthetic and degradative processes, and that synthetic processes are directly proportional to metabolic rate and degradative processes are directly proportional to body mass (Bertalanffy 1957, Fabens 1965). The general equations for length and weight respectively are

$$L = A_L(1 - be^{-rt}) \tag{1}$$

and

$$W = c\left[\left[A_L(1 - be^{-rt})\right]^3\right] \tag{2}$$

where: $b = (1 - L_0/L_A)$;

$L$ = length;

$W$ = weight;

$A_L$ = asymptote of length;

$L_0$ = initial length;

$e$ = base of the natural logarithm;

$t$ = time;

$b$ = constant;

$c$ = constant relating length and weight;

$r$ = growth constant.

The equation for weight is derived by substituting the function relating weight to length ($W = cL^3$) into the length equation. The curves described by these equations are illustrated in Figure 1. The equation for length produces an asymptotic curve that increases at an exponentially decreasing rate as a function of time (Figure 1A). The equation for weight produces an asymptotic sigmoid curve with the inflection point at 30% of asymptotic weight (Figure 1B). Equation (2) can be modified so that the asymptote is in terms of weight. The result is

$$W = c\left[\left[(A_W/c)^{1/3}\ (1 - be^{-rt})\right]^3\right] \qquad (3)$$

in which $A_W$ = asymptote of weight and all other symbols are as explained above for equations (1) and (2).

The other commonly used model for reptile growth is the logistic model. Growth can be logistic-by-length or it can be logistic-by-mass. The general equation for logistic growth is

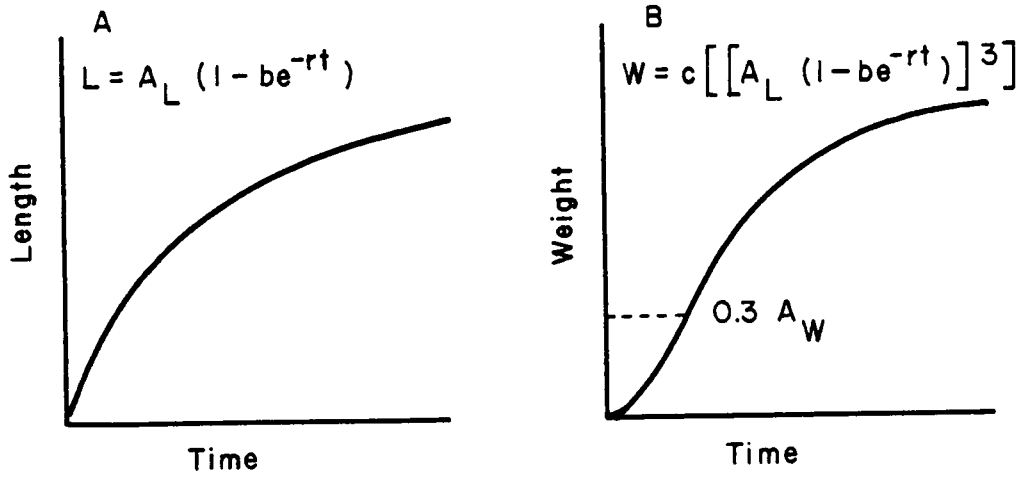



Figure 1. Equations and Growth Curves for the Bertalanffy Growth Model. A. Equation and Growth Curve for Length. B. Equation and Growth Curve for Weight.

$$S = A_S/(1 + be^{-rt}) \quad (4)$$

where: $b = (A_S/A_0) - 1$;

$S$ = size (length or weight);

$A_S$ = asymptote of size;

$A_0$ = initial size.

All symbols are as explained above for equations (1), (2), and (3).

Whether the logistic equation is for length or weight, it produces a symmetrical asymptotic sigmoid curve with its point of inflection at one-half of the asymptote (Figure 2A). If growth is logistic-by-mass, length is evaluated by substituting the function relating length to weight $L = (W/c)^{1/3}$ into the logistic equation for weight. The resulting equation,

$$L = \left[1/c \left[A_W/(1 + be^{-rt})\right]\right]^{1/3} \quad (5)$$

in which $b = (A_W/A_0) - 1$, $W_0$ = initial weight, and all other symbols are as explained above for equations (1), (2), and (3), produces an asymptotic curve with the inflection point at 63% of asymptotic length (Figure 2B). Equation (5) can be modified so that the asymptote is in terms of length. The result is

$$L = \left[1/c \left[cA_L^{\,3}/(1 + be^{-rt})\right]\right]^{1/3} \quad (6)$$

in which all of the symbols are as explained for equation (5).

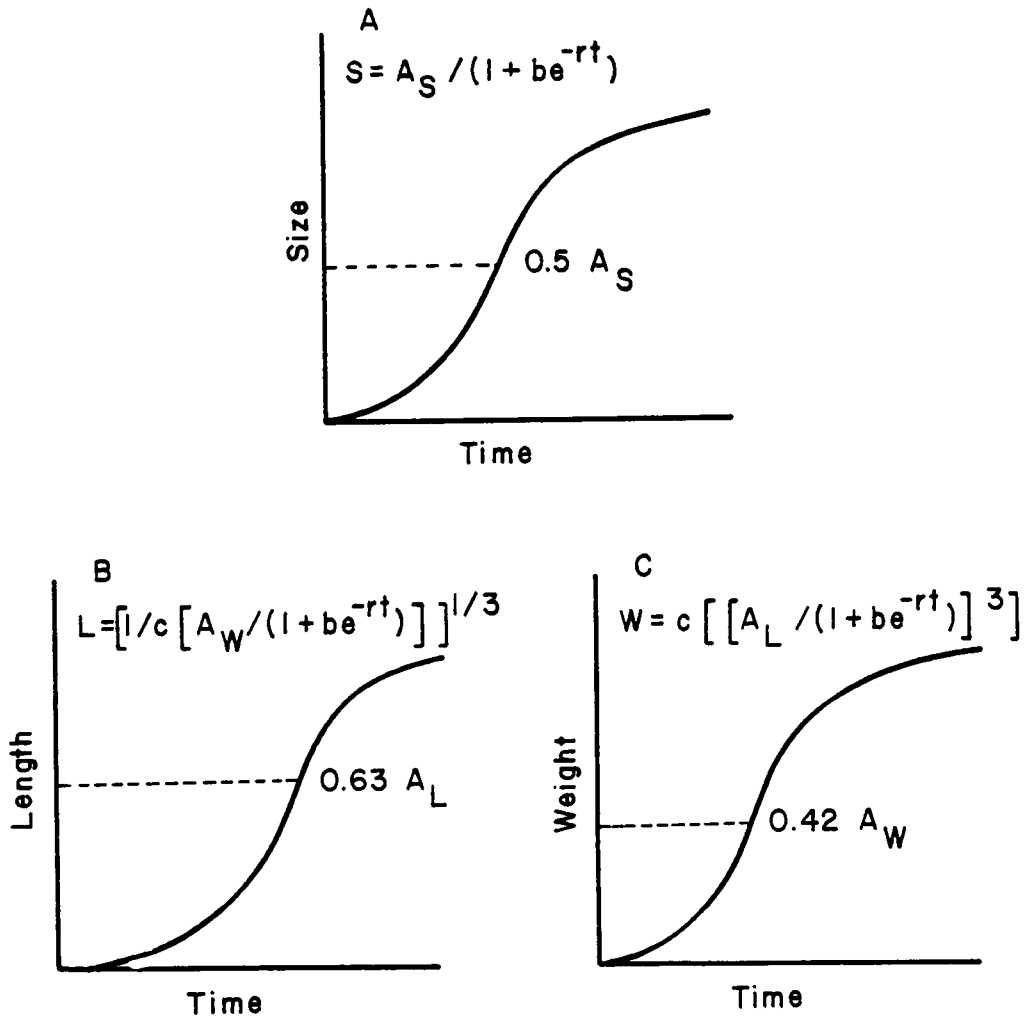



Figure 2. Equations and Growth Curves for the Logistic Growth Model. A. Equation and Growth Curve for Size (Length or Weight). B. Equation and Growth Curve for Length When Growth is Logistic-by-Mass. C. Equation and Growth Curve for Weight When Growth is Logistic-by Length.

If growth is logistic-by-length, weight is evaluated by substituting the function relating weight to length ($W = cL^3$) into the logistic equation for length. The resulting equation,

$$W = c\left[\left[A_I/(1 + be^{-rt})\right]^3\right] \tag{7}$$

in which $b = (A_I/L_0) - 1$, and all other symbols are as explained above for equations (1), (2), (3), produces an asymptotic sigmoid curve with the inflection point at 42% of asymptotic weight (Figure 2C). As with equation (3), equation (7) can be modified so that the asymptote is in terms of weight. The result is

$$W = c\left[\left[A_W/c)^{1/3}/(1 + be^{-rt}\right)\right]^3\right] \tag{8}$$

in which all of the symbols are as explained for equation (7).

Although the general forms of the Bertalanffy and logistic growth models measure growth as a function of time, they can also be used to measure growth as a function of total weight of food consumed by replacing the term for time (t) with a term for total weight of food consumed. This method was used with a modified Bertalanffy growth equation to describe the increase in length in the snake *Elaphe guttata* (Barnard et al. 1979). The modified equation was of the form

$$L = A_L - be^{-rx} \tag{9}$$

in which $b = A_L - A_0$, x = the total weight of food consumed, and all other symbols are as explained above for equations (1), (2), and (3).

Weight in this form of the model is evaluated by using the equation

$$W = c\left[(A_L - be^{-rx})^3\right] \tag{10}$$

in which $b = A_L - L_0$, and all other symbols are as explained above in equations (1), (2), and (3). As with equation (2), equation (10) can be modified so that the asymptote is in terms of weight. The result is

$$W = c\left[\left[(A_W/c)^{1/3} = be^{-rx}\right]^3\right] \tag{11}$$

in which all of the symbols are as explained above in equation (10). Both the general and the modified forms of the Bertalanffy growth model can describe growth as a function of time or as a function of weight of food consumed. Identical results are obtained with the two forms of the equations.

A number of investigations have focused on the problem of fitting growth data from reptiles to the above models. Small, short-lived iguanid lizards appear to have growth curves that are best fit by the logistic-by-mass model, while large long-lived reptiles have growth curves that are best fit by the Bertalanffy growth model (Andrews 1982). Although there are some exceptions, the growth curves of the majority of the populations of *Anolis angusticeps*, *A. carolinensis*, *A. distichus*, and *A. sagrei* studied by Schoener and Schoener (1978) fit the logistic-by-mass model. The growth curve of the lizard *Sceloporus merriami* also fits the logistic-by-mass model (Dunham 1978). Reptiles whose growth pattern have been shown to fit

the Bertalanffy growth model include the snakes *Natrix tigrina* and *Elaphe quadrivirgata* (Fukada 1961), *Elaphe guttata* (Barnard et al. 1979), the turtles *Chrysemys picta* (Wilbur 1975), *Pseudemys scripts* (Gibbons et al. 1981), the lizard *Basiliscus basiliscus* (Van Devender 1978), and the crocodilian *Alligator mississippiensis* (Chabreck and Joanen 1979).

Linear growth models of the general form Y = ax + b are occasionally reported for reptiles. Juveniles of several species of large herbivorous lizards exhibit a constant linear increase in size. *Iguana iguana* and *Ctenosaura similis* exhibit growth rates of 0.27 and 0.36 mm/day respectively for the first two years of life (Van Devender 1982). The snakes *Elaphe obsoleta quadrivittata* (Ford 1974) and *Elaphe guttata* (Barnard et al. 1979) exhibit a linear increase in weight as a function of the total weight of food consumed for the first two years of life. Constant increases in length and weight, however, must obviously be restricted to early growth (Andrews 1982).

*Growth in Snakes*

Studies of growth in snakes can be divided into two categories: field studies and laboratory studies. Field studies provide information about the natural growth patterns of a species. There are, however, some difficulties associated with field work. Assignment of snakes to age groups based on size has been attempted by several investigators (Raney and Roecker 1947, Klauber 1956, Gibbons 1972). Because of differential growth rates of individuals

this assignment could only be made for the first two years of life. Marking animals individually has overcome the problem of age determination, but the difficulty lies in the subsequent recapture of the same individual and this is often difficult.

In spite of the difficulties, field studies have provided some useful information on snake growth patterns. Some of the findings, as would be expected, vary from species to species. Snakes grow faster as juveniles and adolescents than as adults (Klauber 1956). Females of both *Natrix* (=*Nerodia*) *sipedon* and *Natrix* (=*Regina*) *septemvittata* grow faster and achieve a greater maximum size than males (Raney and Roecker 1947). Both males and females of *Thamnophis s. sirtalis*, *T. s. sauritus*, and *T. butleri* grow rapidly for the first year, but the growth rate of the males decreases faster with age (Carpenter 1952). In the black rat snake, *Elaphe o. obsoleta*, there seems to be little sexual dimorphism in the growth rate for the first three years, but with attainment of maturity, growth slows sooner and more rapidly for females (Fitch 1963). Male rattlesnakes average about 1% longer than females at birth. This difference increases to 3% in the following spring and reaches about 15% in fully mature adults of most species (Klauber 1956). As can be plainly seen, specific information about growth in snakes depends a great deal upon the species in question.

Laboratory studies of growth in snakes have addressed questions that are difficult to answer effectively in field situations. Myer and Kowell (1971) found that after six weeks of food deprivation, the weight of four adult kingsnakes, *Lampropeltis getulus*

*floridana*, had only fallen an average of 6.3% below their weight immediately before the pre-deprivation meal. Similar results were obtained with neonate garter snakes *Thamnophis sirtalis* (Myer and Kowell 1973). Apparently snakes are designed to withstand long periods of deprivation without drastic effects. The size that any individual attains apparently depends more on the amount of food consumed than on its age, and the amount of variation among individuals increases as the total amount of food consumed becomes greater (Barnard et al. 1979).

Assimilation efficiencies have been determined in the lab for several species. Caloric assimilation efficiency was 88.9% for the corn snake, *Elaphe guttata* and 83.9% for the hognose snake, *Heterodon platyrhinos*, with no significant different between young and adult animals (Smith 1976). Both caloric assimilation efficiency and assimilation efficiency by weight were independent of food consumption in the blotched water snake, *Natrix* (=*Nerodia*) *erythrogaster transversa*, even though there was a significant decrease in both assimilation efficiency measures with age (Gehrmann 1971). The efficiency of conversion of food to body weight and length was also found to decrease with age in the snake *Spalerosophis cliffordi* (Dmi'el 1967).

*Niche Separation in Nerodia*

The genus *Nerodia* is comprised of eight moderate to large sized semi-aquatic species. The distribution of the genus is largely continuous. The ranges of seven of the eight species overlap

within the area from southern Canada through the United States east of the Rocky Mountains and down the east coast of Mexico to the Yucatan Peninsula. A single species, *N. valida*, has a distribution that is disjunct from the other species and occurs in western Mexico and lower California (Conant 1969, 1975). Although the genus ranges as far north as southern Canada, most of the species are concentrated in the southeastern United States. There is, therefore, a great deal of overlap in the ranges of the species. Due to the semi-aquatic nature of the species, they are likely to be found in the same habitat and are at least potentially competitors for the same resources.

The ecological relationships of four sympatric species of *Nerodia* have been studied in some depth (see Table 2). It was found that the species show some separation in their niche requirements. *Nerodia fasciata* and *N. erythrogaster* prefer similar prey items and display ontogenetic changes in feeding preference from fish to frogs. *Nerodia erythrogaster*, however, is a much larger species and takes larger prey sizes then does *N. fasciata* (Mushinsky et al. 1982). There are also differences in activity time and habitat preferences between the two species. *Nerodia cyclopion* and *N. rhombifera* share similar prey and microhabitat preferences, but differ in their preferred activity time. *Nerodia rhombifera* also eats larger prey than does *N. cyclopion* (Mushinsky et al. 1982).

Sexual as well as species differences are evident in the ecological requirements of some *Nerodia* species. Large females of *N. cyclopion* and *N. rhombifera* eat larger prey than do the smaller

Table 2

Some Ecological Parameters of Four Species of *Nerodia*

| Species | Activity Time[1] | Feeding Preference[2] | Habitat Preference[3] |
|---|---|---|---|
| *N. fasciata* | Primarily diurnal becoming nocturnal in September | Fish, frogs | Generalist |
| *N. erythrogaster* | Nocturnal[2] | Frogs, fish | Sparce vegetation and gently sloping shorelines |
| *N. cyclopion* | Diurnal | Fish | Gently sloping shorelines devoid of vegetation |
| *N. rhombifera* | Nocturnal | Fish | Space vegetation and gently sloping shorelines |

[1]Mushinsky and Hebrard 1977b.

[2]Mushinsky and Hebrard 1977a.

[3]Hebrard and Mushinsky 1978.

conspecific males. This phenomenon is not seen in the species that eat frogs as adults. The typical size of the frogs is such that large females as well as the somewhat smaller males can both ingest the same prey (Mushinsky et al. 1982).

While the adults of the four species discussed above function as four separate feeding units, juveniles of these species can be considered a single feeding unit since all individuals less than 50 cm in snout-vent length feed on the fishes *Gambusia* and *Heterandria* (Mushinsky et al. 1982). Competition among the juveniles could be high if prey abundance should drop for some reason. Since the change to the adult diet seems to require the attainment of a certain size, the rate of growth can pretty well determine when an individual can "escape" from this common feeding pool.

*Experimental Rationale*

As mentioned earlier, there are problems involved in studying growth patterns both in the field and in the laboratory. The problems in these two situations, however, are of different natures. Two major problems with field studies are the lack of accurate knowledge concerning dietary input and fecal output, and the difficulty in following a single individual through time. Because these two difficulties can be overcome under laboratory conditions, it is possible to address some questions that would be difficult to answer under field conditions. This study is laboratory based in order to address the following questions: How do females achieve a greater size than males? How do larger species attain a larger size

than smaller ones? Does the feeding regimen affect the growth pattern? How much variability in growth rates exists among individuals from a single litter?

The answers to the first two questions can take several forms: Individuals of the larger group can be more efficient at using what is consumed, they can eat more than individuals of the smaller group, or they can display a slower decrease in the growth rate with age. These solutions can act singly or in combination in any of the situations. Variability in growth rate can also take a variety of forms. Individuals may vary in the rate of weight and overall length increase, or they may vary in the rate at which various body parts grow in relation to each other. It is the purpose of this study to examine these possibilities in order to determine which ones may be operating in natural populations.

The genus *Nerodia* was chosen as the subject for this study for several reasons. First of all, there is a considerable range in adult body size of species in the genus. Many of the species are sympatric and because of the similarity in their ecological requirements are at least potential competitors. The specific ecological requirements of four of the species of *Nerodia* have been examined in some depth and an examination of their growth rates can add to the understanding of the ecological relationships of the species. *Nerodia* species are also fairly easy to obtain and can be maintained in captivity with relative ease.

# CHAPTER 2

# GENERAL PROCEDURES

## *Subjects and Housing*

Three species of *Nerodia*, *N. fasciata confluens*, *N. c. cyclopion*, and *N. r. rhombifera*, were used as subjects in this growth study. All individuals were captive-born to wild-caught females that had completed gestation in the lab.

The majority of the snakes were housed individually in 31 x 17.2 x 8.3 cm plastic boxes. The boxes were equipped with a water dish and a 10 x 15 cm index card which could be used as a shelter. A few of the snakes were specially housed in order to address specific questions. Details of the housing of these snakes can be found in the procedure of the appropriate experiment.

## *Weighing and Measuring*

All subjects were sexed, weighed, and measured as soon as possible after birth. Sexing in newborn snakes was accomplished by applying pressure to the base of the tail which everted the hemipenes in males. The sex of these snakes was later confirmed by probing the post cloacal region of the tail after the snakes had reached an appropriate size. Only one of the over 60 snakes was misidentified as to sex during the initial sexing procedure.

Snakes were measured by gently, but firmly stretching them along a meter stick. Both snout-vent length (SVL) and total

length (L) were measured to the nearest millimeter and tail length (TL) was determined by subtracting SVL from L. Snakes were measured every four weeks during the study using the procedure described above.

Most of the snakes were weighed once per week and all were weighed to the nearest 0.01 g. The number of days allowed to elapse between feeding and weighing varied from experiment to experiment but was never less than four. The weight (W) of a snake for any four week period was taken as the average of the weekly weights during that period, the first and last days' weights inclusive. The averaging was used to avoid the problem of sudden weight loss that occurs when snakes shed and to diminish the effect of fluctuations in weight due to water gain or loss. Some snakes were weighed only once every four weeks because of the special experimental treatment they received. Details of these experiments can be found in the procedure of the appropriate experiment.

*Feeding*

All snakes were maintained on a diet of fathead minnows, *Pimephales promelas*, or a combination of fathead minnows and mosquitofish, *Gambusia affinis*. All food items were presented live to the snakes after being weighed. Each food item was patted dry with a paper towel, placed in a dry petri dish, and weighed to the nearest milligram on an analytical balance. After weighing, food items were placed in a snake's water dish and left for 24 hours. At the end of this period, all uneaten food items were removed. The weight of the

food given to the snakes was gradually increased as the snakes increased in size.

*Dietary Analysis*

The dry weight of food consumed was determined by drying 70 individuals of each food item. These items spanned the range of food sizes offered to the snakes. Each food item was patted dry with a paper towel and weighed while still alive. The food item was then killed by placing it in 60°C water, and then wrapped individually in aluminum foil, being careful to leave an opening in the top to allow moisture to escape. The foil packet containing the food item was then dried to constant weight in a laboratory oven set at 60°C. The dried food item was then removed from the foil packet and weighed. The proportion of dry weight for each item was determined by the following formula:

$$\text{Proportion of Dry Weight} = \frac{\text{Dry weight of item}}{\text{Wet weight of item}}$$

The average proportion of dry weight for each kind of food item was used to calculate the dry weight of food consumed for that particular food item. The dried food items were subsequently ground to a fine powder and analyzed for caloric contant by bomb calorimetry. These figures were used in the calculation of the total calories consumed.

In several experiments, a feces analysis was also made. For the purposes of feces collection, the shelter was removed from the cages. Feces were collected for four week periods at various times throughout the experiments. The sides and bottom of each cage were

scraped to ensure collection of as much of the fecal material as possible. Fecal samples were collected separately for each group according to the sex, species, and feeding regimen of the snakes. Samples were dried to constant weight at 60°C in a laboratory oven. The dry weight of the feces wsa then taken and used to determine dietary assimilation efficiencies by weight using the formula

$$\text{Assimilation Efficiency by Weight} = \frac{\text{Dry weight of food consumed} - \text{Dry weight of the feces}}{\text{Dry weight of food consumed}} \times 100$$

Dried feces were subsequently ground to a fine powder and analyzed for caloric content by bomb calorimetry. Caloric assimilation efficiencies were calculated using the following formula:

$$\text{Caloric Assimilation Efficiency} = \frac{\text{Caloric content of food consumed} - \text{Caloric content of feces}}{\text{Caloric content of food consumed}} \times 100$$

# CHAPTER 3

## GROWTH MODELS AND GROWTH IN *NERODIA*

### *Introduction*

Growth in various species of reptiles has been shown to fit several growth models which differ in their predictions as to when growth is most rapid (see pages 16-17). *Nerodia fasciata* from Shelby County, Tennessee provided enough data to evaluate the ability of these models to estimate changes in size as a function of time and as a function of the weight of food consumed. These data constitute the results of experiment 1. The amount of data available from the other species was insufficient to evaluate the growth models, but due to their close taxonomic relationship to *N. fasciata*, it can be assumed, at least temporarily, that their growth follows the predictions of the same growth model.

In addition to their use in evaluating the growth models, the data from *N. fasciata* were also used in evaluating sexual and individual variation in growth. These subjects are discussed in Chapter 4 and Chapter 5 respectively.

### *Materials and Methods*

*Subjects and procedures.* Subjects for experiment 1 consisted of 14 (eight male and six female) broad-banded watersnakes, *Nerodia fasciata confluens*, that were captive born to a wild caught female from Shelby County, Tennessee. The snakes were born September 9, 1979

and were initially weighed and measured on September 14, 1979. The snakes were initially maintained on a diet of mosquitofish but were switched to fathead minnows at either seven or eight months of age when the snakes had grown too large to be efficiently fed with mosquitofish.

The snakes were fed twice per week and were weighed on the fourth day following the first feeding session of the week. The second feeding of the week immediately followed weighing. L and SVL measurements were made once every four weeks. Feces were collected during the thirteenth, twenty-first, and twenty-fifth months after birth.

This experiment was designed primarily to examine the relationship between food consumption and growth in relation to established growth models. The data were analyzed to see how well they conformed to the predictions of the linear, Bertalanffy, and logistic growth models. This experiment was also designed to examine sexual and individual variation in growth rate among siblings. The collection and analysis of the feces allowed an examination of the relationship between assimilation efficiency and growth rate. The latter three subjects will be examined in later chapters.

*Data analysis.* Growth data for W, L, SVL, and TL as a function of time and as a function of the total weight of food consumed were analyzed using the Bertalanffy and logistic growth models. A linear analysis as a function of the total weight of food consumed was also made. The slope of the linear regression line represents

the average production-ingestion ratio (P-I ratio) for the time period covered by the regression line. The P-I ratio is the increase in the growth parameter (W, L, SVL, or TL) per gram of food consumed and can be calculated as follows:

$$\text{P-I Ratio} = \frac{\text{Increase in the growth parameter}}{\text{Weight of food consumed during the growth period}}$$

The increase in the growth parameter is in grams in the case of W and in millimeters in the cases of L, SVL, and TL. The P-I ratios used here differ from those of Smith (1976) in that the ratios in this study are not expressed as a percentage of the amount of food consumed. This modification was made because percent has no meaning in relation to L, SVL, and TL and the weight of food consumed since two different scales of measurement (mm and g) are involved. The P-I ratio provides a convenient means of expressing growth in terms of how much increase in size is realized per gram of food consumed.

The data were tested for their conformity to the Bertalanffy and logistic models primarily by comparison of the $r^2$ values and the amount of variation unexplained by the model (Sum of Squares Error = SSE) of each model for the growth parameters W, L, SVL, and TL. Comparisons were also made of the predictions of the models for asymptotes and initial sizes.

*Results*

*Comparisons of growth models.* Although the actual values differ, the general pattern of the scatter plots of W, L, SVL, and TL for both males and females is the same. This situation applies whether the data are plotted as a function of food weight or as a function of time. Because of the similarity of the results for the sexes, the relationship between the models and the data are illustrated using only the male data. Also since the patterns of growth for L, SVL, and TL are similar, SVL is used in some cases to illustrate the relationship between the models and the data for length. The data for growth for all of the growth parameters in females, and for growth in L and TL in males are included in the appropriate tables.

Data for W, L, SVL, and TL as a function of food weight for the first four years of growth are shown in Figures 3 and 4. The lines in these figures represent the best linear regression line that can be drawn for each data set. Obviously the linear model does a poor job of describing the variation in the data for this period of time. Despite the fact that a straight line does not fit the entire data set, it can be used to describe smaller portions of the data. Table 3 compares the regression lines fitted to one, two, three, and four years of growth data. Not only does the correspondence of the linear regression and the data, as measured by the $r^2$ value, decrease as larger time units are employed, but the estimates of the starting values of the growth parameters are progressively further from the actual mean values. Use of the linear model with

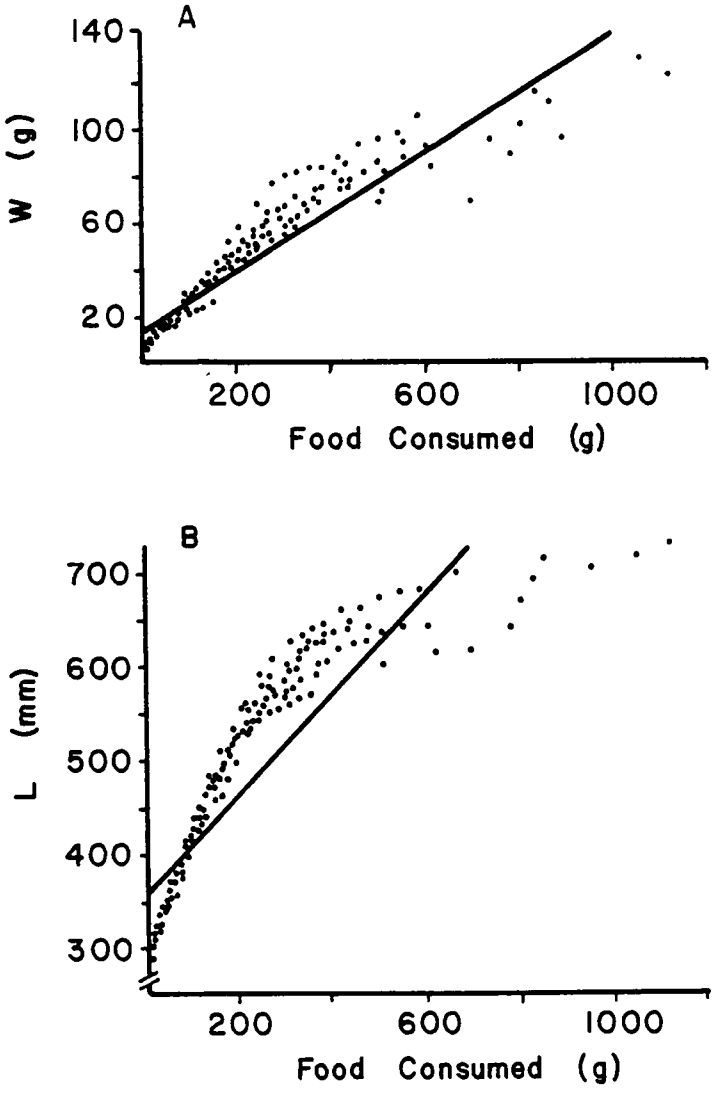



Figure 3. The Linear Growth Model Fitted to the Weight (W) and Total Length (L) Data for Male *Nerodia fasciata* from Shelby County, Tennessee. A. The Data for Weight as a Function of Food Consumed. B. The Data for Total Length as a Function of Food Consumed.

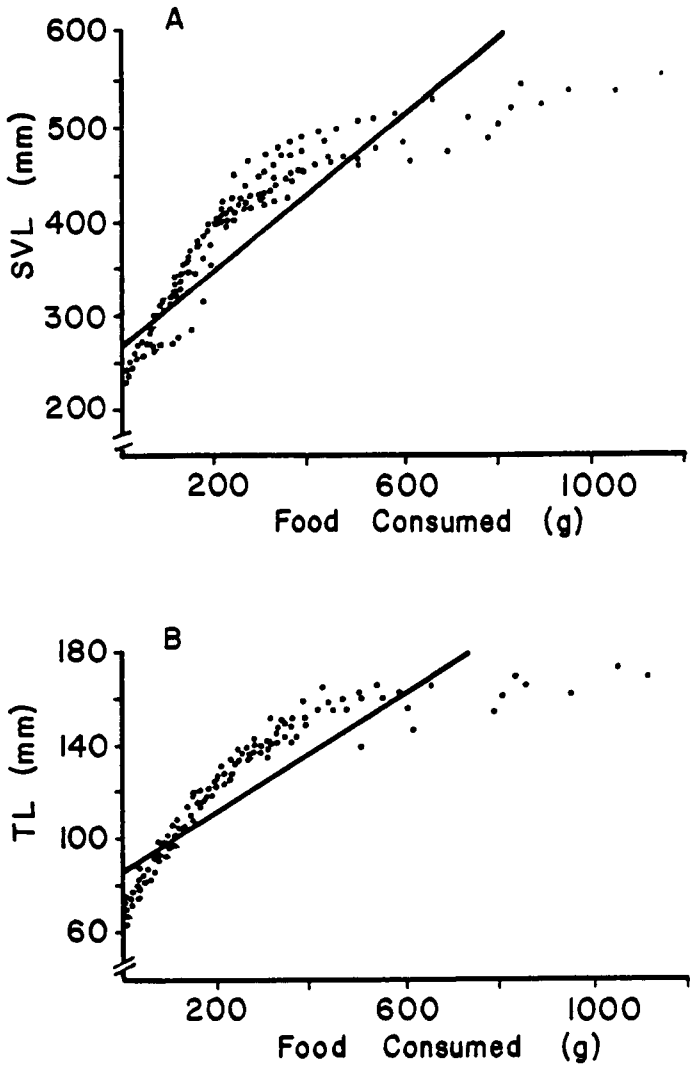



Figure 4. The Linear Growth Model Fitted to the Snout-Vent Length (SVL) and Tail Length (TL) Data for Male *Nerodia fasciata* from Shelby County, Tennessee. A. The Data for Snout-Vent-Length as a Function of Food Consumed. B. The Data for Tail Length as a Function of Food Consumed.

Table 3

$r^2$ Values and Estimates of Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) at Birth for *Nerodia fasciata* from Shelby County, Tennessee Using the Bertalanffy Growth Model

| Sex | Parameter | Mean Value at Birth | Estimate of Mean Value at Birth | | | | $r^2$ | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 Year's Data | 2 Years' Data | 3 Years' Data | 4 Years' Data | 1 Year's Data | 2 Years' Data | 3 Years' Data | 4 Years' Data |
| ♂ | W (g) | 5.8 | 6.9 | 8.2 | 10.1 | 12.8 | 0.942 | 0.964 | 0.947 | 0.912 |
| | L (mm) | 276 | 288 | 322 | 339 | 356 | 0.967 | 0.923 | 0.845 | 0.783 |
| | SVL (mm) | 208 | 221 | 243 | 255 | 267 | 0.880 | 0.913 | 0.849 | 0.796 |
| | TL (mm) | 68 | 69 | 77 | 82 | 86 | 0.934 | 0.930 | 0.839 | 0.764 |
| ♀ | W (g) | 6.0 | 6.7 | 9.2 | 11.4 | 13.9 | 0.983 | 0.976 | 0.964 | 0.959 |
| | L (mm) | 274 | 286 | 324 | 339 | 363 | 0.977 | 0.926 | 0.877 | 0.797 |
| | SVL (mm) | 221 | 221 | 254 | 276 | 297 | 0.970 | 0.913 | 0.829 | 0.760 |
| | TL (mm) | 63 | 65 | 72 | 75 | 79 | 0.939 | 0.896 | 0.855 | 0.789 |

even smaller time units should produce even greater correspondence between the model and the data. Use of the linear model for periods of up to one year, however, is reasonable.

In contrast to the linear model, the Bertalanffy and the logistic models describe asymptotic curves and therefore are more likely to show a high correspondence to the data. Growth as a function of time and as a function of food weight produce quite different scatter plots and fitting the models to the two types of data produced different results. Figure 5 shows the Bertalanffy, logistic-by-length, and logistic-by-mass models fitted to the data for W as a function of food weight for male *N. fasciata*. Figure 6 shows the three models fitted to the same data as a function of time. Figures 7 and 8 show the models fitted to the data for SVL. It is obvious that the scatter about the regression lines in the plots of size on time is much greater than that about the regression lines in the plots of size on food weight. This result is due to the fact that growth as a function of time does not compensate for the different amounts of food consumed by individuals. Plotting growth as a function of food weight compensates for the differences in food consumption rates, but the information concerning the time frame is lost.

Whether the data is plotted as a function of time or as a function of food weight, the total amount of variation among the data points is the same since it involves the same size data. The difference in the two plots is in how much of the total variation can be explained by the use of any particular model. The unexplained variation (SSE) can then be used as a measure of the lack of

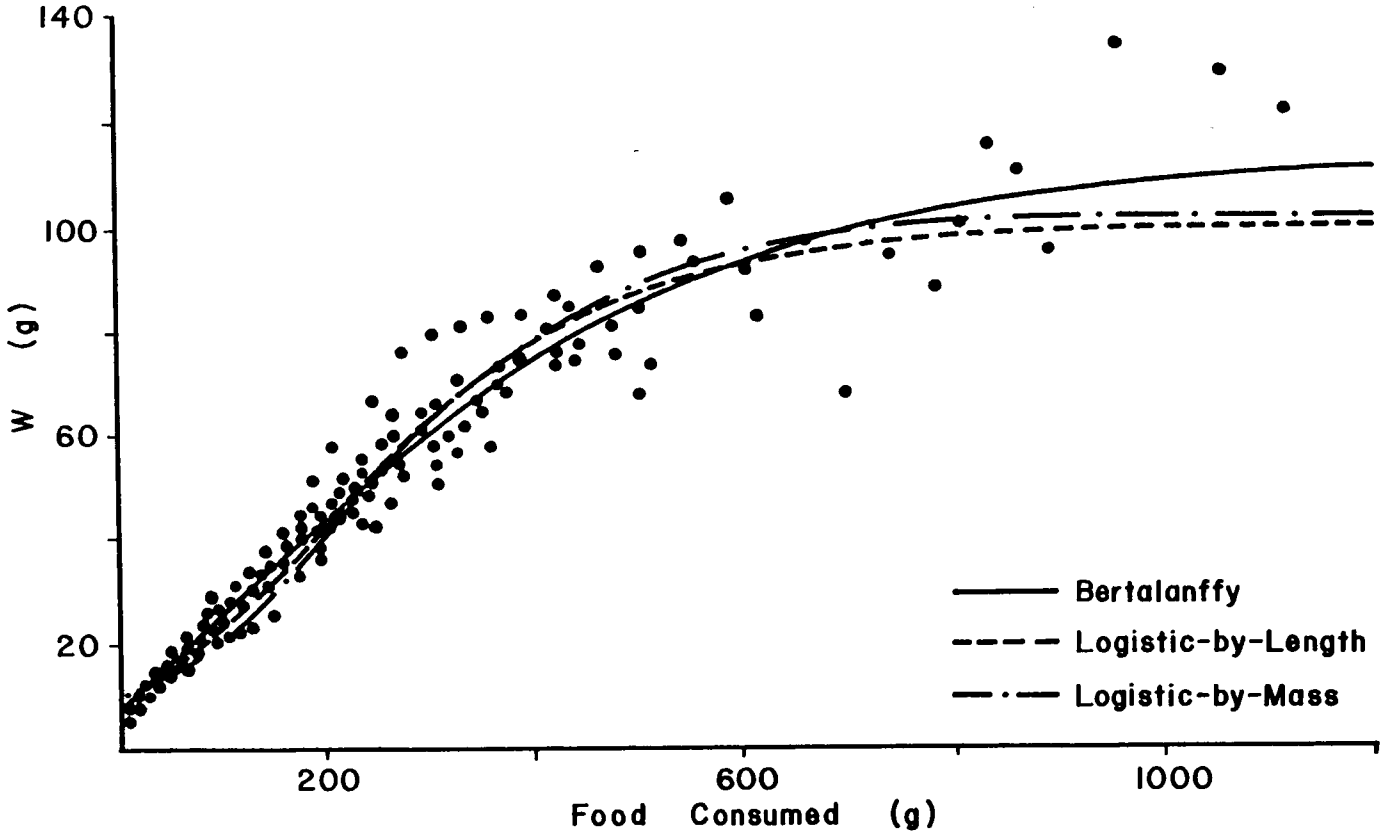



Figure 5. Growth Models Fitted to the Data for Weight (W) as a Function of Food Consumed for male *Nerodia fasciata* from Shelby County, Tennessee.

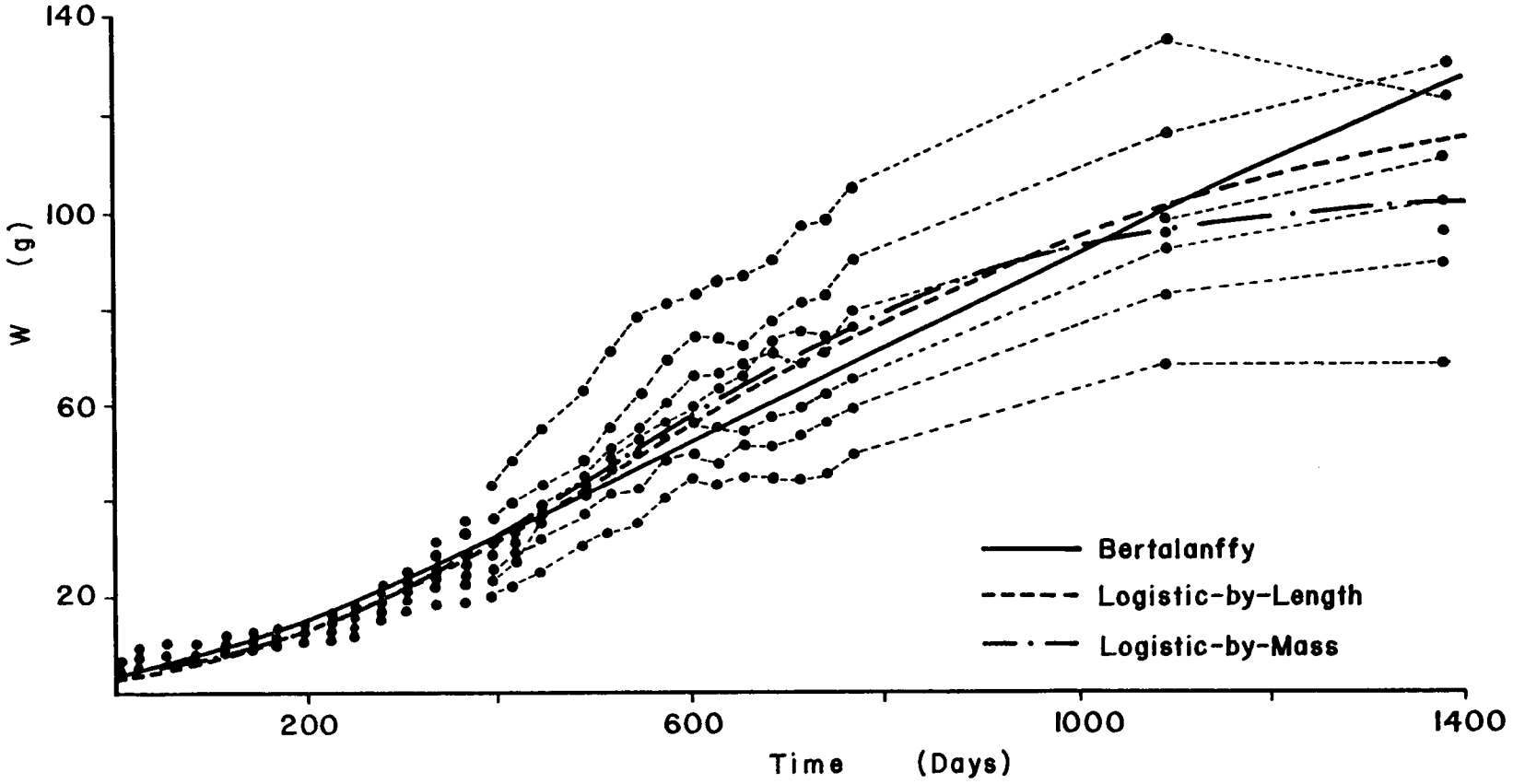



Figure 6. Growth Models Fitted to the Data for Weight (W) as a Function of Time for Male *Nerodia fasciata* from Shelby County, Tennessee.

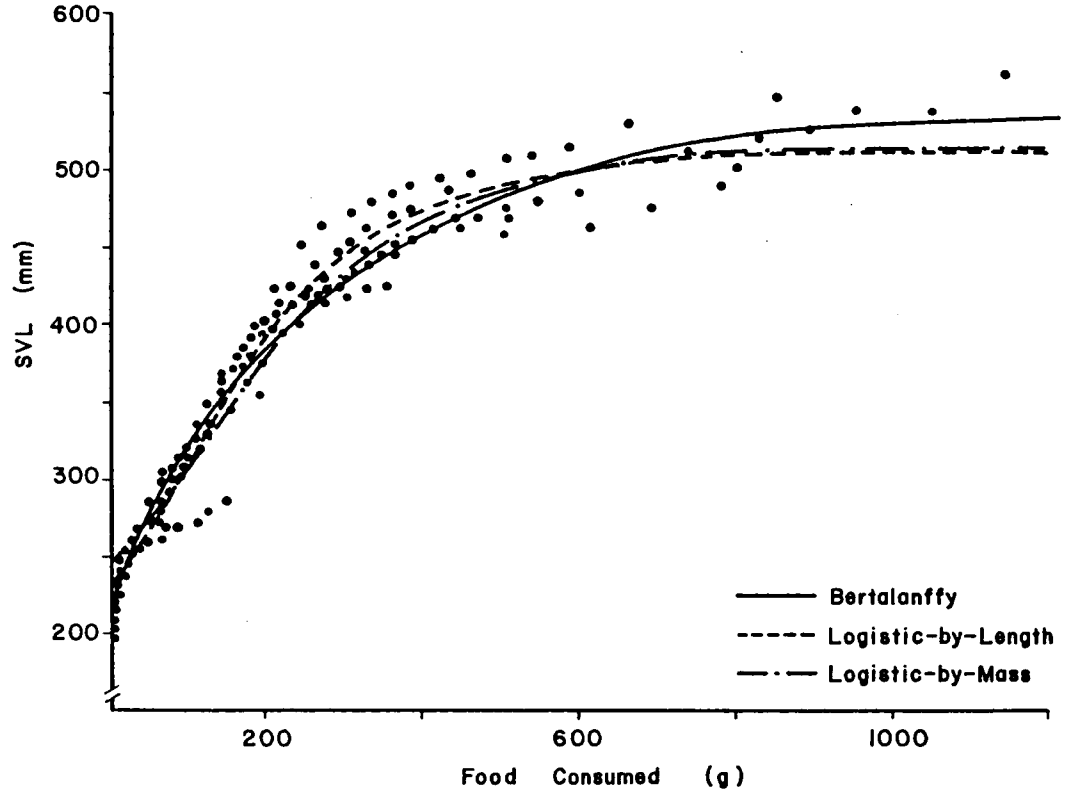



Figure 7. Growth Models Fitted to the Data for Snout-Vent Length (SVL) as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee.

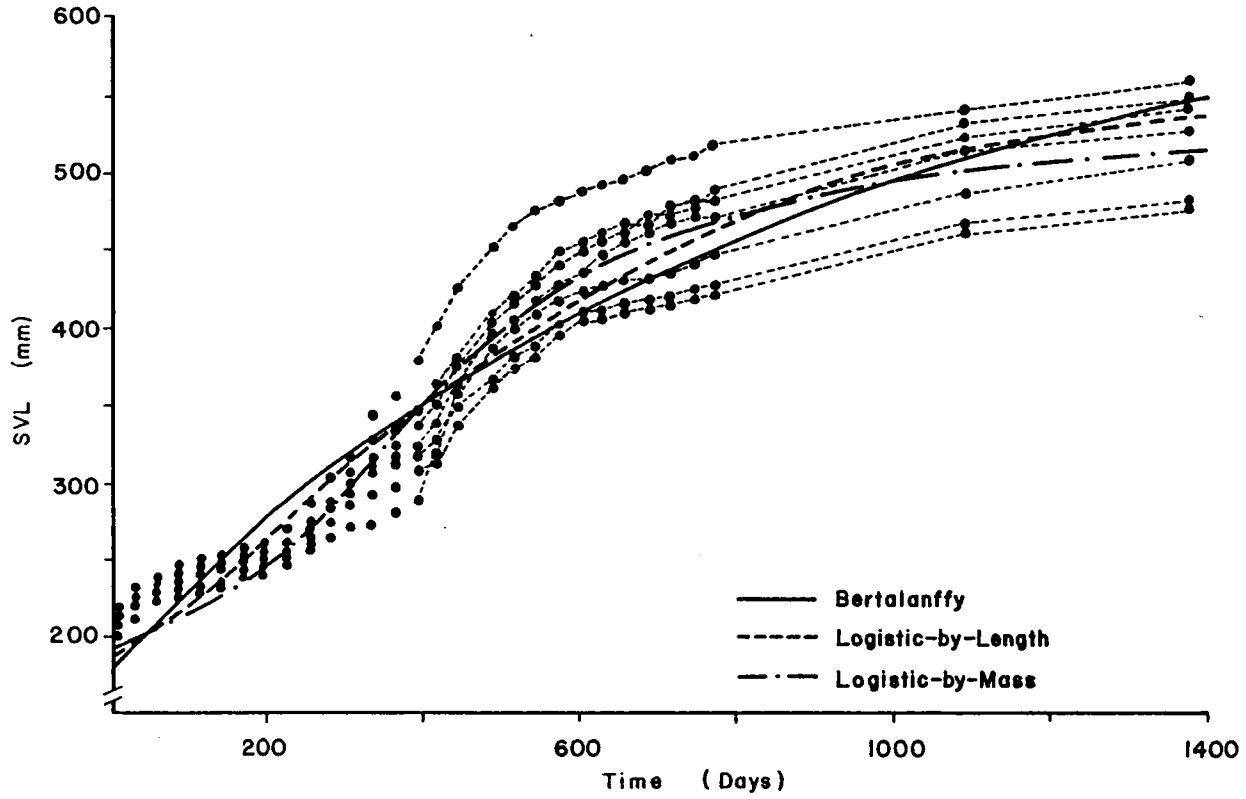



Figure 8. Growth Models Fitted to the Data for Snout-Vent Length (SVL) as a Function of Time for Male *Nerodia fasciata* from Shelby County, Tennessee.

correspondence between a model and the data. Generally the SSE for each of the three models is smaller when size is evaluated as a function of food weight than when it is evaluated as a function of time (see Table 4). Because of the greater correspondence between the data and the models, size as a function of food weight makes for a better test of the three growth models.

The diagrams of the three growth models fitted to the data in Figures 5 and 7 give very little indication of which model provides a better fit of the data. To distinguish among the models, it is necessary to examine the $r^2$ values and the SSE for each model (see Table 4). In nearly every case, the Bertalanffy model had a smaller SSE than the other models. Also a comparison of the estimates of size at birth generated by the models and the mean size at birth for any of the growth parameters (see Table 4) shows that the Bertalanffy model generally made the best estimate. Growth in these snakes therefore can be said to correspond to the Bertalanffy growth model.

*Manipulation of the parameters of the Bertalanffy growth model.* The two most important parameters of the Bertalanffy growth model in terms of describing growth are the asymptote and the growth constant r. In order to show the effect that these two parameters have on the shape of the growth curve, their values were manipulated using equations 8 and 9 (see page 15) with some simulated food consumption data. The results of these manipulations are shown in Figures 9 and 10. In Figure 9, the asymptote for SVL of curves A and B was set at 800 mm. The growth constant for curve A was set at

Table 4

Comparisons of Growth Models on Data for *Nerodia fasciata* from Shelby County, Tennessee

| Sex | Parameter | Model* | Method | $r^2$ | Error Sum of Squares (SSE) | Estimate of Asymptote | Estimate of Value at Birth | Mean Value at Birth |
|---|---|---|---|---|---|---|---|---|
| ♂ | W (g) | Bert. | Time | 0.940 | 29864.44 | 210.5 | 4.4 | 5.8 |
| | | | Food | 0.985 | 7313.15 | 112.6 | 7.4 | |
| | | L-L | Time | 0.950 | 25032.93 | 125.2 | 4.9 | |
| | | | Food | 0.981 | 9499.76 | 98.5 | 8.2 | |
| | | L-M | Time | 0.953 | 23466.89 | 103.1 | 5.9 | |
| | | | Food | 0.980 | 9826.28 | 102.2 | 11.9 | |
| | L (mm) | Bert. | Time | 0.993 | 290124.73 | 837 | 235 | 276 |
| | | | Food | 0.999 | 45154.49 | 698 | 282 | |
| | | L-L | Time | 0.994 | 231270.78 | 718 | 245 | |
| | | | Food | 0.999 | 49984.68 | 670 | 293 | |
| | | L-M | Time | 0.995 | 204872.81 | 682 | 257 | |
| | | | Food | 0.997 | 138766.31 | 679 | 331 | |
| | SVL (mm) | Bert. | Time | 0.993 | 192874.50 | 652 | 180 | 208 |
| | | | Food | 0.998 | 52013.64 | 534 | 215 | |
| | | L-L | Time | 0.994 | 153607.12 | 551 | 187 | |
| | | | Food | 0.998 | 54738.09 | 511 | 223 | |

Table 4 (Continued)

| Sex | Parameter | Model* | Method | $r^2$ | Error Sum of Squares (SSE) | Estimate of Asymptote | Eatimate of Value at Birth | Mean Value at Birth |
|---|---|---|---|---|---|---|---|---|
| | | L-M | Time | 0.995 | 136388.97 | 516 | 195 | |
| | | | Food | 0.996 | 102279.96 | 511 | 249 | |
| | TL (mm) | Bert. | Time | 0.992 | 19991.16 | 199 | 56 | 68 |
| | | | Food | 0.999 | 3602.90 | 168 | 67 | |
| | | L-L | Time | 0.993 | 15769.08 | 172 | 58 | |
| | | | Food | 0.999 | 3398.06 | 162 | 70 | |
| | | L-M | Time | 0.994 | 13783.13 | 165 | 62 | |
| | | | Food | 0.996 | 9280.89 | 164 | 80 | |
| ♀ | W (g) | Bert. | Time | 0.983 | 12254.58 | 203.5 | 3.5 | 6.0 |
| | | | Food | 0.970 | 21148.03 | 165.0 | 7.3 | |
| | | L-L | Time | 0.980 | 14442.58 | 201.1 | 4.5 | |
| | | | Food | 0.946 | 38438.81 | 140 | 8.6 | |
| | | L-M | Time | 0.981 | 13754.72 | 209.9 | 8.7 | |
| | | | Food | 0.973 | 19203.25 | 188.7 | 18.4 | |
| | L (mm) | Bert. | Time | 0.997 | 112621.27 | 1404 | 232 | 274 |
| | | | Food | 0.999 | 35317.86 | 819 | 287 | |

Table 4 (Continued)

| Sex | Parameter | Model* | Method | $r^2$ | Error Sum of Squares (SSE) | Estimate of Asymptote | Estimate of Value at Birth | Mean Value at Birth |
|---|---|---|---|---|---|---|---|---|
| | | L-L | Time | 0.988 | 73149.73 | 909 | 246 | |
| | | | Food | 0.998 | 74080.25 | 756 | 300 | |
| | | L-M | Time | 0.996 | 152217.52 | 865 | 299 | |
| | | | Food | 0.988 | 414642.97 | 819 | 377 | |
| | SVL (mm) | Bert. | Time | 0.996 | 95250.45 | 858 | 174 | 211 |
| | | | Food | 0.998 | 40778.64 | 626 | 223 | |
| | | L-L | Time | 0.998 | 62103.31 | 669 | 188 | |
| | | | Food | 0.997 | 70859.68 | 595 | 235 | |
| | | L-M | Time | 0.995 | 117294.59 | 674 | 234 | |
| | | | Food | 0.989 | 288328.18 | 640 | 294 | |
| | TL (mm) | Bert. | Time | 0.994 | 9030.69 | 322 | 54 | 63 |
| | | | Food | 0.996 | 6289.90 | 178 | 65 | |
| | | L-L | Time | 0.995 | 7769.74 | 201 | 57 | |
| | | | Food | 0.995 | 8111.17 | 165 | 68 | |
| | | L-M | Time | 0.994 | 9153.16 | 186 | 64 | |
| | | | Food | 0.988 | 18497.03 | 176 | 81 | |

*Bert. = Bertalanffy Growth Model; L-L = Logistic-by-Length growth Model; L-M = Logistic-by-Mass Growth Model.

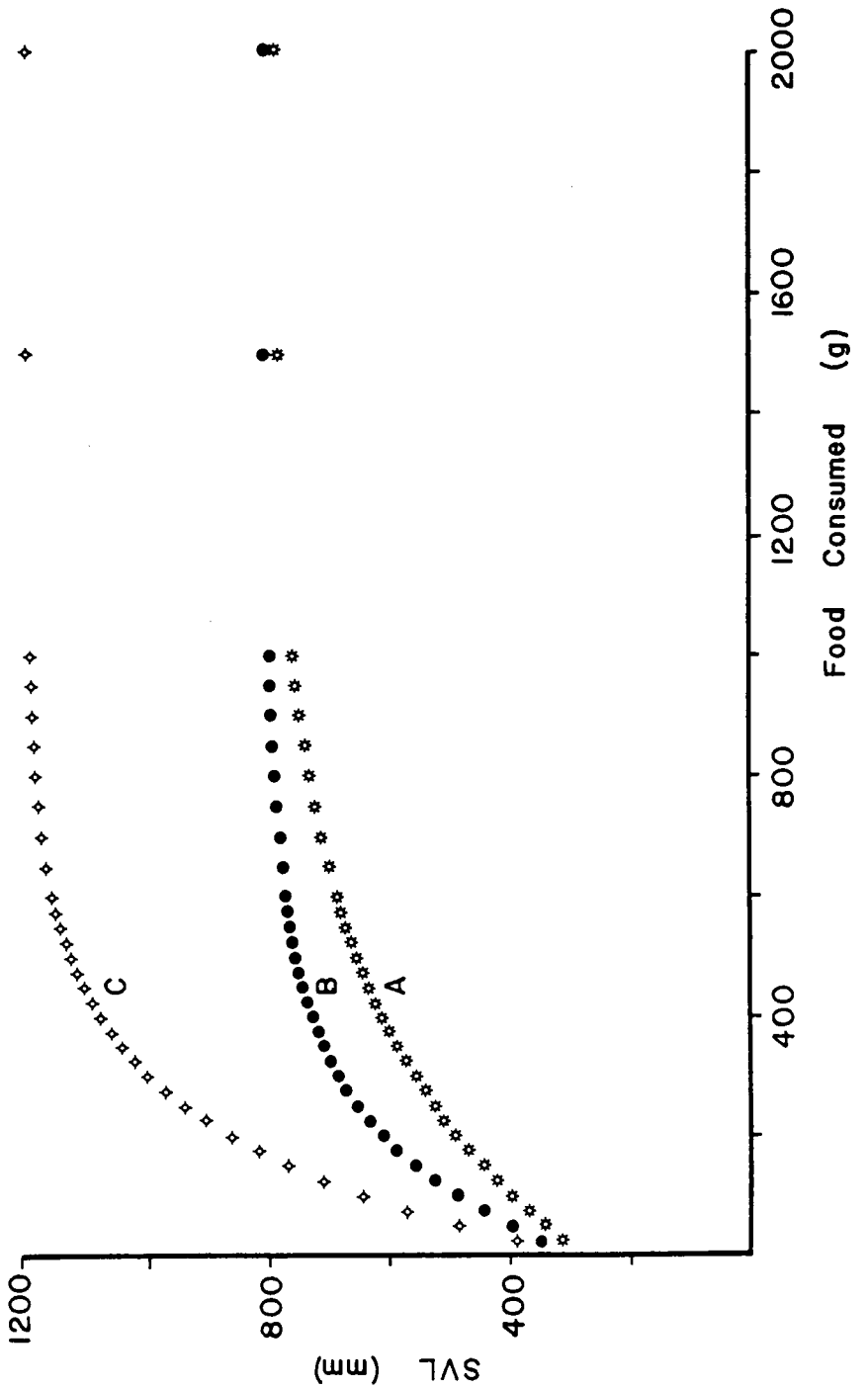



Figure 9. Simulated Growth Curves for Snout-Vent Length (SVL) Using the Bertalanffy Growth Model.

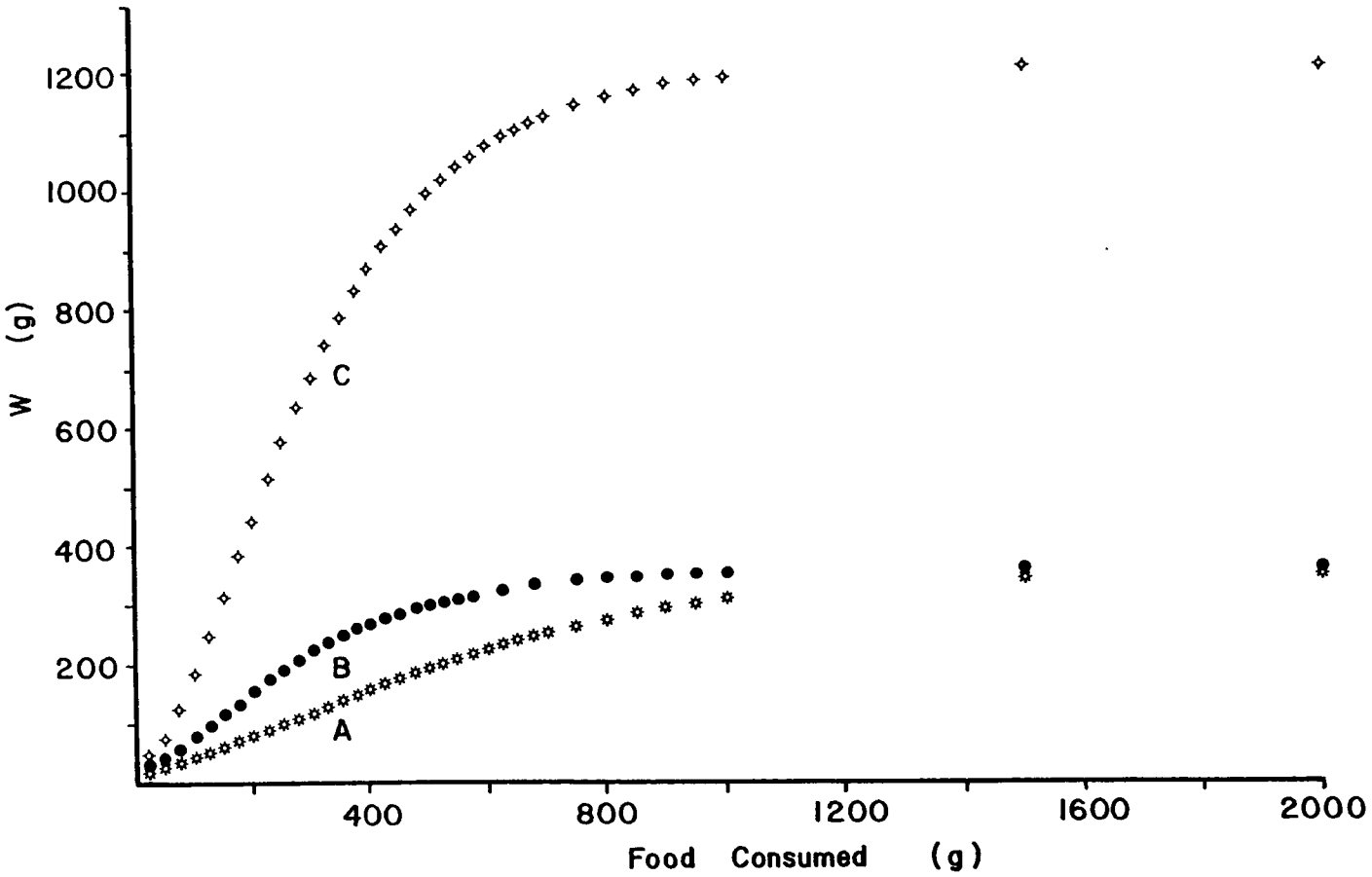



Figure 10. Simulated Growth Curves for Weight (W) Using the Bertalanffy Growth Model.

0.0025 and that for curve B was set at 0.005. The result of this manipulation is that both curves approach 800 mm as a maximum, but curve B approaches it at a much more rapid rate and shows a more rapid decline in the growth rate as it nears the maximum. In fact, since the growth constant of curve A is only half that of curve B, it takes twice as much food to reach 90% of the asymptote (720 mm) in curve A as it does to reach the same point in curve B.

The asymptote for curve C was set at 1200 mm and the growth constant was set at 0.005. Because the growth constant of curves B and C are identical, the two curves approach their respective asymptotes at the same relative rate and show the same rapid decline as they near their asymptotes. Since the asymptote of curve C is greater than that of curve B, curve C increases at an absolute faster rate. At 375 g of food, curve C has increased to 1059 mm, from an original SVL of 280 mm. Curve B has only increased to 720 mm from the same original SVL.

Curves A, B, and C in Figure 10 are the corresponding W curves for the SVL curves A, B, and C respectively in Figure 9. In addition to the parameter values set for the SVL curves, the value of the constant c in equation 9 (see page 15) was set at $7 \times 10^{-7}$ for all of the curves. As in Figure 9, curves A and B in Figure 10 approach the same asymptote, but curve B approaches it at a much more rapid rate. Also as in Figure 9, curves B and C approach their respective asymptotes at the same relative rate, but the difference in the asymptotes for W is much greater than the difference for SVL. This result is due to the fact that snakes become progressively heavier per unit

length as they increase in length. Because of the greater difference in their asymptotes, the difference in the absolute rate of increase in curves B and C is greater for W than it was for SVL. At 375 g of food, curve C had increased to 831 g from an original weight of 15 g. Curve B had only increased to 262 g from the same original weight.

*Discussion*

While it is appropriate under the conditions of this experiment to evaluate growth as a function of the total weight of food consumed, it is traditionally evaluated as a function of time. This difference is due to the fact that growth curves are normally constructed from field data instead of from laboratory data. Several points are of importance in comparing field studies with this study. First of all in the field, a reliable growth curve can be constructed for a population in as little as two growing seasons since animals of different ages can be tracked at one time. This situation circumvents the need to follow one particular individual until it reaches its full adult size. Second, the growth curve constructed from field data can be used as an estimate of the growth rate of individuals in that population. The growth curve in this study cannot be used in this way for two reasons: Repeated measures on the same animals violate the assumption of independence of observations required of regression analysis, and the animals in this study were raised in the lab under conditions that can hardly be considered natural. The effects that these conditions had on the growth of the snakes cannot be known with very much accuracy. As a consequence of

the two conditions stated above, the actual values generated for the growth curves in this study can only be applied to the animals in this study.

Since it seems that growth curves constructed from data from captive animals cannot be applied with any certainty to free-living animals, why bother collecting the data? There are two advantages to conducting growth studies in the lab: The amount of food consumed by any individual can be accurately measured in the lab, and individuals can be compared with one another with reasonable control of the variables that can confound individual differences in the field. Differences in the feeding rate are largely responsible for the variation in growth rates among snakes (Wharton 1966, Smith 1976, Barnard et al. 1979). Observing growth under laboratory conditions is the only way to control this major source of variation in growth rates. Measuring growth as a function of time is the most accurate means available for field studies. Laboratory studies can use the weight of food consumed which is a more proximate factor controlling growth.

Since the pattern of growth of the snakes in this study is most closely described by the Bertalanffy growth model, something should be said about what this actually means. The implications of growth by the Bertalanffy growth model is that growth in length will be greatest for the youngest animals and gradually decrease with age (see Figure 1A, page 13). In terms of food consumption, the P-I ratio for length should be greatest at birth and gradually decrease. In contrast the logistic-by-length model predicts that the rate of growth in length will increase until the animal reaches 50% of

asymptotic length and then the rate will begin to decrease (see Figure 2A, page 15). The logistic-by-mass model has the growth rate increasing until 63% of asymptotic length is reached. Growth in weight follows the same general pattern in the three models as growth in length. The rate of growth in weight increases in the Bertalanffy model until 30% of asymptotic weight is reached and the rate increases in the logistic-by-length and logistic-by-mass models until 42% and 50% of asymptotic weight respectively are reached.

For an animal that must reach a certain size in a short period of time, it would certainly be advantageous to grow according to the logistic-by-mass model. Long-lived animals are probably not under any pressure for very rapid growth and are more likely to have growth patterns that correspond to the Bertalanffy model. In fact, a reasonably long life expectancy is probably a prerequisite for growth by the Bertalanffy model. Of course, there can be many intermediate cases whose growth are more closely described by the logistic-by-length model. There is also no reason why growth cannot fall between the predictions of the models since animals are not restricted by the constraints of a mathematical model (Kaufmann 1981). This fact can explain why the growth in TL in males is more closely fit by the logistic-by-length model when W, L, and SVL are more closely fit by the Bertalanffy model (see Table 4, page 42).

The observations on the changes in the Bertalanffy growth model brought about by changes in the asymptote and growth constant have important implications for comparisons of different groups. These groups can be different species, populations, or sexes. Since

the values of the growth constant r are directly comparable among groups regardless of the size of the animals (Ricklefs 1968, Andrews 1976), it is important to know what the differences between the groups means in terms of growth. Generally the large the value of r, the more rapidly the animal will approach its asymptote. By comparing r values as well as the P-I ratios, the differences in relative as well as the absolute rates of growth between groups can be determined. These rates are examined in Chapter 4.

# CHAPTER 4

## GROWTH PATTERNS IN *NERODIA*

*Introduction*

Data from three separate experiments were used in the analysis of growth in *N. fasciata*, *N. cyclopion*, and *N. rhombifera*. Experiment 1 was discussed in relation to growth models in Chapter 3 and is discussed here in relation to sexual variation in growth.

Experiment 2 was designed primarily to examine the effect that the feeding regimen has on the growth rate. In addition, data from this experiment allow the examination of sexual, species, and individual variation in growth rate. The species comparisons are of particular interest since the snakes in this experiment are all offspring of females that were collected within 100 m of each other. An examination of the response of these potentially competing individuals to similar conditions in the lab can therefore, at least potentially, give some insight into how these species interact in the wild. Data are also available for an examination of the relationship between assimilation efficiency and growth rate.

Experiment 3 was designed to examine growth under circumstances in which the snakes had the opportunity to set their own feeding level. In addition, since these snakes are from the same litter of *N. fasciata* used in experiment 2, the data from this experiment represent another feeding regimen that can be compared with the two

included in that experiment. Sexual and individual variation in growth rate can also be examined.

*Materials and Methods*

*Experiment 1.* The subjects and procedures for experiment 1 were discussed earlier (see Chapter 3). In Chapter 3, the data from these snakes were discussed in relation to several growth models. In this chapter, only the information pertinent to sexual variation in growth will be discussed.

*Experiment 2.* Subjects for this experiment consisted of eight green water snakes, *Nerodia c. cyclopion*, 15 diamondback water snakes, *N. r. rhombifera*, and 12 broad-banded water snakes, *N. fasciata confluens*. Gravid female snakes were collected June 28 and 29, 1980 at Reelfoot Lake, Lake County, Tennessee. These snakes were kept in the laboratory at temperatures ranging from 19°C to 26°C during the gestation period. The *N. c. cyclopion* were born October 4, 1980, the *N. fasciata confluens* were born October 3, 1980, and the *N. r. rhombifera* were born October 15, 1980.

Snakes from all three species were allocated to one of two feeding groups taking care that both sexes were equally represented in each group. One group was fed once per week while the other group was fed an equal amount but in two feeding sessions per week. For purposes of discussion, the once-per-week group is referred to as the intermediate meal size group and the twice-per-week group is

referred to as the small meal size group. Both groups were maintained on an exclusive diet of fathead minnows.

The snakes were weighed on the fourth day after feeding in both groups. The second feeding session of the week for the small meal size group immediately followed weighing. Measurements of L and SVL were made once every four weeks. Feces were collected during the first, eighth, and twelfth months after birth.

*Experiment 3.* Subjects for this experiment consisted of six (three male and three female) broad-banded water snakes, *N. fasciata confluens*, which were captive-born to a wild-caught female from Reelfoot Lake, Lake County, Tennessee. These six animals were part of the litter of *N. fasciata confluens* used in experiment 2. These snakes were separated from their littermates at birth to be used in a "free access" study designed to determine the natural feeding patterns of this species.

The snakes were housed individually in 31 x 15 x 15 cm wooden boxes to which a 32 x 31 x 31 cm plexiglass aquarium was attached. The bottom of the aquarium was lined with gravel and a pool of water 2.5 cm deep was created. This apparatus was designed to simulate natural conditions and allow the snakes the opportunity to "hunt" for their prey.

A set number of fathead minnows were weighed as a group and introduced into the pool and left for 24 hours. The snakes were originally given five fish each, but this number was increased as the

snakes increased in size. The fish remaining the next day were weighed as a group and the difference between this weight and the weight of the fish first introduced was taken as the weight of fish consumed. This procedure was repeated every other day. In relation to growth and feeding regimen, this group is referred to as the large meal size group.

The snakes were weighed once every four weeks so that the feeding regimen would be disrupted as little as possible. Measurements of L and SVL were made every four weeks. No feces collections were made.

*Data Analysis*

Growth data for W, L, SVL, and TL as a function of total weight of food consumed were analyzed using the Bertalanffy growth model for time periods greater than one year, and the linear model for time periods of one year or less duration. Comparisons of slopes (P-I ratios) of the linear regressions by the t-test for parallelism provided the means of analyzing feeding regimen, sexual, species, and individual variation in growth rates by the linear model. Comparisons of the predicted asymptotes and the growth constants (r) along with their 95% confidence intervals provided the means of analyzing variation in growth by the Bertalanffy model.

Comparisons were made of the increase in weight per unit length (W/SVL) as a function of $SVL^2$ by the linear model. The slopes of these regression lines were compared between groups and between individuals by the t-test for parallelism. Both caloric and

assimilation efficiencies by weight (see page 28 for calculation formulas) were determined to examine the relationship between assimilation efficiency and growth rate.

*Results*

*Feeding regimen and growth.* Comparisons of the P-I ratios of all of the growth parameters (W, L, SVL, and TL) appear by groups (species and sex) in Table 5. Variation in growth, however, is discussed separately for length and weight in order to present a clearer picture of how the change in feeding regimen affects each growth parameter. Since the data concerning the feeding regimen and growth were only collected for a maximum of one year, analysis was made using only the linear growth model.

*Analysis of length increases.* The P-I ratios for all of the length measures for male *N. fasciata* were significantly greater for the intermediate meal size group than for the large meal size group. Comparisons of the P-I ratios of the intermediate and small meal size groups as well as the large and small meal size groups revealed no significant differences (Figure 11). The differences between the P-I ratios for TL for the large and small meal size groups, however, approached significance (see Table 5).

The results for female *N. fasciata* differed from those of the males. The P-I ratios for all of the length measures for the females were significantly greater for the intermediate meal size group than for the large or for the small meal size groups. The

Table 5

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) by Meal Size for Two Species of *Nerodia* from Lake County, Tennessee

| Groups | Parameter | Meal Size | P-I Ratio | t | df | p |
|---|---|---|---|---|---|---|
| *N. fasciata* male | W | Large<br>Intermediate | 0.2190<br>0.2154 | 0.50 | 97 | 0.6205 |
| Large x Intermediate Meal Size (12 months) | L | Large<br>Intermediate | 1.2345<br>1.6158 | 3.58 | 97 | 0.0005 |
| | SVL | Large<br>Intermediate | 1.0055<br>1.2637 | 3.23 | 97 | 0.0017 |
| | TL | Large<br>Intermediate | 0.2291<br>0.3521 | 4.37 | 97 | 0.0001 |
| Large x Small Meal Size (10 months) | W | Large<br>Small | 0.2334<br>0.2109 | 2.65 | 62 | 0.0101 |
| | L | Large<br>Small | 1.6677<br>1.8478 | 1.61 | 62 | 0.1115 |
| | SVL | Large<br>Small | 1.3422<br>1.4653 | 1.42 | 62 | 0.1618 |
| | TL | Large<br>Small | 0.3254<br>0.3824 | 1.95 | 62 | 0.0554 |
| Intermediate x Small Meal Size (10 months) | W | Intermediate<br>Small | 0.2290<br>0.2109 | 1.74 | 73 | 0.0860 |
| | L | Intermediate<br>Small | 2.0520<br>1.8478 | 1.39 | 73 | 0.1678 |
| | SVL | Intermediate<br>Small | 1.6151<br>1.4653 | 1.41 | 73 | 0.1633 |
| | TL | Intermediate<br>Small | 0.4369<br>0.3824 | 1.24 | 73 | 0.2191 |

Table 5 (Continued)

| Groups | Parameter | Meal Size | P-I Ratio | t | df | p |
|---|---|---|---|---|---|---|
| *N. fasciata* female | W | Large<br>Intermediate | 0.2614<br>0.2393 | 3.16 | 83 | 0.0022 |
| Large x Intermediate Meal Size (12 months) | L | Large<br>Intermediate | 0.9747<br>1.8146 | 9.77 | 83 | 0.0001 |
| | SVL | Large<br>Intermediate | 0.8145<br>1.4605 | 9.25 | 83 | 0.0001 |
| | TL | Large<br>Intermediate | 0.1603<br>0.3541 | 7.77 | 83 | 0.0001 |
| Large x Small Meal Size (8 months) | W | Large<br>Small | 0.2690<br>0.1859 | 5.22 | 41 | 0.0001 |
| | L | Large<br>Small | 1.4808<br>2.0563 | 3.11 | 41 | 0.0034 |
| | SVL | Large<br>Small | 1.2183<br>1.7451 | 3.85 | 41 | 0.0004 |
| | TL | Large<br>Small | 0.2625<br>0.3112 | 0.87 | 41 | 0.3879 |
| Intermediate x Small Meal Size (8 months) | W | Intermediate<br>Small | 0.2536<br>0.1859 | 5.30 | 41 | 0.0001 |
| | L | Intermediate<br>Small | 2.6326<br>2.0563 | 3.07 | 41 | 0.0038 |
| | SVL | Intermediate<br>Small | 2.1502<br>1.7451 | 3.11 | 41 | 0.0034 |
| | TL | Intermediate<br>Small | 0.4824<br>0.3112 | 2.57 | 41 | 0.0139 |

Table 5 (Continued)

| Groups | Parameter | Meal Size | P-I Ratio | t | df | p |
|---|---|---|---|---|---|---|
| *N. rhombifera* male | W | Intermediate | 0.1817 | 3.83 | 74 | 0.0003 |
| | | Small | 0.1455 | | | |
| Intermediate x Small Meal Size (10 months) | L | Intermediate | 1.1871 | 1.77 | 74 | 0.0811 |
| | | Small | 1.0411 | | | |
| | SVL | Intermediate | 0.8294 | 1.82 | 74 | 0.0727 |
| | | Small | 0.7279 | | | |
| | TL | Intermediate | 0.3577 | 1.12 | 74 | 0.2649 |
| | | Small | 0.3133 | | | |
| *N. rhombifera* female | W | Intermediate | 0.2084 | 1.73 | 86 | 0.0870 |
| | | Small | 0.1861 | | | |
| Intermediate x Small Meal Size (10 months) | L | Intermediate | 1.3789 | 1.02 | 86 | 0.3086 |
| | | Small | 1.2443 | | | |
| | SVL | Intermediate | 1.0379 | 0.84 | 86 | 0.4007 |
| | | Small | 0.9555 | | | |
| | TL | Intermediate | 0.3411 | 1.40 | 86 | 0.1658 |
| | | Small | 0.2888 | | | |

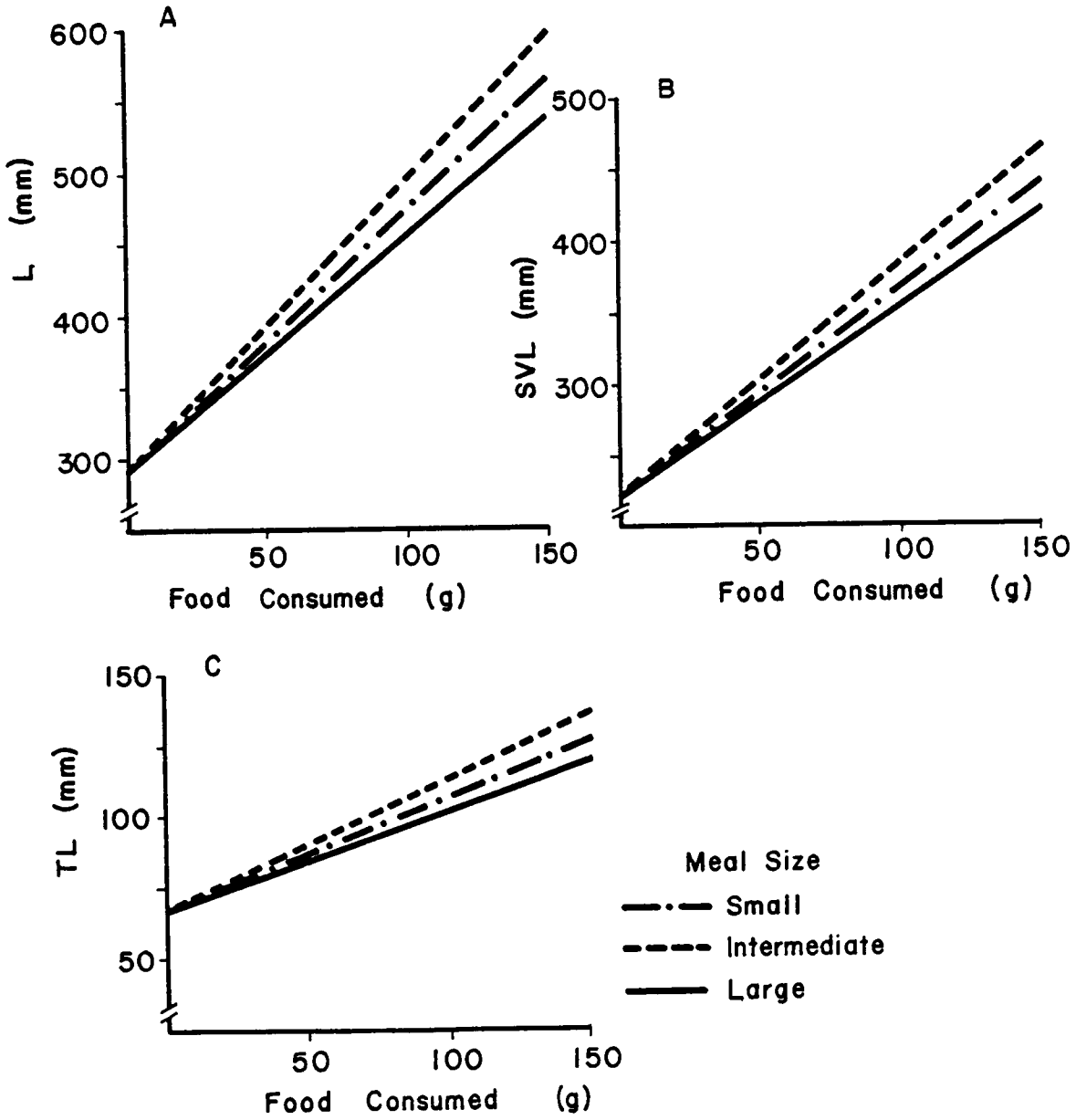



Figure 11. Effect of the Feeding Regimen on Growth in Length in Male *Nerodia fasciata* from Lake County, Tennessee. A. The Effect on Total Length (L). B. The Effect on Snout-Vent Length (SVL). C. The Effect on Tail Length (TL). Data Represent the First 10 Months of Growth.

P-I ratios were also significantly greater for the small meal size group than for the large meal size group for L and SVL, but not for TL (Figure 12).

Male and female *N. rhombifera* in the intermediate and small meal size groups did not have significantly different P-I ratios for any of the length measures (Figures 13 and 14). The differences in the P-I ratios for L and SVL in males, however, did approach significance (see Table 5).

It is apparent that the effect that the feeding regimen has on the rate of growth in length depends on the species as well as the sex of the animal. Female *N. fasciata* are apparently best at using food energy for growth in length when it is consumed in small sized meals than when it is comsumed in large ones. Male *N. fasciata* show the same trend although the magnitude of their response to changing meal size is not as great as in females. This fact is evident from the lack of significant differences between most of the meal size groups in males. The shift in the P-I ratio with changing meal size could be caused by either a shift in the proportion of the diet that is used for other purposes (e.g., more energy for maintenance or for growth in weight) or by a drop in the assimilation efficiency so that more of the energy consumed is excreted in the feces. Judging by the relative sizes of the shift in the ratios, it seems evident that male and female *N. fasciata* proportion the use of the food energy available to them in different ways.

The feeding regimen has little affect on the allocation of food energy for various purposes in *N. rhombifera*, at least within

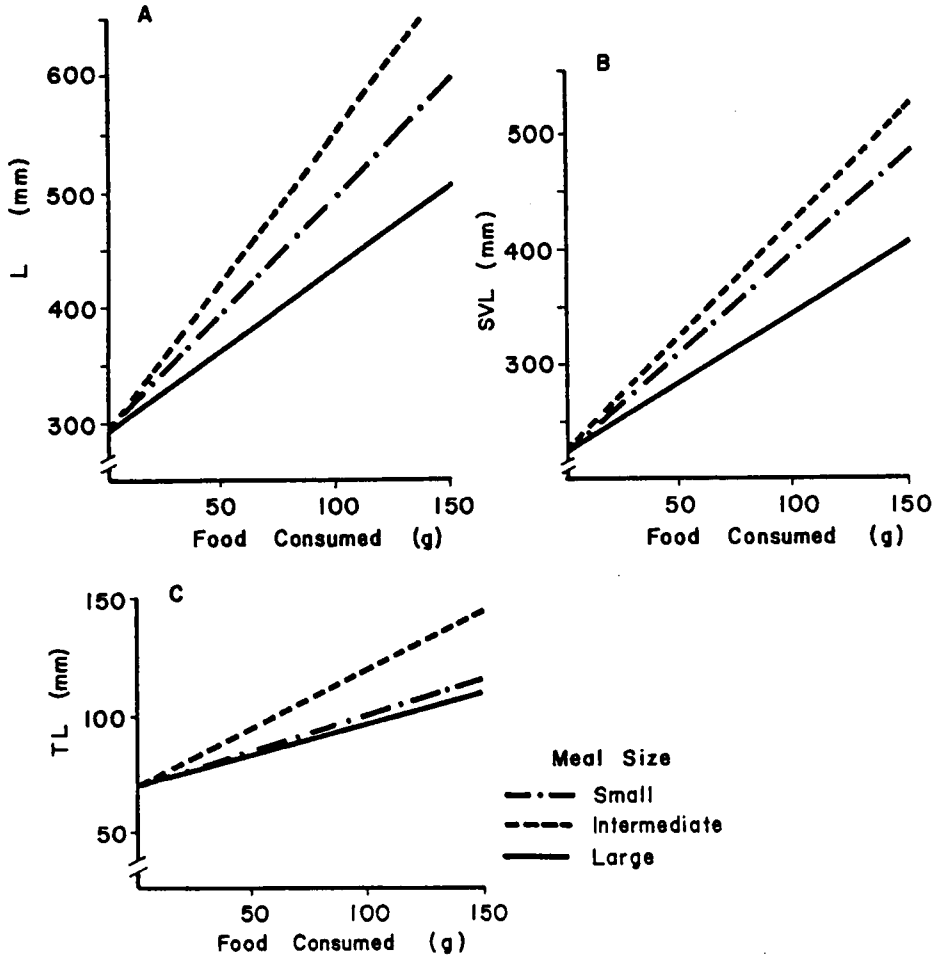



Figure 12. Effect of the Feeding Regimen on Growth in Length in Female *Nerodia fasciata* from Lake County, Tennessee. A. The Effect on Total Length (L). B. The Effect on Snout-Vent Length (SVL). C. The Effect on Tail Length (TL). Data Represent the First Eight Months of Growth.

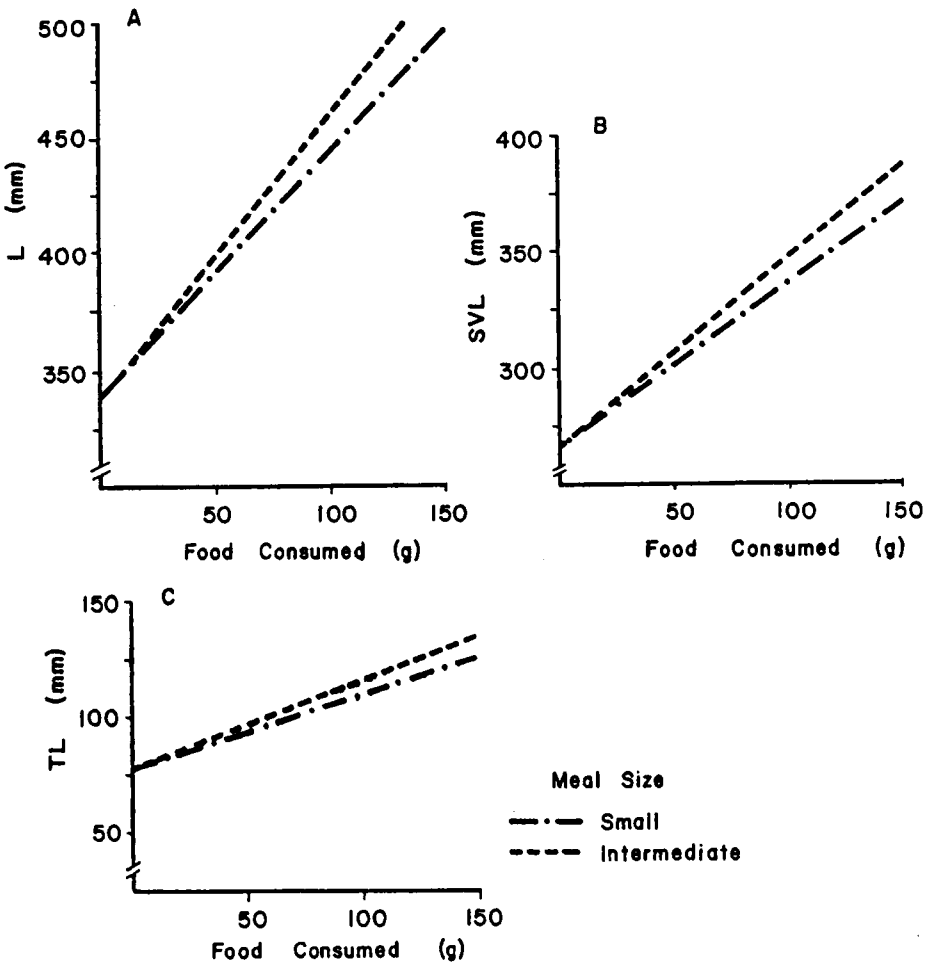



Figure 13. Effect of the Feeding Regimen on Growth in Length in Male *Nerodia rhombifera*. A. The Effect on Total Length (L). B. The Effect on Snout-Vent Length (SVL). C. The Effect on Tail Length (TL). Data Represent the First 10 Months of Growth.

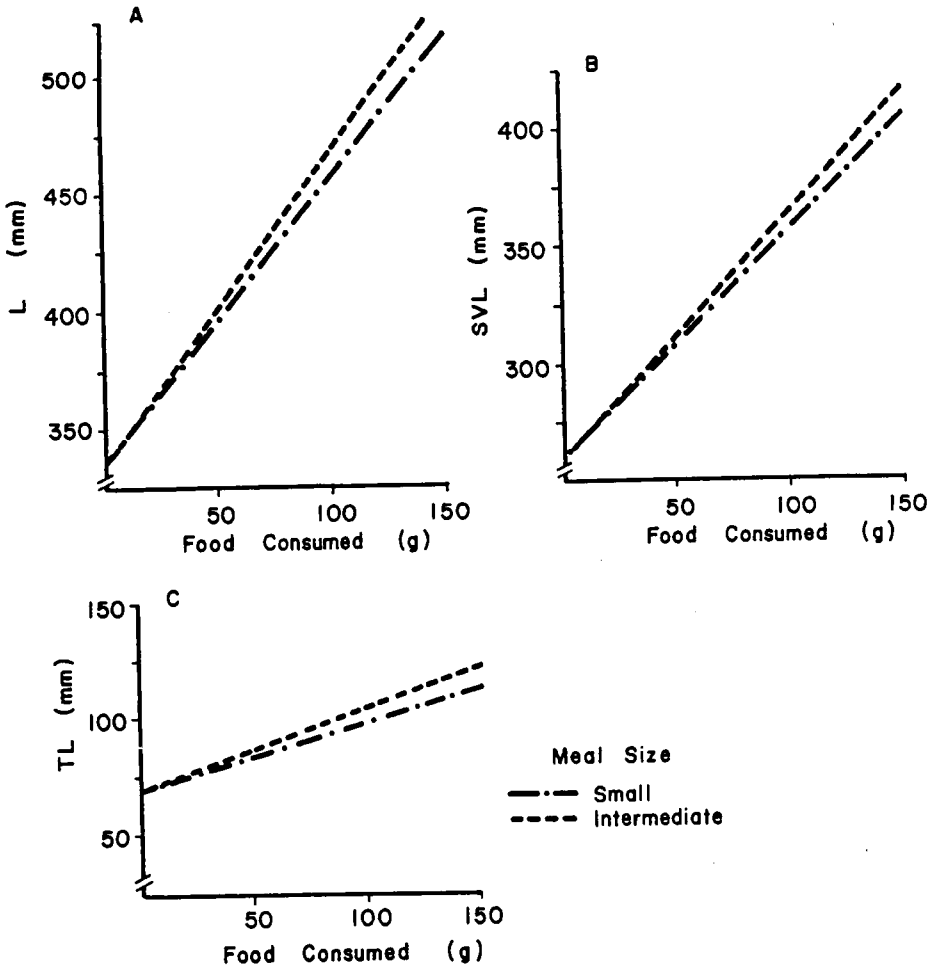



Figure 14. Effect of the Feeding Regimen on Growth in Length in Female *Nerodia rhombifera*. A. The Effect on Total Length (L). B. The Effect on Snout-Vent Length (SVL). C. The Effect on Tail Length (TL). Data Represent the First 10 Months of Growth.

the range of meal sizes presented here. It is of interest, however, that the same trend in P-I ratio changes evident in *N. fasciata* is indicated by the *N. rhombifera* data (see Figures 11 through 14). Further discussion of meal size and the allocation of energy for growth can be found in the following two sections.

*Analysis of weight increases.* The P-I ratios for increases in weight showed a different trend in relation to the feeding regimen than did the P-I ratios for increases in length. In both male and female *N. fasciata*, the highest P-I ratios were found in the large meal size group followed by the intermediate meal size group, then the small meal size group (Figure 15). In the females, there was a statistically significant difference among all of the meal size groups, while in the males a significant difference occurred only between the large and the small meal size groups (see Table 5, pages 57-59). In *N. rhombifera*, a significant difference occurred only between the P-I ratios of the males although the difference in the P-I ratios of the females approached significance (see Table 5). The trend in *N. rhombifera* is the same as that found in *N. fasciata*: the larger the meal size, the higher the P-I ratio (Figure 16).

As with increases in length, the effect of the feeding regimen on the P-I ratio for increases in weight differs for each species and each sex. The sexual differences are largely a matter of magnitude. The difference in the P-I ratios is greater in females than in males in *N. fasciata*, and greater in males than in females in *N. rhombifera* (see Figures 15 and 16). It is apparent that *N. fasciata* and

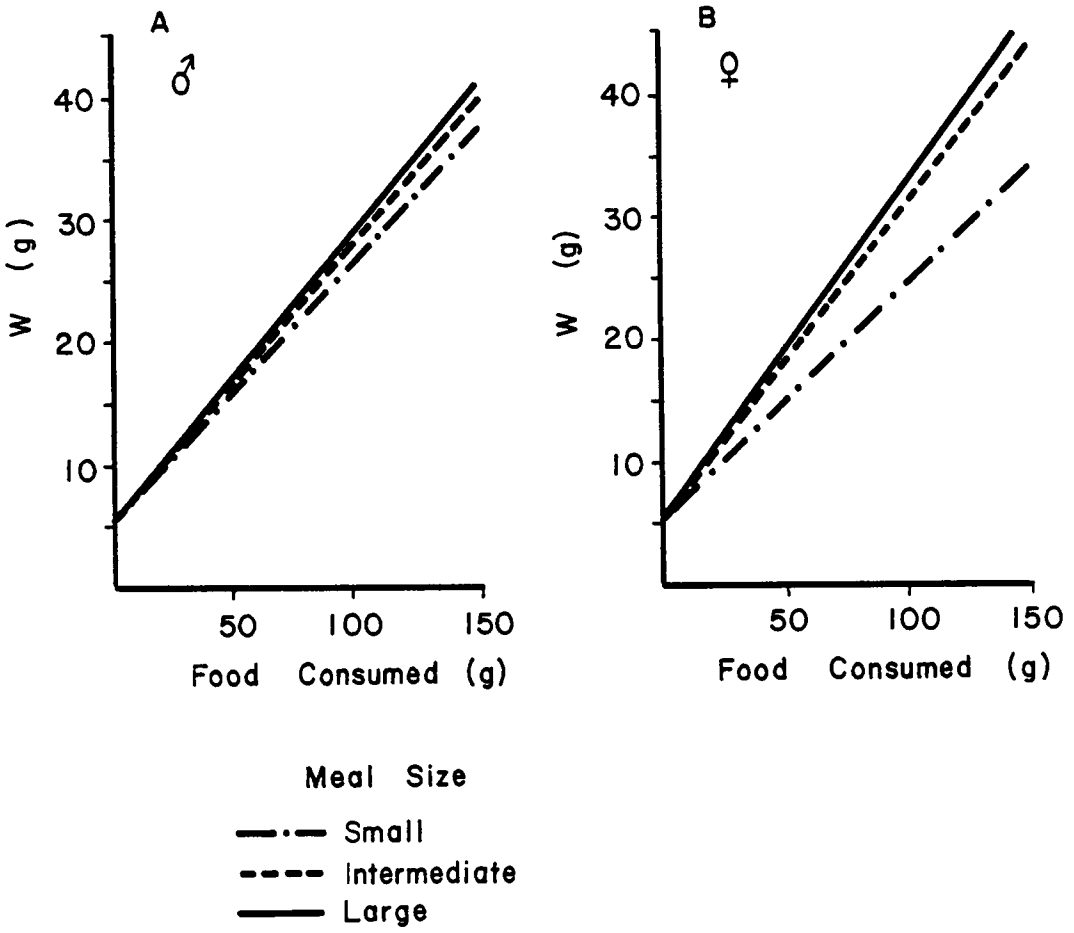



Figure 15. Effect of the Feeding Regimen on Growth in Weight (W) in *Nerodia fasciata* from Lake County, Tennessee. A. The Effect in Males. B. The Effect in Females. Data for Males Represent the First 10 Months of Growth. Data for Females Represent the First Eight Months of Growth.

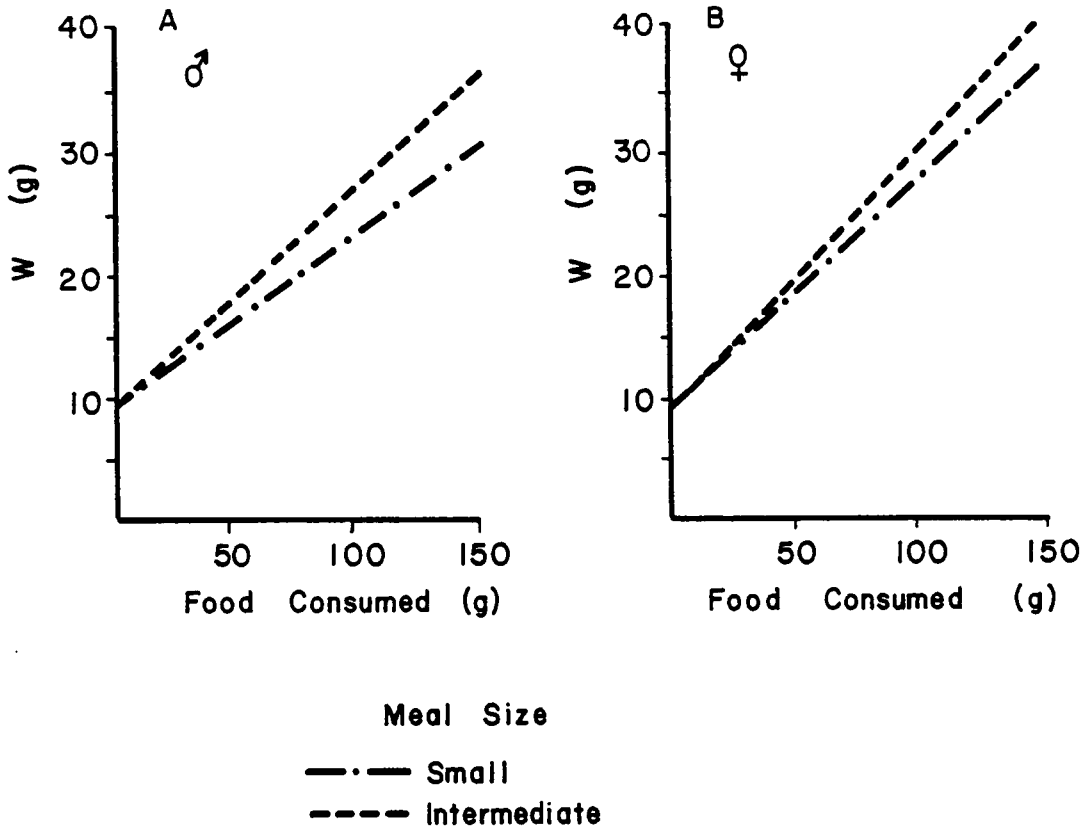



Figure 16. Effect of the Feeding Regimen on Growth in Weight (W) in *Nerodia rhombifera*. A. The Effect in Males. B. The Effect in Females. Data Represent the First 10 Months of Growth.

*N. rhombifera* do not respond in identical manners at least as far as which sex responds more vigorously to a change in meal size.

It is of interest that while the large meal size groups showed the lowest P-I ratios for increases in length, they showed the highest P-I ratios for increases in weight. This phenomenon lends support to the idea of a shift in the proportion of the diet allocated to various bodily functions with a shift in the meal size. A result of the different trends in increases in length and weight with changing meal size is a difference in the weight per unit length (W/SVL) among the meal size groups (see Table 6). In both male and female *N. fasciata*, the large meal size group increased in W/SVL at a significantly faster rate than did males and females respectively in the intermediate and small meal size groups. The intermediate and small meal size groups were not significantly different. The greater increase in W/SVL in the large meal size group resulted in the snakes of that group being heavier-bodied at any given SVL than snakes in the intermediate or small meal size groups (Figure 17). Comparisons of W/SVL for *N. rhombifera* showed a significant difference between meal size groups for the females, but not for the males (see Table 6). The significant change in the females was apparently due to the fact that a change in meal size affected primarily their P-I ratio for W and not for SVL, which resulted in a large change in W/SVL. Males, on the other hand, showed large changes for W and SVL in the same direction which resulted in very little change in W/SVL (see Table 5, pages 57-59). A summary of the results of the effect of feeding regimen on the pattern of growth can be found in Table 7.

Table 6

Comparisons of the Rate of Increase in Weight Per Unit Length (W/SVL) for *Nerodia fasciata* and *N. rhombifera* by Meal Size

| Species | Sex | Meal Size | Slope* ($\times 10^7$) | t | df | p |
|---|---|---|---|---|---|---|
| *N. fasciata* | ♂ | Large<br>Intermediate | 8.41<br>6.45 | 5.50 | 66 | 0.0001 |
| | | Large<br>Small | 8.41<br>6.76 | 3.19 | 46 | 0.0020 |
| | | Intermediate<br>Small | 6.45<br>6.76 | 0.91 | 59 | 0.3688 |
| | ♀ | Large<br>Intermediate | 9.27<br>5.66 | 8.25 | 51 | 0.0001 |
| | | Large<br>Small | 9.27<br>5.71 | 7.58 | 41 | 0.0001 |
| | | Intermediate<br>Small | 5.66<br>5.71 | 0.28 | 41 | 0.7812 |
| *N. rhombifera* | ♂ | Intermediate<br>Small | 8.70<br>9.05 | 0.74 | 73 | 0.4601 |
| | ♀ | Intermediate<br>Small | 7.10<br>6.15 | 2.08 | 84 | 0.0407 |

*The numbers presented here are the values of the slopes of the regression of W/SVL on $SVL^2$.

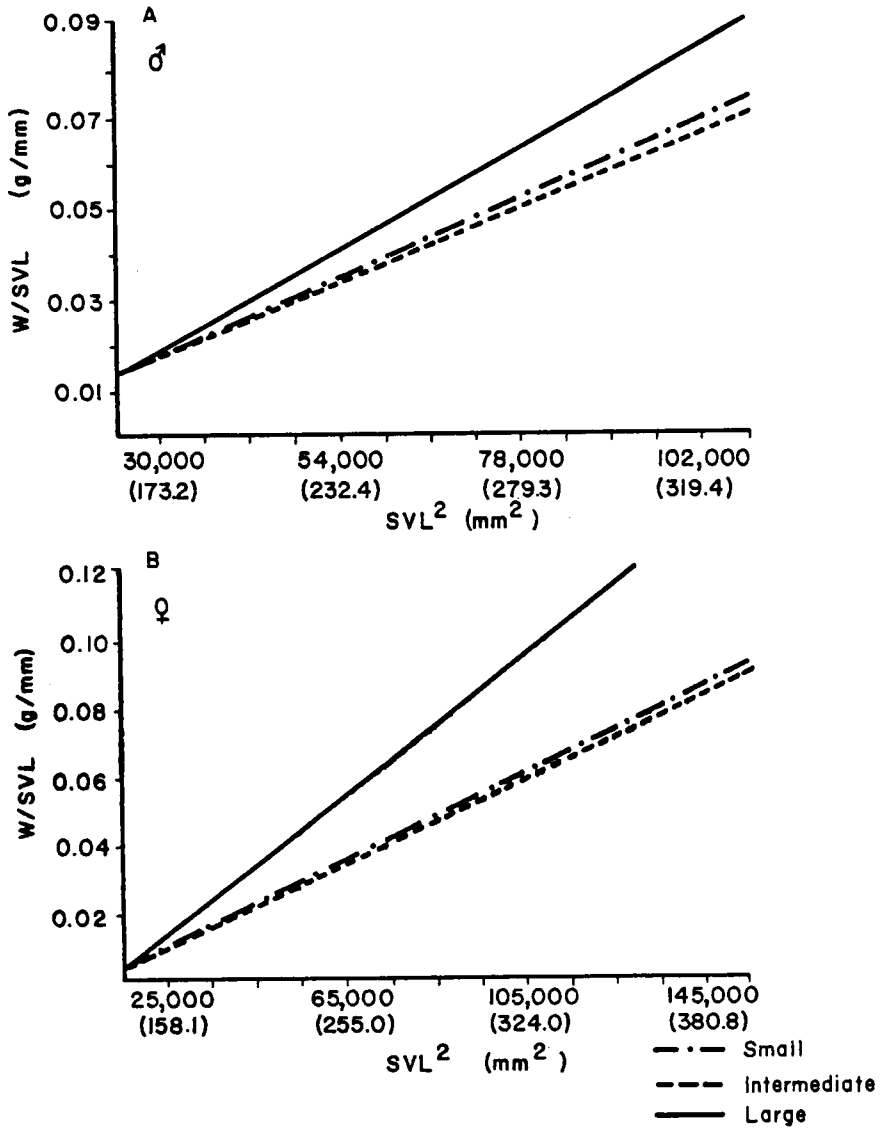



Figure 17. Effect of the Feeding Regimen on the Rate of Increase in Weight Per Unit Length (W/SVL) for *Nerodia fasciata* from Lake County, Tennessee. A. The Effect in Males. B. The Effect in Females. Data for Males Represent the First 10 Months of Growth. Data for Females Represent the First Eight Months of Growth. Numbers in parentheses are Snout-Vent Lengths (SVL).

Table 7

Summary of the Results of the Effect of the Feeding Regimen on the Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), Tail Length (TL), and Weight Per Unit Length (W/SVL) in Two Species of *Nerodia* from Lake County, Tennessee[1,2]

| Species | W | L | SVL | TL | W/SVL |
|---|---|---|---|---|---|
| *N. fasciata* (♂) | | | | | |
| Large Meal Size x Intermediate Meal Size | NS (L) | S*** (I) | S** (I) | S*** (I) | S*** (I) |
| Large Meal Size x Small Meal Size | S* (L) | NS (S) | NS (S) | NS (S) | S** (L) |
| Small Meal Size x Intermediate Meal Size | NS (I) | NS (I) | NS (I) | NS (I) | NS (SM) |
| *N. fasciata* (♀) | | | | | |
| Large Meal Size x Intermediate Meal Size | S** (L) | S*** (I) | S*** (I) | S*** (I) | S*** (L) |
| Large Meal Size x Small Meal Size | S*** (L) | S** (SM) | S*** (SM) | NS (SM) | S*** (L) |
| Small Meal Size x Intermediate Meal Size | S*** (I) | S** (I) | S** (I) | S* (I) | NS (SM) |
| *N. rhombivera* (♂) | | | | | |
| Small Meal Size x Intermediate Meal Size | S*** (I) | NS (I) | NS (I) | NS (I) | NS (I) |
| *N. rhombifera* (♀) | | | | | |
| Small Meal Size x Intermediate Meal Size | NS (I) | NS (I) | NS (I) | NS (I) | S* (I) |

Table 7 (Continued)

[1]S* = Significant difference, $p < 0.05$.
S** = Significant difference, $p < 0.005$.
S*** = Significant difference, $p < 0.0005$
[2]NS = No significant difference, $p > 0.05$.
[2]Symbols in parentheses represent the meal size with the higher P-I ratio for that growth parameter:

I = Intermediate meal size.
L = Large meal size.
SM = Small Meal Size

*Sexual Variation in Growth*

*Introduction.* Sexual variation not only applies to growth rates, but also to the rate of food consumption. Both parameters are discussed in the following sections. Comparisons of the P-I ratios of all of the growth parameters (W, L, SVL, and TL) appear by groups (species, population, and feeding regimen) in Table 8. Variation in growth, however, is discussed separately for length and weight in order to present a clearer picture of how sex affects each growth parameter. Discussion of the linear model analysis is followed by discussion of the Bertalanffy model analysis for both large length and weight. Due to insufficient data for the other groups, only data for *N. fasciata* from Shelby County, Tennessee and *N. fasciata*, *N. cyclopion*, and *N. rhombifera* fed the intermediate meal size were analyzed using the Bertalanffy growth model.

*Rate of food consumption.* For the most part, the snakes in the various experiments in this study were offered a set amount of food at each feeding. Under these conditions, a striking difference in the consumption rate of males and females would not be expected. In spite of this fact, some differences did emerge and these results, along with those of experiment 3, gave some indication of the sexual variation in food consumption rate that can be expected in natural populations.

Of the snakes that were offered a set amount of food at each feeding, only the *N. cyclopion* showed a sexual difference in the average weight of food consumed during the first year. During this

Table 8

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) by Sex for Three Species of *Nerodia*

| Groups | Parameter | Sex | P-I Ratio | t | df | p |
|---|---|---|---|---|---|---|
| *N. fasciata* | W | ♀ | 0.2143 | 5.46 | 192 | 0.0001 |
| | | ♂ | 0.1844 | | | |
| Shelby County, Tennessee male x female (12 months) | L | ♀ | 1.4657 | 3.47 | 178 | 0.0007 |
| | | ♂ | 1.3420 | | | |
| | SVL | ♀ | 1.1722 | 6.72 | 192 | 0.0001 |
| | | ♂ | 0.9035 | | | |
| | TL | ♀ | 0.2935 | 3.26 | 178 | 0.0013 |
| | | ♂ | 0.3339 | | | |
| Lake County, Tennessee Large Meal Size male x female (12 months) | W | ♀ | 0.2615 | 6.07 | 86 | 0.0001 |
| | | ♂ | 0.2190 | | | |
| | L | ♀ | 0.9747 | 3.16 | 86 | 0.0022 |
| | | ♂ | 1.2345 | | | |
| | SVL | ♀ | 0.8145 | 2.91 | 86 | 0.0046 |
| | | ♂ | 1.0055 | | | |
| | TL | ♀ | 0.1603 | 2.97 | 86 | 0.0039 |
| | | ♂ | 0.2291 | | | |
| Lake County, Tennessee Intermediate Meal Size male x female (12 months) | W | ♀ | 0.2393 | 3.45 | 94 | 0.0009 |
| | | ♂ | 0.2154 | | | |
| | L | ♀ | 1.8146 | 1.81 | 94 | 0.0734 |
| | | ♂ | 1.6158 | | | |
| | SVL | ♀ | 1.4605 | 2.35 | 94 | 0.0207 |
| | | ♂ | 1.2637 | | | |
| | TL | ♀ | 0.3541 | 0.07 | 94 | 0.9452 |
| | | ♂ | 0.3521 | | | |

Table 8 (Continued)

| Groups | Parameter | Sex | P-I Ratio | t | df | p |
|---|---|---|---|---|---|---|
| *N. fasciata* | W | ♀ | 0.1859 | 2.35 | 41 | 0.0234 |
| | | ♂ | 0.2187 | | | |
| Lake County, Tennessee Small Meal Size male x female (8 months) | L | ♀ | 2.0563 | 0.43 | 41 | 0.6674 |
| | | ♂ | 2.1369 | | | |
| | SVL | ♀ | 1.7451 | 0.35 | 41 | 0.7293 |
| | | ♂ | 1.6984 | | | |
| | TL | ♀ | 0.3112 | 2.25 | 41 | 0.0302 |
| | | ♂ | 0.4386 | | | |
| *N. cyclopion* | W | ♀ | 0.2253 | 8.33 | 108 | 0.0001 |
| | | ♂ | 0.1679 | | | |
| Intermediate Meal Size male x female (12 months) | L | ♀ | 1.4632 | 1.77 | 108 | 0.0789 |
| | | ♂ | 1.3343 | | | |
| | SVL | ♀ | 1.1617 | 2.82 | 108 | 0.0058 |
| | | ♂ | 1.0028 | | | |
| | TL | ♀ | 0.3015 | 1.44 | 108 | 0.1534 |
| | | ♂ | 0.3316 | | | |
| *N. rhombifera* | W | ♀ | 0.1925 | 2.19 | 108 | 0.0310 |
| | | ♂ | 0.1745 | | | |
| Intermediate Meal Size male x female (12 months) | L | ♀ | 1.1507 | 2.43 | 108 | 0.0167 |
| | | ♂ | 0.9758 | | | |
| | SVL | ♀ | 0.8666 | 3.67 | 108 | 0.0004 |
| | | ♂ | 0.6800 | | | |
| | TL | ♀ | 0.2841 | 0.42 | 108 | 0.6723 |
| | | ♂ | 0.2958 | | | |
| *N. rhombifera* | W | ♀ | 0.1861 | 3.01 | 76 | 0.0036 |
| | | ♂ | 0.1455 | | | |
| Small Meal Size male x female (10 months) | L | ♀ | 1.2443 | 1.49 | 76 | 0.1391 |
| | | ♂ | 1.0411 | | | |

Table 8 (Continued)

| Groups | Parameter | Sex | P-I Ratio | t | df | p |
|---|---|---|---|---|---|---|
| | SVL | ♀ | 0.9555 | 2.26 | 76 | 0.0266 |
| | | ♂ | 0.7279 | | | |
| | TL | ♀ | 0.2888 | 0.63 | 76 | 0.5274 |
| | | ♂ | 0.3133 | | | |

time, *N. cyclopion* females fed the intermediate meal size consumed an average of 154.8 g of fish while the males consumed only 109.8 g. This difference is significant ($t = 3.34$, $df = 6$, $p < 0.02$), but during the same period *N. fasciata* and *N. rhombifera* males and females from Lake County, Tennessee fed the intermediate meal size did not differ in their consumption rates. Male *N. fasciata* consumed an average of 156.3 g of fish while the females consumed an average of 153.2 g ($t = 0.71$, $df = 5$, $p > 0.50$), and male *N. rhombifera* consumed an average of 156.5 g of fish while the females consumed an average of 148.5 g ($t = 0.75$, $df = 6$, $p > 0.40$). When allowed to eat as much as they would take, male *N. fasciata* from Lake County, Tennessee consumed an average of 168.4 g of fish during the first year while the females consumed an average of 360.5 g. The difference between these numbers is significant ($t = 3.93$, $df = 4$, $p < 0.02$). Since these snakes were from the same litter of *N. fasciata* mentioned above, it would seem that providing the snakes with a set amount of food at each feeding upset the natural feeding patterns of the snakes.

Even under artificial feeding conditions, differences in the consumption rate of males and females may emerge in time. *Nerodia fasciata* from Shelby County, Tennessee showed no sexual differences in the amount of food consumed during the first two years ($t = 1.04$, $df = 12$, $p > 0.20$), but during the third year, females consumed an average of 409.1 g of fish while the males consumed an average of 258.2 g. These numbers are significantly different ($t = 2$, $df = 10$, $p < 0.05$). Given all of the above data, it would appear that in the

species studied, there is a tendency for the females to consume more than the males.

*Analysis of length increases.* Sexual variation in increases in length for *N. fasciata* from Shelby County, Tennessee are shown in Figure 18. In both L and SVL, females have a significantly higher P-I ratio than the males, and in TL males have a significantly higher P-I ratio than the females (see Table 8). The results illustrate the general trends in increases in length for all of the experimental groups. The differences between males and females, however, are not always significant and do not always follow these trends.

Sexual variation in L for all of the remaining experimental groups are shown in Figure 19. All of the groups had higher P-I ratios for females than for males with the exception of the *N. fasciata* fed the large and the small meal sizes. Of those groups having higher P-I ratio for females than for males only *N. rhombifera* fed the intermediate meal size showed a significant difference between the sexes. Of those groups having a higher P-I ratio for males, only *N. fasciata* fed the large meal size had a significant difference between the sexes (see Table 8).

The results for SVL were similar to those for L (see Figure 20). For this parameter, all of the groups had higher P-I ratios for females than for males with the exception of *N. fasciata* fed the large meal size. Only *N. fasciata*, *N. cyclopion*, and *N. rhombifera* fed the intermediate meal size, and *N. rhombifera* fed the small meal size had significantly higher P-I ratios for females than for males.

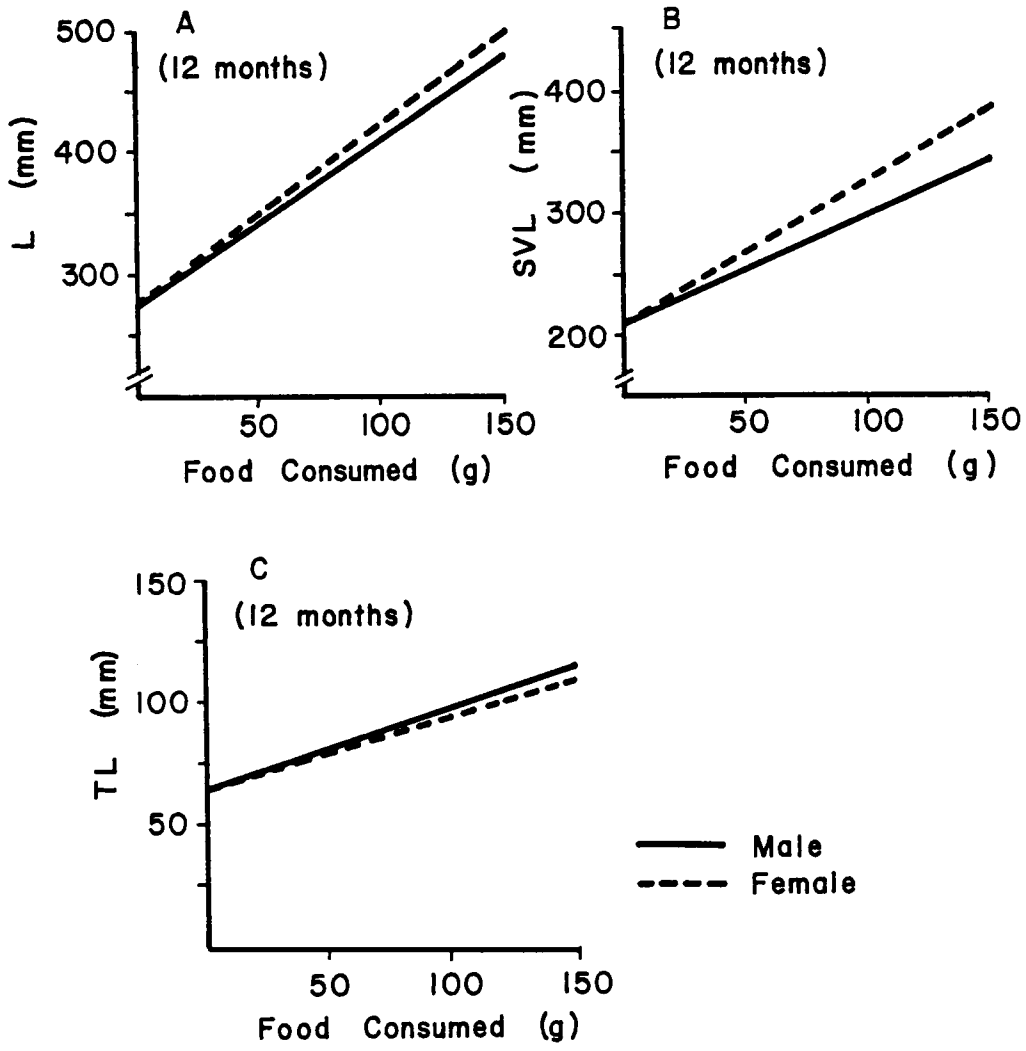



Figure 18. Sexual Variation in Growth in Length in *Nerodia fasciata* from Shelby County, Tennessee. A. Variation in Total Length (L). B. Variation in Snout-Vent Length (SVL). C. Variation in Tail Length (TL).

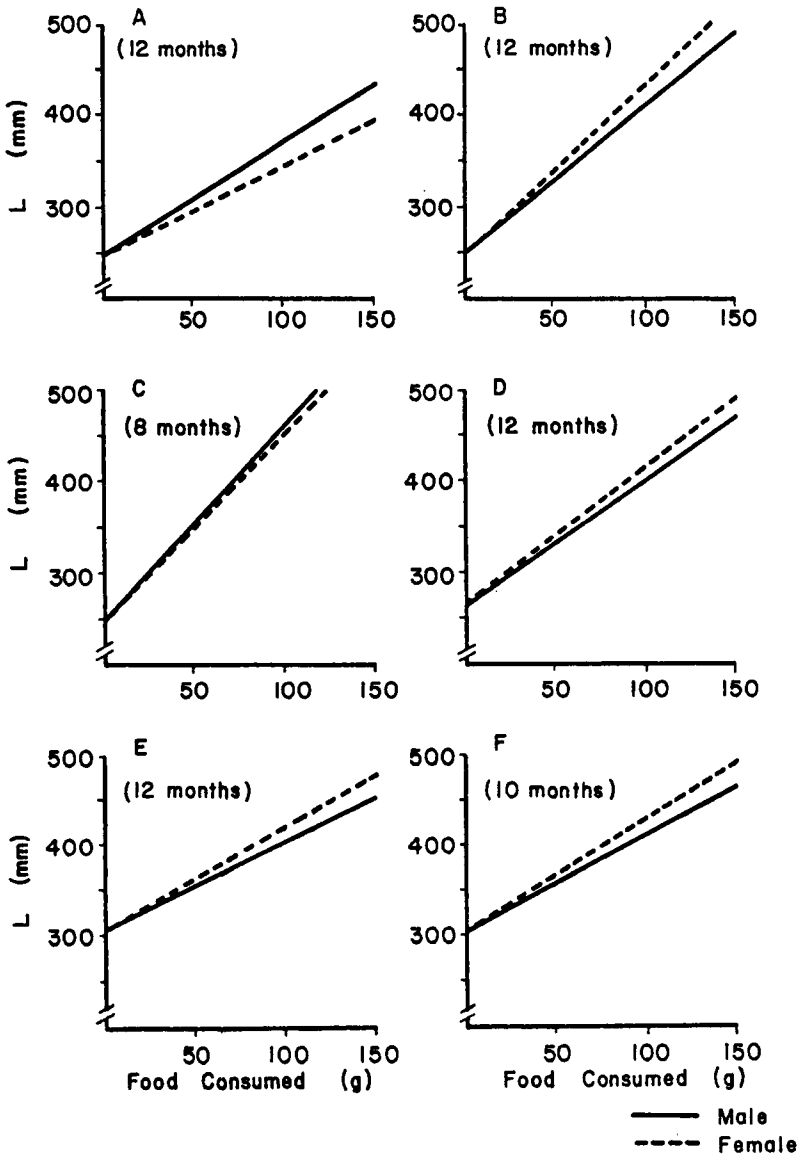



Figure 19. Sexual Variation in Growth in Total Length (L) in Snakes of the Genus *Nerodia* from Lake County, Tennessee. A. *N. fasciata* Large Meal Size. B. *N. fasciata* Intermediate Meal Size. C. *N. fasciata* Small Meal Size. D. *N. cyclopion* Intermediate Meal Size. E. *N. rhombifera* Intermediate Meal Size. F. *N. rhombifera* Small Meal Size.

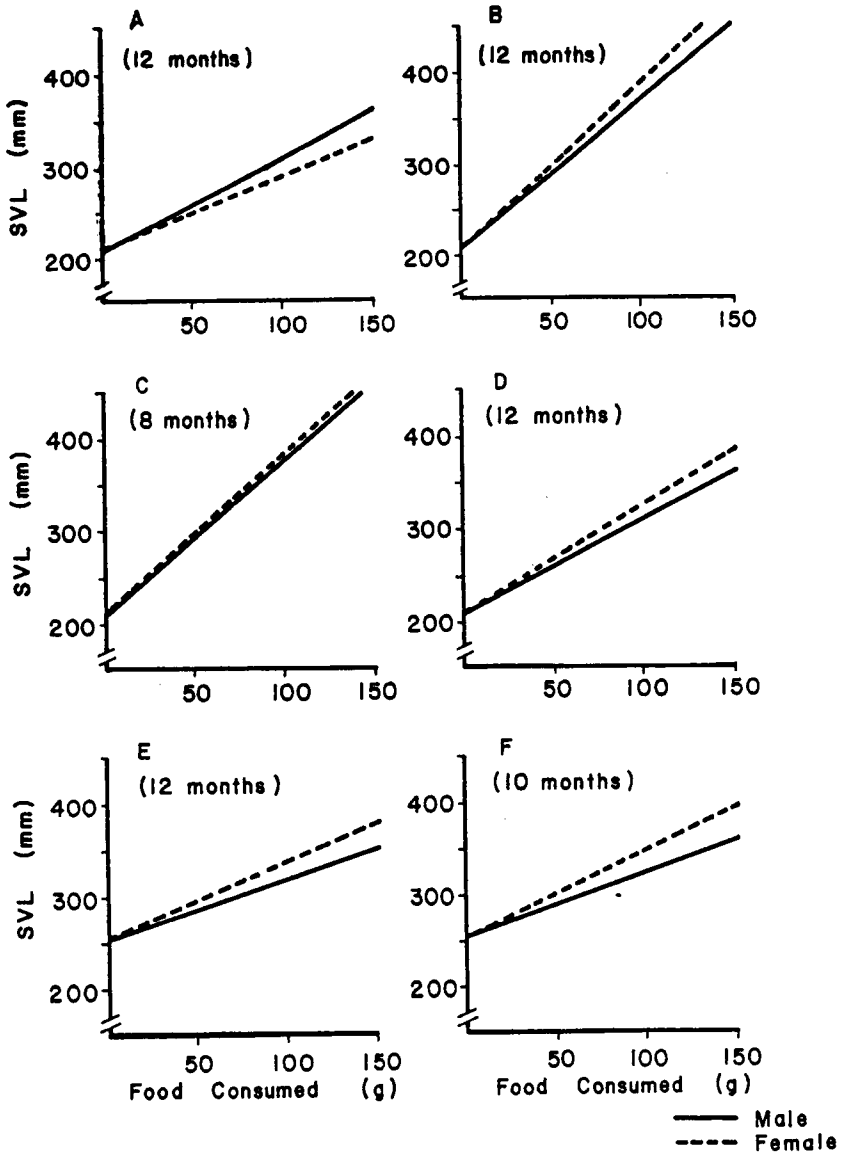



Figure 20. Sexual Variation in Growth in Snout-Vent Length (SVL) in Snakes of the Genus *Nerodia* from Lake County, Tennessee. A. *N. fasciata* Large Meal Size. B. *N. fasciata* Intermediate Meal Size. C. *N. fasciata* Small Meal Size. D. *N. cyclopion* Intermediate Meal Size. E. *N. rhombifera* Intermediate Meal Size. F. *N. rhombifera* Small Meal Size.

*Nerodia fasciata* fed the large meal size had a significantly higher P-I ratio for males than for females (see Table 8).

The differences as to which sex had the higher P-I ratio for increases in L and SVL is related to the difference in the magnitude of the response of the two sexes to changing meal size. It was established earlier (see pages 61 and 68) that the magnitude of the response of *N. fasciata* to changing meal size was greater for females than for males, and that the energy allocated for length increases changes with meal size. In the present case the most energy was allocated to length increases with the intermediate meal size, followed by the small and then the large meal sizes. Given this information, it is reasonable to expect the male and female P-I ratios for L and SVL to change in relation to each other, even to the point of changing order. *Nerodia rhombifera* on the other hand generally showed smaller changes in the P-I ratios with changing meal size than did *N. fasciata* (see Table 5, pages 57-59). This fact can explain why the relationship of the P-I ratio for L and SVL of male and female *N. rhombifera* remains nearly the same when the meal size is changed (see Figures 19E, 19F, 20E, and 20F).

The results for TL differed from those for L and SVL in that males generally had a higher P-I ratio than did the females (Figure 21). The same phenomena that explain the relationship of the growth of the sexes in L and SVL can be used for TL. In *N. fasciata* the largest differences in the P-I ratios for TL between males and females exist in the meal size groups that allocate proportionately less energy for increases in length (the large and small meal size

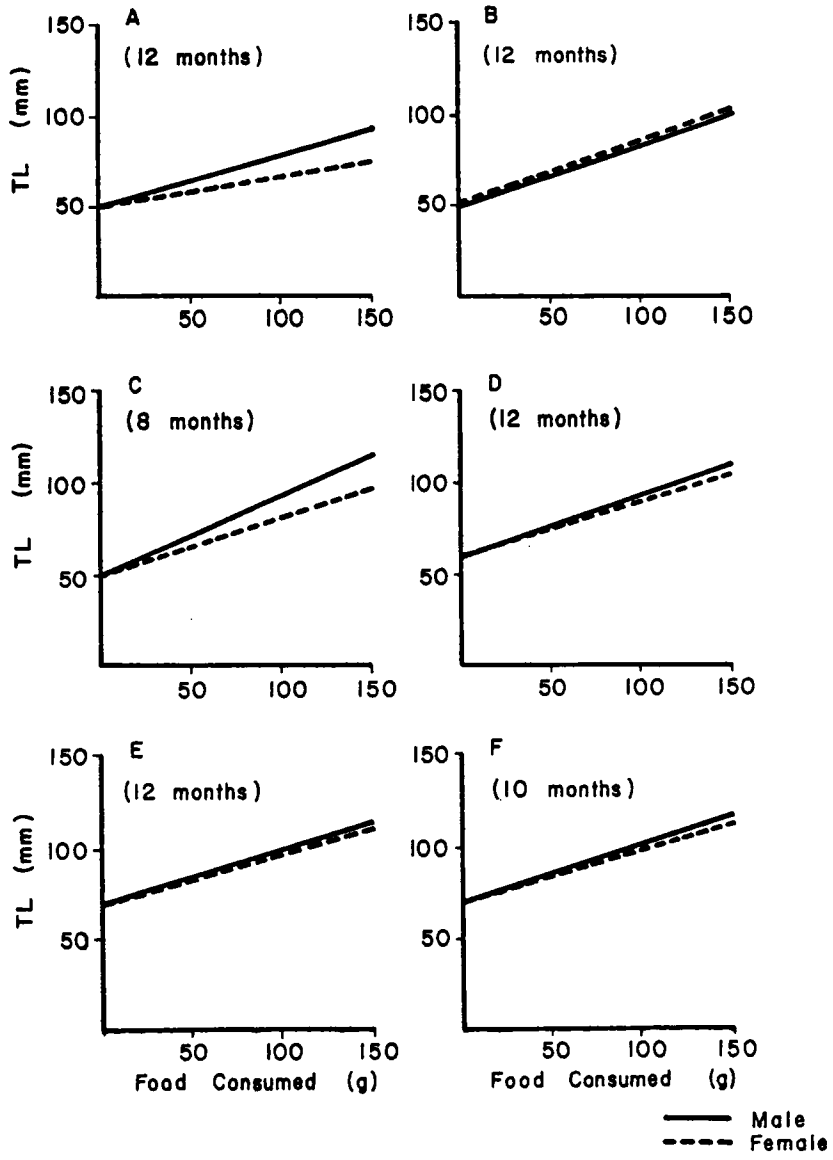



Figure 21. Sexual Variation in Growth in Tail Length (TL) in Snakes of the Genus *Nerodia* from Lake County, Tennessee. A. *N. fasciata* Large Meal Size. B. *N. fasciata* Intermediate Meal Size. C. *N. fasciata* Small Meal Size. D. *N. cyclopion* Intermediate Meal Size. E. *N. rhombifera* Intermediate Meal Size. F. *N. rhombifera* Small Meal Size.

groups), and is smallest in the intermediate meal size group where proportionately more energy is allocated to increases in length (see Figures 21A through 21C). The changes in the relationship of the P-I ratios for TL for males and females in the three meal size groups is therefore brought about because of the greater response of the females to changing meal size. The relationship of the P-I ratios for TL in male and female *N. rhombifera* remains nearly the same in both meal size groups (see Figures 21E and 21F).

Relative growth rates are more accurately compared with one another when data are available for all size classes of the animals in question (Andrews 1982). The truth of this statement can be seen in Table 9. Estimates of the asymptotes and the growth constants (r) for the four growth parameters change as more years of data are added to the model. As the growth curves near the asymptote, the change in the estimates of the asymptote and r become smaller. This trend is especially evident in the males which essentially had reached their full adult size at the end of three years. The females still show large changes in the estimates of the asymptote and r between the third and fourth years.

Because the estimates of the Bertalanffy model reach reliable levels only after growth is nearly complete, the values presented for most of the experimental groups probably do not represent the true values for their growth. Only the values for *N. fasciata* from Shelby County, Tennessee can be assumed to be reasonably accurate. They are probably more accurate for the males since the females appear to be still growing at a significant rate. Estimates of the

Table 9

Estimates of the Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for *Nerodia fasciata* from Shelby County, Tennessee from the Bertalanffy Growth Model

| | | 1 Year | | 2 Years | | 3 Years | | 4 Years | |
|---|---|---|---|---|---|---|---|---|---|
| Sex | Parameter | Estimate | r | Estimate | r | Estimate | r | Estimate | r |
| ♂ | W (g) | 40.1 | 0.0097 | 108.6 | 0.0039 | 105.2 | 0.0041 | 112.7 | 0.0039 |
| | L (mm) | 672 | 0.0044 | 711 | 0.0041 | 699 | 0.0043 | 698 | 0.0042 |
| | SVL (mm) | 369 | 0.0097 | 537 | 0.0039 | 532 | 0.0041 | 534 | 0.0039 |
| | TL (mm) | 264 | 0.0010 | 180 | 0.0037 | 172 | 0.0042 | 168 | 0.0044 |
| ♀ | W (g) | 82.5 | 0.0060 | 113.3 | 0.0045 | 126.5 | 0.0040 | 164.4 | 0.0033 |
| | L (mm) | 624 | 0.0060 | 752 | 0.0041 | 775 | 0.0037 | 819 | 0.0031 |
| | SVL (mm) | 490 | 0.0060 | 573 | 0.0041 | 595 | 0.0040 | 626 | 0.0033 |
| | TL (mm) | 133 | 0.0059 | 165 | 0.0037 | 170 | 0.0034 | 178 | 0.0028 |

asymptotes and r values for the other experimental groups are presented since in some cases they do reflect the general relationship of the relative growth rates of males and females.

The growth constant r is a measure of the rate at which the size of an animal approaches the asymptote. The larger the value of r, the faster the size will approach the asymptote (see pages 41 and 47). As stated above, male *N. fasciata* from Shelby County, Tennessee had essentially reached their full adult size at the end of three years, while the females were still growing. The males therefore had reached their asymptote in less time than it took for the females. The males should have a larger value of r than the females for each of the growth parameters. Table 10 shows that for every growth parameter, the value of r is greater for males than for females. These results are significant at the 0.05 level since the 95% confidence intervals of the r values do not overlap.

These results are opposite to the results for absolute growth rates. The P-I ratios were generally higher for females than for males for L and SVL. Although the females grow at an absolute faster rate, they grow for a longer period of time and consequently have a slower relative growth rate than the males. These results hold for *N. fasciata* from Lake County, Tennessee and for *N. cyclopion* generally although the differences are not significant. The r values indicate that the reverse may be true for *N. rhombifera* (see Table 10). Only two years' data have been collected for these snakes and judging from the estimated asymptotes and the reported adult sizes for these species, they are a long way from completing their

Table 10

Estimates of Asymptotes and Growth Constant Values (r) for Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) from the Bertalanffy Growth Model for Three Species of *Nerodia*

| Species | Meal Size | Sex | Age (Years) | Parameter | Estimate of Asymptote: Value (mm) | Estimate of Asymptote: 95% Confidence Interval (mm) | Estimate of r: Value | Estimate of r: 95% Confidence Interval |
|---|---|---|---|---|---|---|---|---|
| *N. fasciata* Shelby County, Tennessee | ---- | ♂ | 4 | L | 698 | 687-708 | 0.0042 | 0.0040-0.0045 |
| | | | | SVL | 534 | 523-544 | 0.0039 | 0.0036-0.0042 |
| | | | | TL | 168 | 165-171 | 0.0044 | 0.0041-0.0046 |
| *N. fasciata* Shelby County, Tennessee | ---- | ♀ | 4 | L | 819 | 802-836 | 0.0031 | 0.0029-0.0033 |
| | | | | SVL | 626 | 614-638 | 0.0033 | 0.0031-0.0035 |
| | | | | TL | 178 | 170-187 | 0.0028 | 0.0024-0.0032 |
| *N. fasciata* Lake County, Tennessee | Intermediate | ♂ | 2 | L | 624 | 594-654 | 0.0071 | 0.0059-0.0083 |
| | | | | SVL | 495 | 474-516 | 0.0067 | 0.0058-0.0077 |
| | | | | TL | 130 | 121-138 | 0.0085 | 0.0063-0.0108 |
| *N. fasciata* | Intermediate | ♀ | 2 | L | 710 | 693-728 | 0.0060 | 0.0056-0.0065 |
| | | | | SVL | 568 | 555-582 | 0.0061 | 0.0056-0.0065 |
| | | | | TL | 142 | 135-149 | 0.0058 | 0.0048-0.0067 |

Table 10 (Continued)

| Species | Meal Size | Sex | Age (Years) | Parameter | Estimate of Asymptote: Value (mm) | Estimate of Asymptote: 95% Confidence Interval (mm) | Estimate of r: Value | Estimate of r: 95% Confidence Interval |
|---|---|---|---|---|---|---|---|---|
| *N. cyclopion* | Intermediate | ♂ | 2 | L | 602 | 558-645 | 0.0057 | 0.0044-0.0070 |
| | | | | SVL | 472 | 432-512 | 0.0051 | 0.0038-0.0064 |
| | | | | TL | 134 | 126-142 | 0.0078 | 0.0060-0.0097 |
| *N. cyclopion* | Intermediate | ♀ | 2 | L | 695 | 673-718 | 0.0055 | 0.0049-0.0061 |
| | | | | SVL | 555 | 538-573 | 0.0053 | 0.0048-0.0059 |
| | | | | TL | 140 | 134-147 | 0.0062 | 0.0051-0.0072 |
| *N. rhombifera* | Intermediate | ♂ | 2 | L | 722 | 684-759 | 0.0032 | 0.0027-0.0038 |
| | | | | SVL | 569 | 531-608 | 0.0027 | 0.0021-0.0033 |
| | | | | TL | 165 | 153-177 | 0.0048 | 0.0036-0.0061 |
| *N. rhombifera* | Intermediate | ♀ | 2 | L | 724 | 676-773 | 0.0038 | 0.0030-0.0047 |
| | | | | SVL | 576 | 538-615 | 0.0035 | 0.0027-0.0043 |
| | | | | TL | 151 | 140-162 | 0.0050 | 0.0036-0.0064 |

growth. This situation is particularly evident in *N. rhombifera* which attains a maximum length of 1600 mm (Mount 1975). Recent measurements on these same individuals confirm the fact that they are still growing at a significant rate. The asymptotes and r values of these groups therefore may not represent their true relative growth rates.

As would be expected for a group that has an absolute faster growth rate and grows for a longer period of time, female *N. fasciata* from Shelby County, Tennessee had larger estimated asymptotes than the males (see Table 10). The differences in the asymptotes were significant at the 0.05 level. Not enough time has passed in order to determine the true values of the asymptotes for the other experimental groups. The general relationship of the adult sizes of the sexes are evident in the data for *N. fasciata* from Lake County, Tennessee and *N. cyclopion*. The estimates of the asymptotes for the males and females are already significantly different ($p \leq 0.05$) despite the short duration of the data collection. The *N. rhombifera* males and females apparently have not had enough time to grow so that the size trends in the adults are evident (see Table 10). Graphical representation of the growth curves for male and female *N. fasciata* from Shelby County, Tennessee appear in Figures 22 through 24. Browth curves for the other experimental groups are not shown, but they follow the same general pattern of those illustrated.

While the females increase in L and SVL at a faster absolute and a slower relative rate, males increase in TL at a faster absolute and relative rate. Since the body parts of males and females are

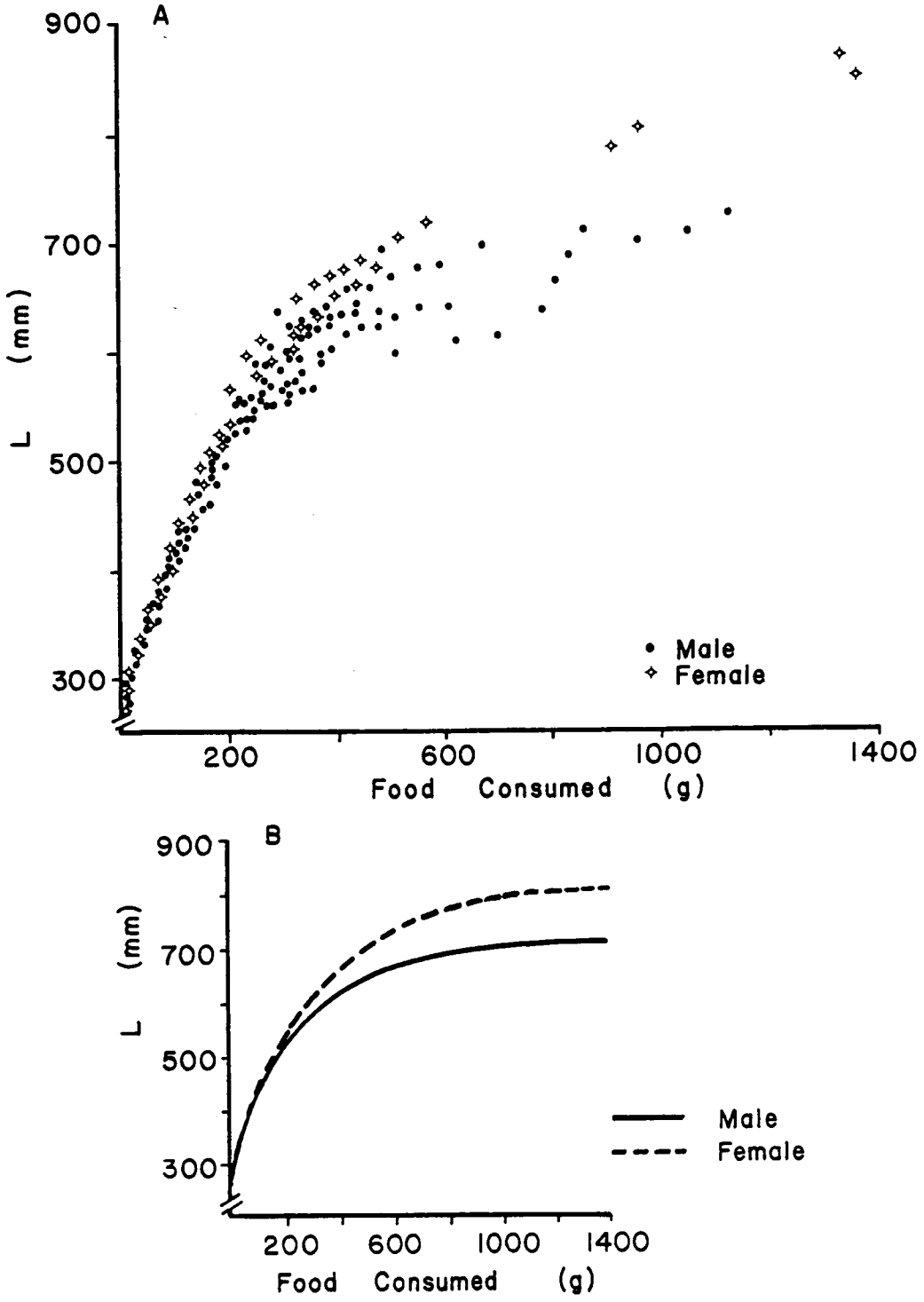



Figure 22. Sexual Variation in Growth in Total Length (L) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines.

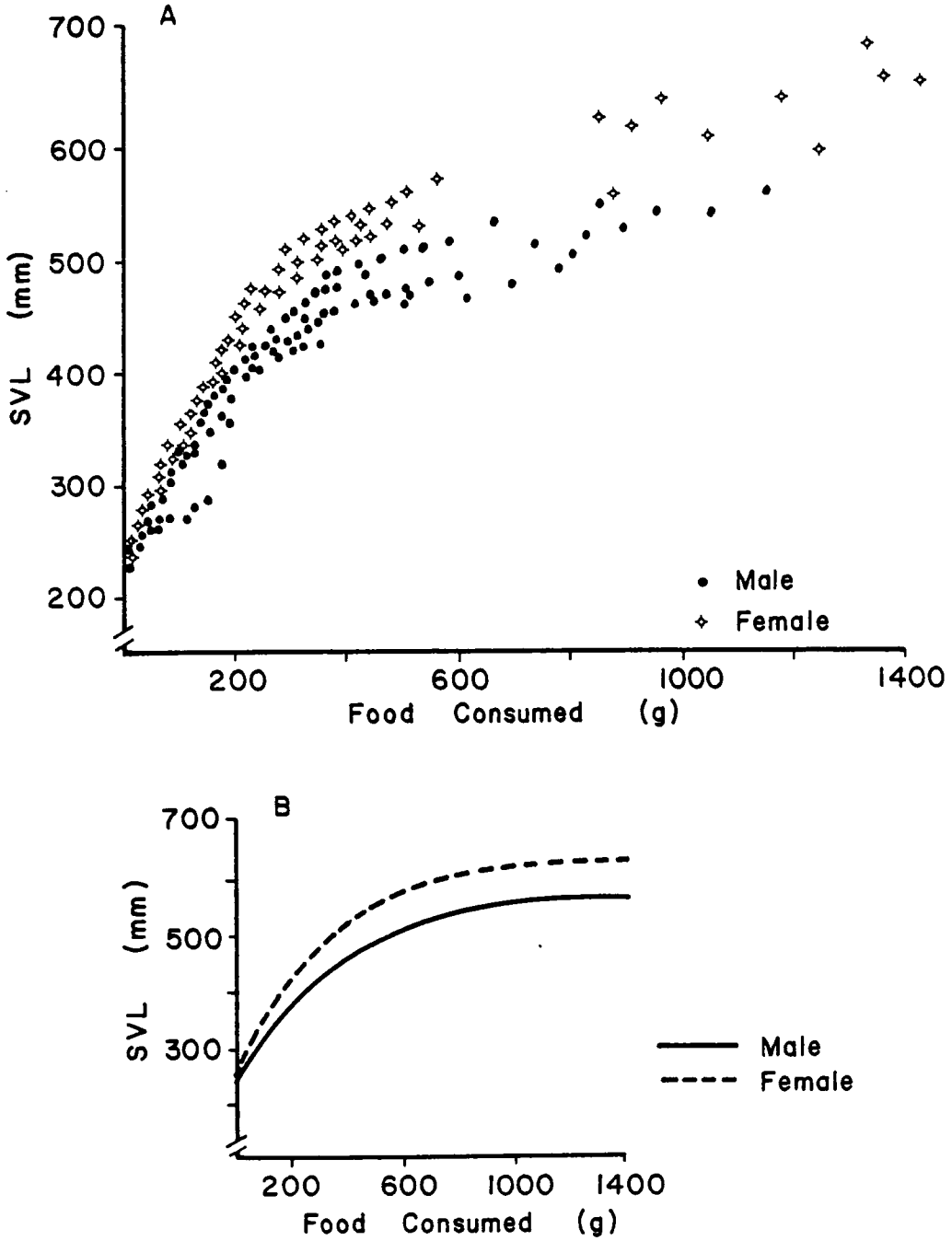



Figure 23. Sexual Variation in Growth in Snout-Vent Length (SVL) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines.

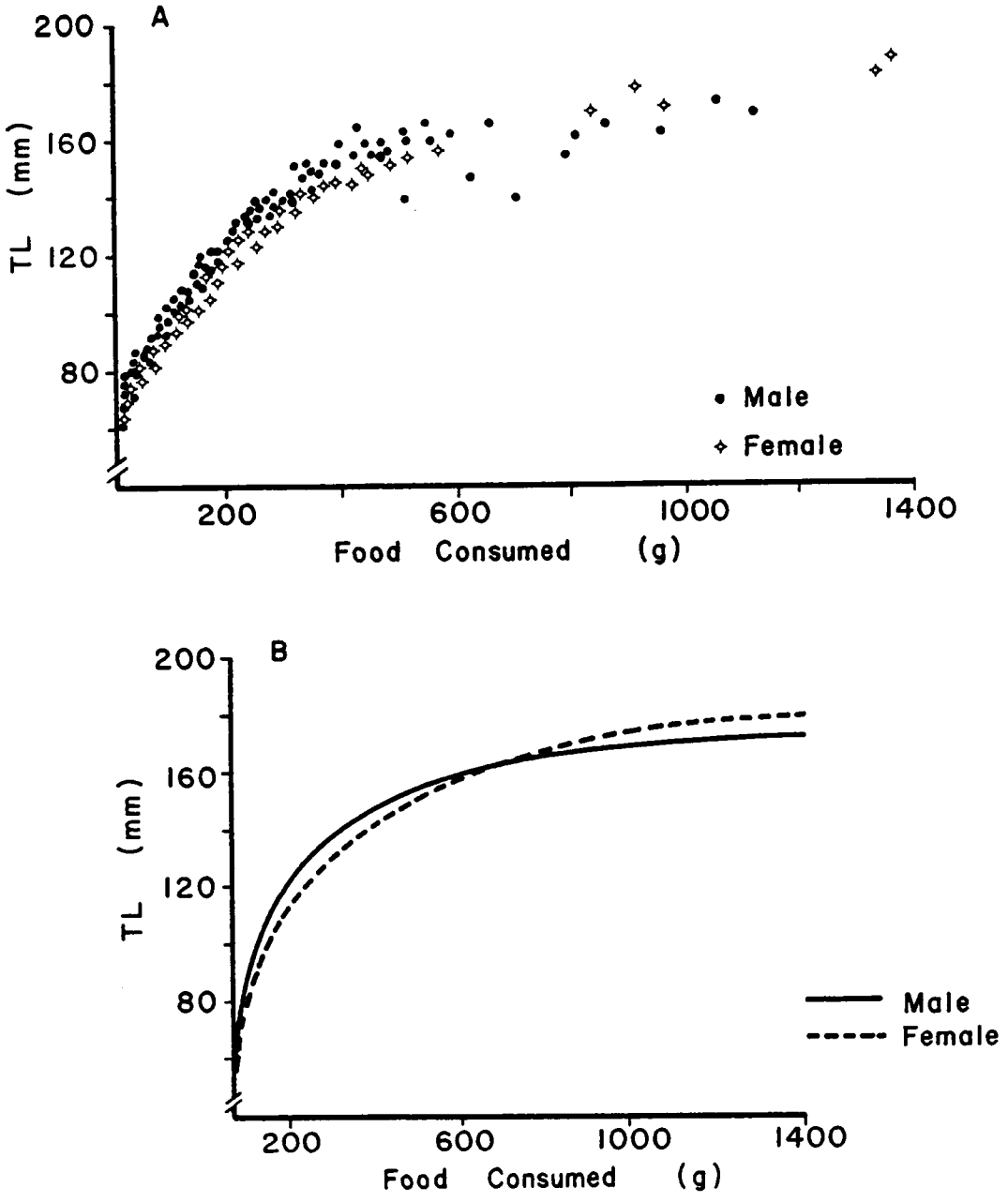



Figure 24. Sexual Variation in Growth in Tail Length (TL) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines.

growing at proportionately different rates, it is of interest to examine how increases in length are proportioned between the body parts. Any increase in L must be divided between SVL and TL. Figure 25 shows the data for SVL as a function of L. Figure 25A shows the individual data points and Figure 25B shows the resultant regression lines for male and female *N. fasciata* from Shelby County, Tennessee. Although the difference in the slopes of the regression lines is small, it is significant ($t = 11.86$, $df = 362$, $p = 0.0001$). What the slopes indicate is that for every 1 mm increase in L, SVL increases 0.79 mm in females and 0.75 mm in males. The linearity of the relationship between L and SVL indicates that the proportion of increases in L that is attributed to SVL is independent of the size of the snake. Whether the snake is a newborn or an adult, a 1 mm increase in L always produces the same increase in SVL. A corollary to the idea of the proportion of the increase attributed to SVL being independent of size is that it is also independent of the absolute growth rate. This is true simply because a newborn snake grows at a faster rate than an adult and it has already been established that there is no difference between these two size classes. The relationship between SVL and L and SVL and TL stated above applied principally to snakes subjected to the same feeding regimen. A change in the feeding regimen may cause a slight shift in the proportion of the increase in L attributed to SVL and TL. A significant shift occurred only in male *N. fasciata* fed the large and intermediate meal sizes. The general relationship between males and females remains the same regardless of the shift (see Table 11).

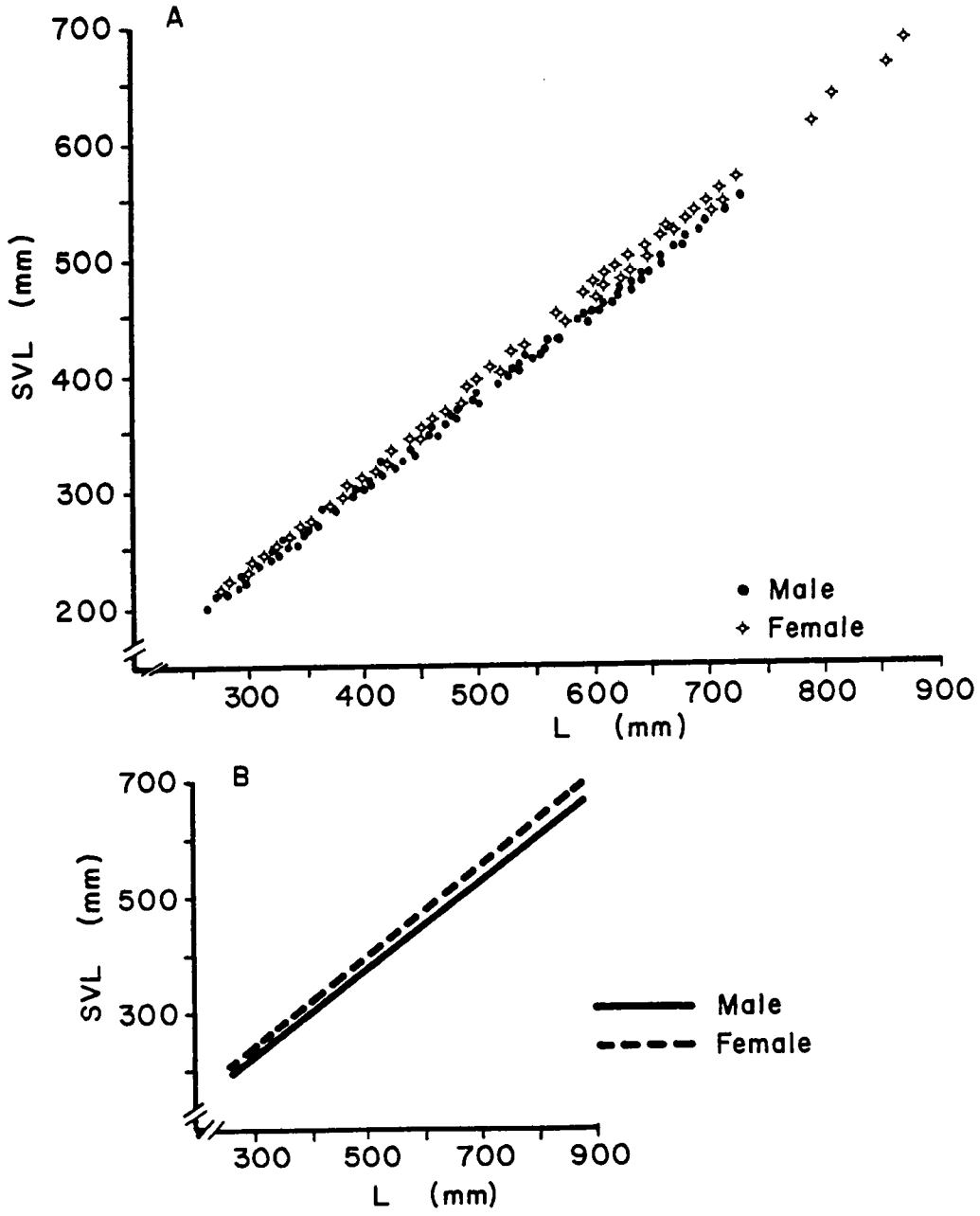



Figure 25. The Relationship Between Snout-Vent Length (SVL) and Total Length (L) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines.

Table 11

The Effect of Meal Size on the Proportion of the Increase in Total Length (L) Attributed to Snout-Vent Length (SVL) and Tail Length (TL) in *Nerodia fasciata* and *N. rhombifera*

| Species | Sex | Meal Size | Slope of SVL on L | Slope of TL on L | t | df | p |
|---|---|---|---|---|---|---|---|
| *N. fasciata* | ♂ | Large | 0.80 | 0.20 | 2.86 | 73 | 0.0051 |
| | | Intermediate | 0.78 | 0.22 | | | |
| Lake County, Tennessee | | | | | | | |
| | | Large | 0.80 | 0.20 | 1.31 | 62 | 0.1936 |
| | | Small | 0.79 | 0.21 | | | |
| | | Intermediate | 0.78 | 0.22 | 1.44 | 73 | 0.1539 |
| | | Small | 0.79 | 0.21 | | | |
| | ♀ | Large | 0.82 | 0.18 | 0.58 | 51 | 0.5635 |
| | | Intermediate | 0.81 | 0.19 | | | |
| | | Large | 0.82 | 0.18 | 0.66 | 41 | 0.5088 |
| | | Small | 0.83 | 0.17 | | | |
| | | Intermediate | 0.81 | 0.19 | 1.06 | 41 | 0.2956 |
| | | Small | 0.83 | 0.17 | | | |

Table 11 (Continued)

| Species | Sex | Meal Size | Slope of SVL on L | Slope of TL on L | t | df | p |
|---|---|---|---|---|---|---|---|
| *N. rhombifera* | ♂ | Intermediate | 0.69 | 0.31 | 0.42 | 73 | 0.6791 |
| | | Small | 0.70 | 0.30 | | | |
| | ♀ | Intermediate | 0.74 | 0.26 | 1.32 | 84 | 0.1893 |
| | | Small | 0.76 | 0.24 | | | |

The relationship between TL and L is shown in Figure 26. Since all of the increase in L not attributed to SVL must be attributed to TL, males showed a greater proportion of the increase in L going to TL than did the females. For every 1 mm increase in L, TL increased 0.25 mm in males and 0.21 mm in females. As with SVL, this relationship remains the same regardless of the size or growth rate of the snakes, but may be affected by meal size (see Table 11). Figures 27 through 29 show the relationships between SVL and L and TL and L for the other experimental groups. Although the proportions vary from group to group, the proportion of the increase in L attributed to TL is always greater in males. The differences between males and females are significant in every case.

*Analysis of weight increases.* The P-I ratios for increases in W were higher for females than for males in every experimental group except for *N. fasciata* fed the small size (see Figures 30 and 31). All of the differences in the P-I ratios including the instance in which the males had the higher P-I ratio were significant (see Table 8, pages 74-76). The change in the relationship of the P-I ratios for W for male and female *N. fasciata*, as with the relationships for L and SVL (see page 82), is related to the difference in the magnitude of the response of the two sexes to changing meal size. The magnitude of the response was greater for females than for males and in the one instance resulted in the reversal in the relationship of the P-I ratios for the sexes.

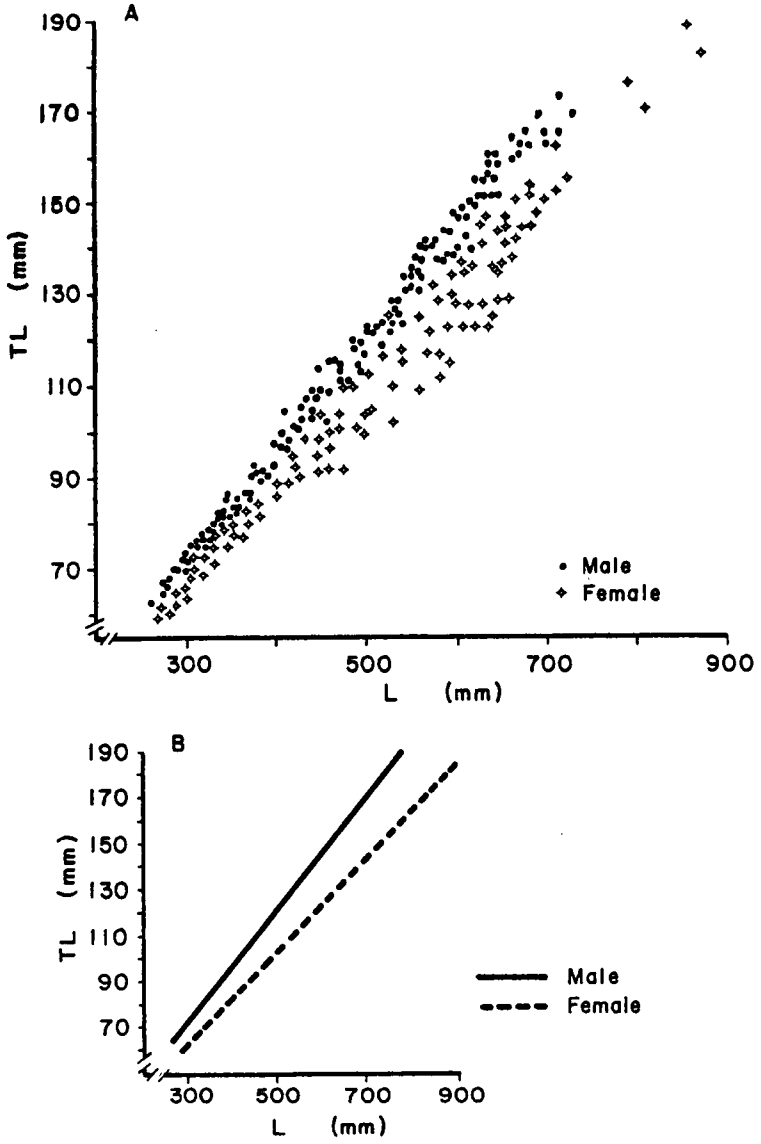



Figure 26. The Relationship Between Tail Length (TL) and Total Length (L) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines.

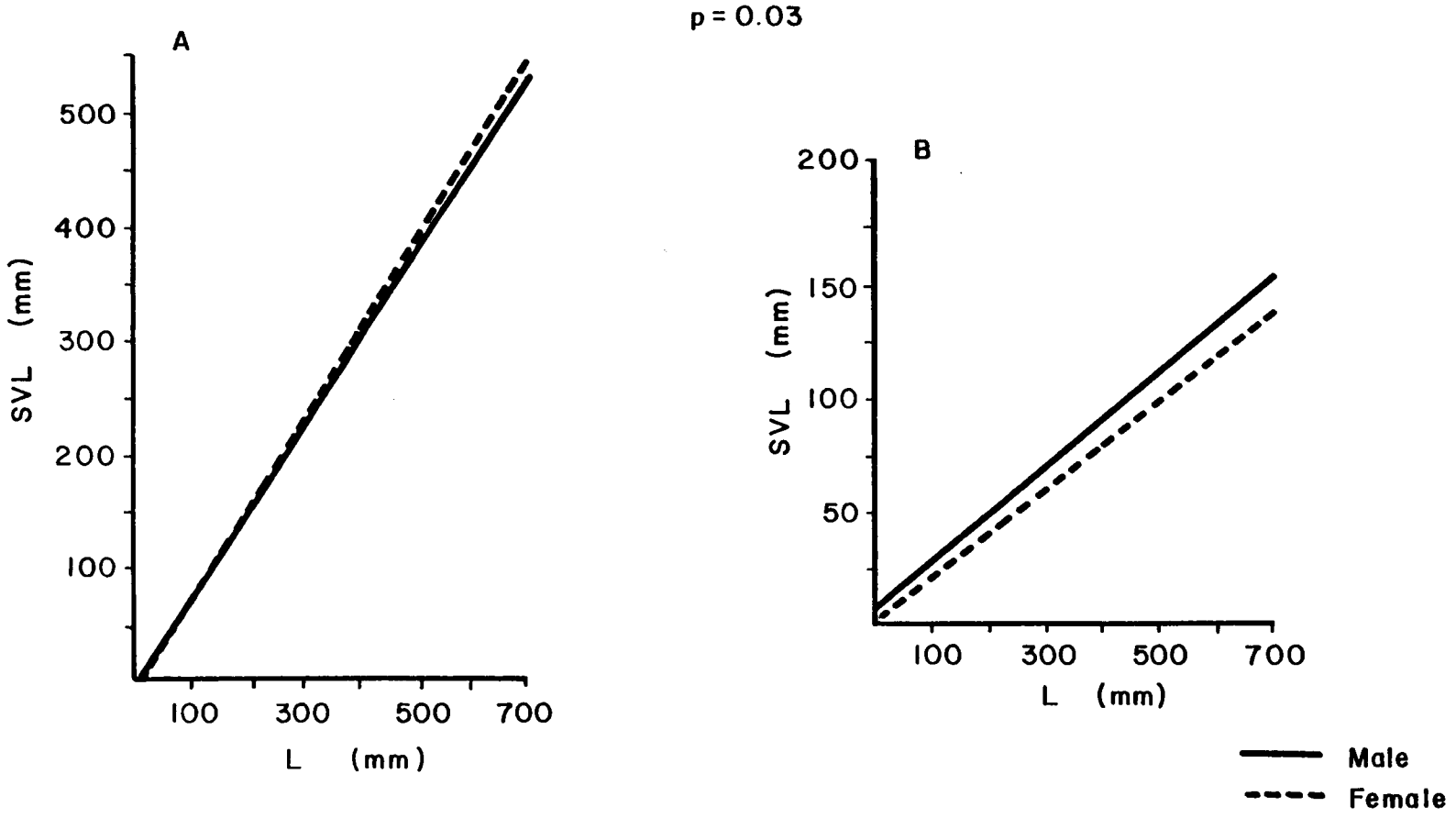



Figure 27. The Relationship Between Snout-Vent Length (SVL) and Total Length (L) and Tail Length (TL) and Total Length in *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size. A. SVL and L. B. TL and L.

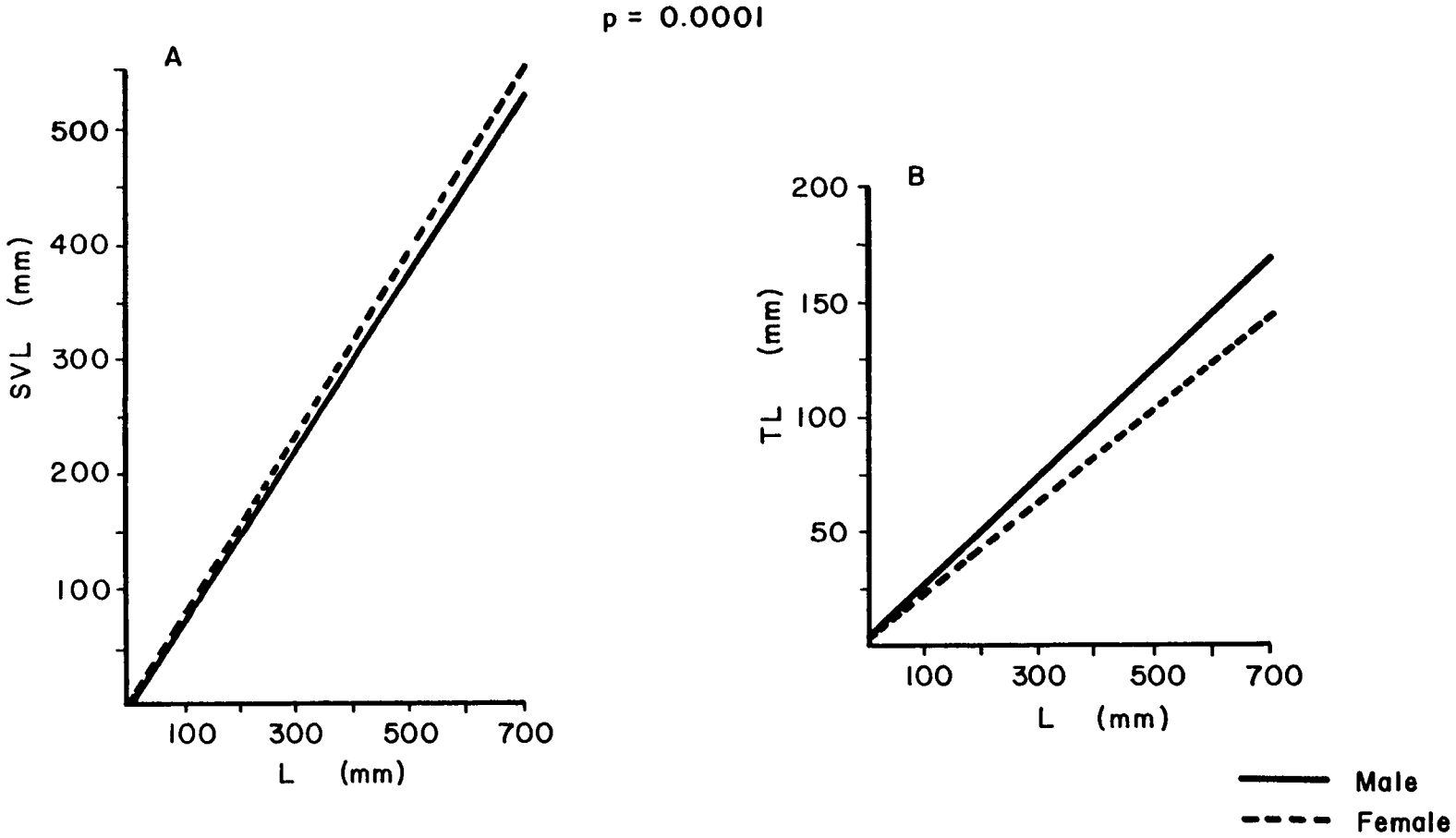



Figure 28. The Relationship Between Snout-Vent Length (SVL) and Total Length (L) and Tail Length (TL) and Total Length in *Nerodia cyclopion* Fed the Intermediate Meal Size. A. SVL and L. B. TL and L.

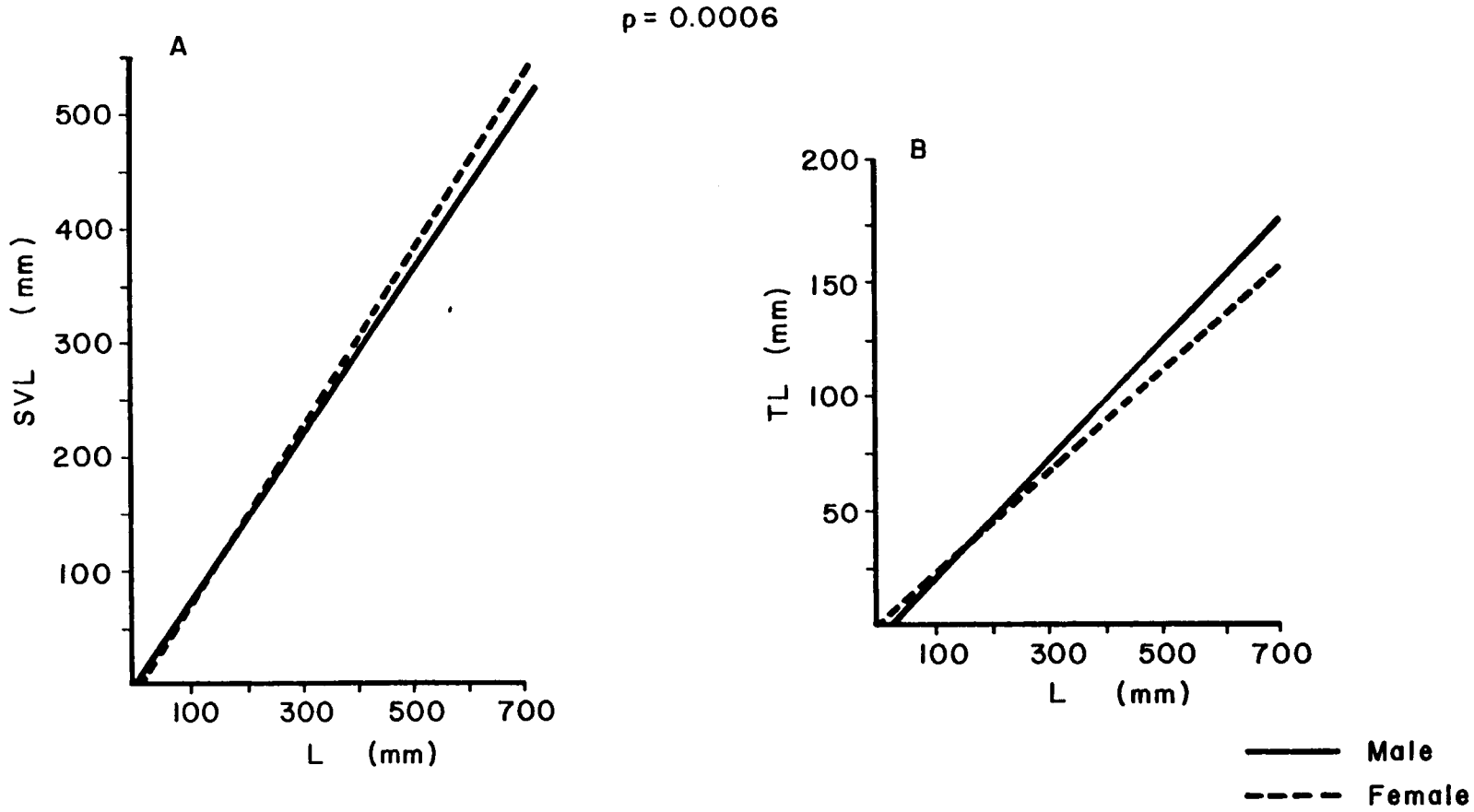



Figure 29. The Relationship Between Snout-Vent Length (SVL) and Total Length (L) and Tail Length (TL) and Total Length in *Nerodia rhombifera* Fed the Intermediate Meal Size. A. SVL and L. B. TL and L.

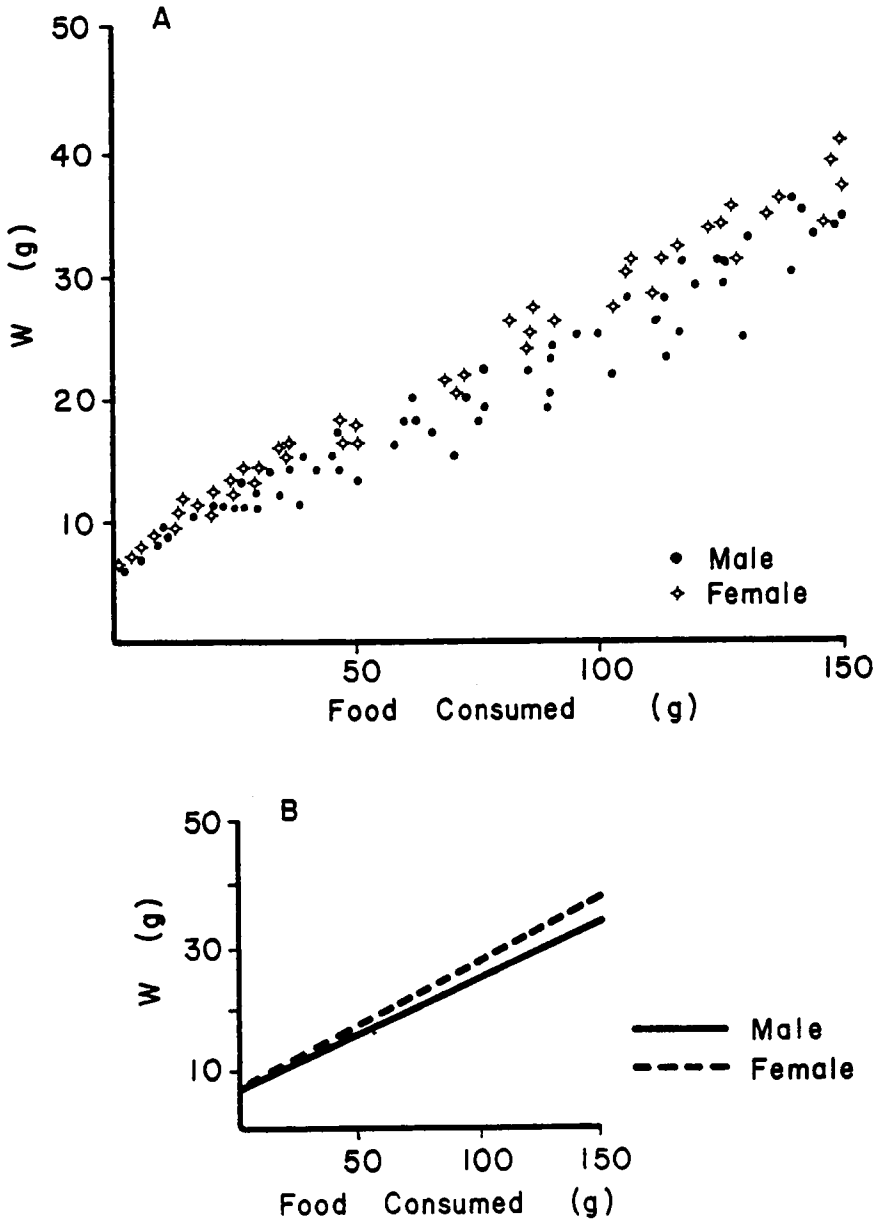



Figure 30. Sexual Variation in Growth in Weight (W) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines.

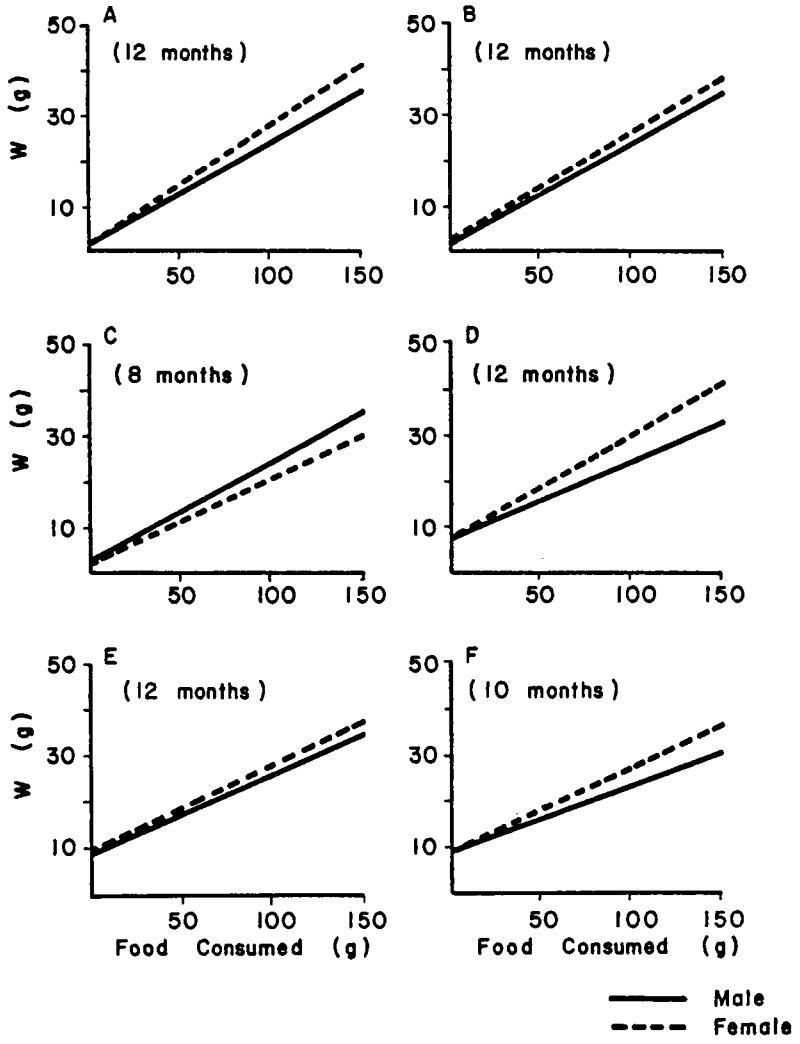



Figure 31. Sexual Variation in Growth in Weight (W) in Snakes of the Genus *Nerodia* from Lake County, Tennessee. A. *N. fasciata* Large Meal Size. B. *N. fasciata* Intermediate Meal Size. C. *N. fasciata* Small Meal Size. D. *N. cyclopion* Intermediate Meal Size. E. *N. rhombifera* Intermediate Meal Size. F. *N. rhombifera* Small Meal Size.

In terms of relative growth, males grew faster than females. The relationships of the relative growth rates are not surprising considering that W is linearly related to L (see page 12) and the relative growth rate for L was faster for males. The growth curves for W for male and female *N. fasciata* from Shelby County, Tennessee are shown in Figure 32. The estimate of the asymptote of W is significantly greater for females than for males (Table 12). The asymptote for W is greater for females in all of the experimental groups with the exception of *N. rhombifera*. As mentioned earlier, only the values for *N. fasciata* males from Shelby County, Tennessee can be assumed to represent accurate measures of the parameters of the growth curve (see page 84). Although some of the experimental groups show the general relationship of male and female adult sizes as seen in natural populations, the values presented in Table 12 probably do not represent the true values for the growth curves.

The relationship of W/SVL of male and female *N. fasciata* from Shelby County, Tennessee is shown in Figure 33. The rate of increase in W/SVL was greater for males than for females and resulted in males being heavier-bodied than females at all SVLs. The same results obtained for the other experimental groups, but the magnitude of the difference between males and females varied with meal size (Figures 34 and 35). In fact, in *N. fasciata* from Lake County, Tennessee, significant differences existed between the sexes in the intermediate and small meal size groups, but not in the large meal size group. The magnitude of the difference between male and female *N. rhombifera*

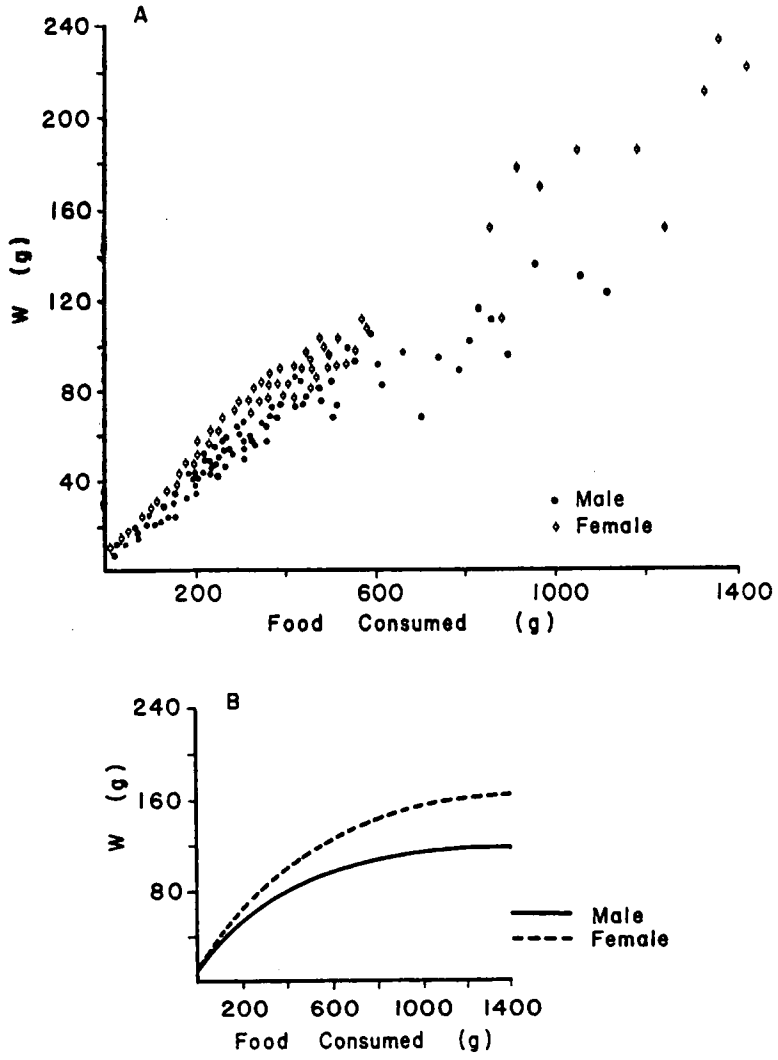



Figure 32. Sexual Variation in Growth in Weight (W) in *Nerodia fasciata* from Shelby County, Tennessee. Data Represent Four Years of Growth. A. The Data. B. The Regression Lines.

Table 12

Estimates of Asymptotes for Weight (W) from the Bertalanffy Growth Model for Three Species of *Nerodia*

| Species | Meal Size | Sex | Age (Years) | Predicted Asymptote W (g) | Predicted Asymptote 95% Confidence Interval (g) |
|---|---|---|---|---|---|
| *N. fasciata* Shelby County, Tennessee | ---- | ♂ | 4 | 112.7 | 111.2-114.2 |
| *N. fasciata* Shelby County, Tennessee | ---- | ♀ | 4 | 164.4 | 160.6-168.3 |
| *N. fasciata* Lake County, Tennessee | Intermediate | ♂ | 2 | 87.7 | 85.4-90.1 |
| *N. fasciata* Lake County, Tennessee | Intermediate | ♀ | 2 | 110.1 | 107.7-112.6 |
| *N. cyclopion* | Intermediate | ♂ | 2 | 79.3 | 77.8-80.7 |
| *N. cyclopion* | Intermediate | ♀ | 2 | 116.1 | 114.3-117.9 |
| *N. rhombifera* | Intermediate | ♂ | 2 | 147.7 | 145.6-149.5 |
| *N. rhombifera* | Intermediate | ♀ | 2 | 138.3 | 134.4-142.2 |

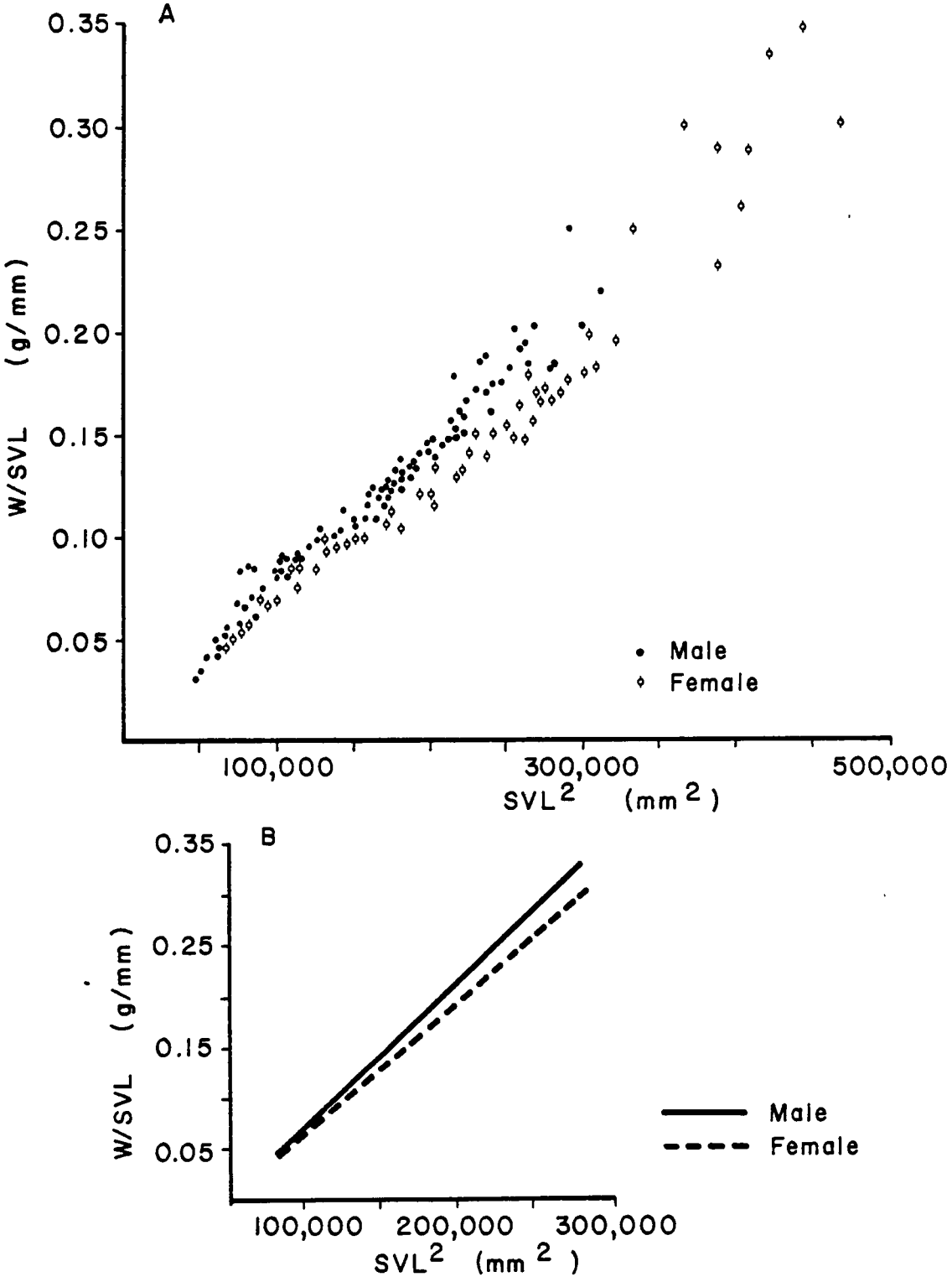



Figure 33. Sexual Variation in Weight Per Unit Length (W/SVL) in *Nerodia fasciata* from Shelby County, Tennessee. A. The Data. B. The Regression Lines.

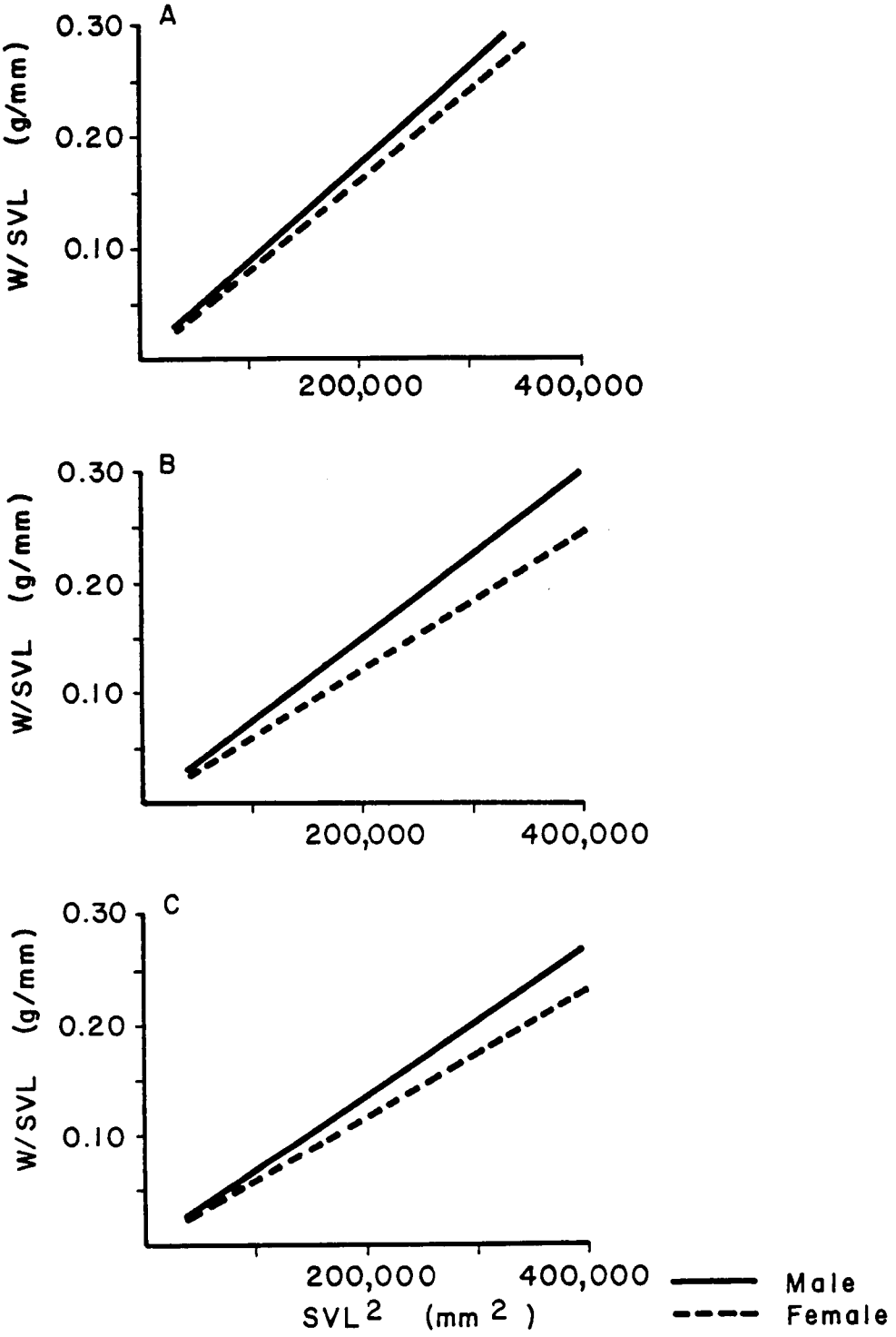



Figure 34. Sexual Variation in Growth in Weight Per Unit Length (W/SVL) for *Nerodia fasciata* from Lake County, Tennessee. A. Large Meal Size. B. Intermediate Meal Size. C. Small Meal Size.

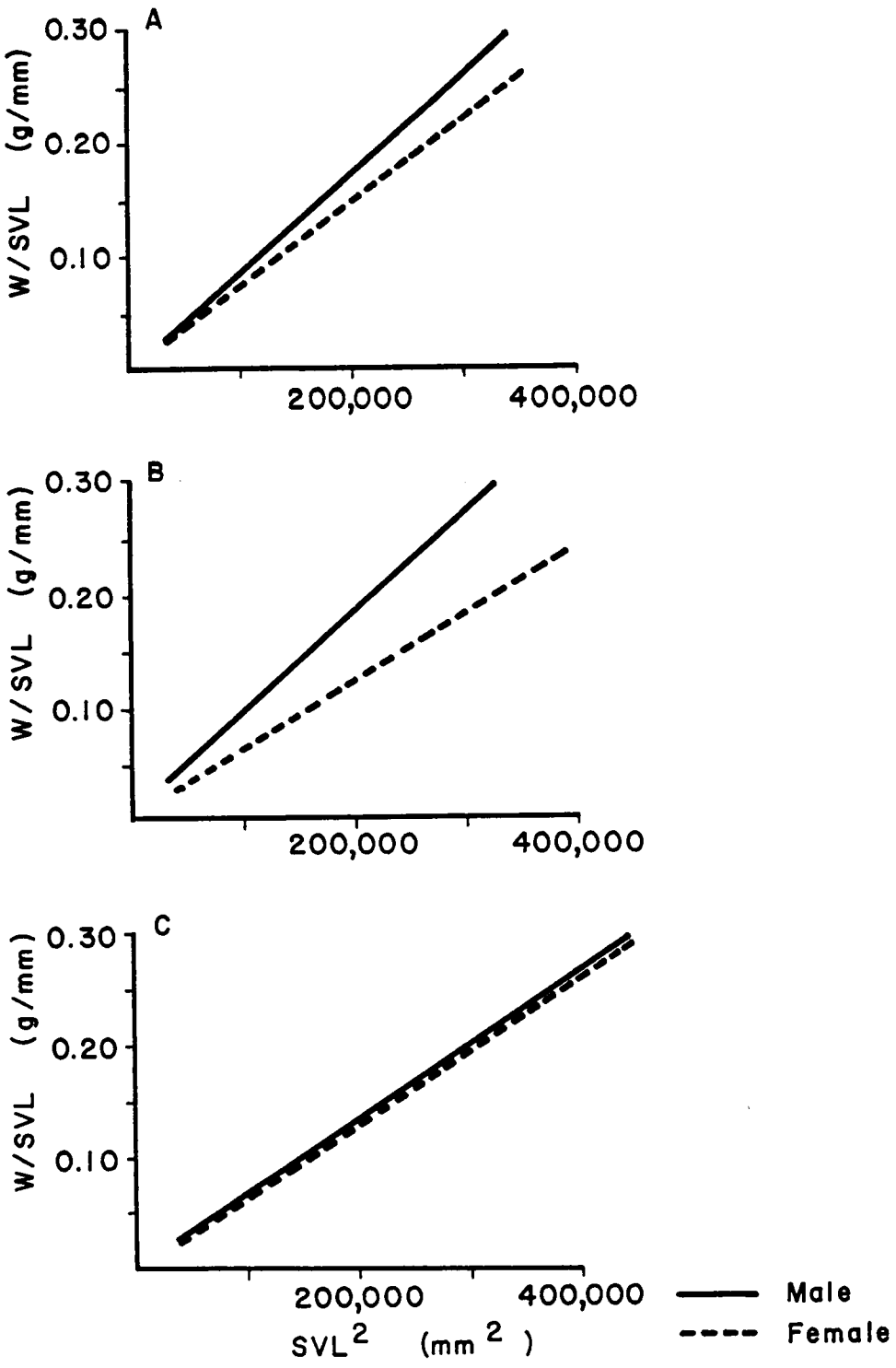



Figure 35. Sexual Variation in Growth in Weight Per Unit Length (W/SVL) in *Nerodia rhombifera* and *N. cyclopion*. A. *N. rhombifera* Intermediate Meal Size. B. *N. rhombifera* Small Meal Size. C. *N. cyclopion* Intermediate Meal Size.

was also greater in the small meal size group than in the intermediate meal size group (see Table 13).

The results for W/SVL for the sexes are unusual in view of the fact that females are heavier-bodied than males for all lengths in natural populations (Klauber 1956, Semlitsch and Gibbons 1982). The discrepancy between the results for natural populations and the snakes in this study probably reflects the differences in the feeding regimens of the groups. The *N. fasciata* from Lake County, Tennessee illustrate this point. The difference between males and females was smallest in the large meal size group where the snakes were allowed to a large extent to set their own feeding level. When the snakes were offered food on a restricted feeding schedule, the rate of increase in W/SVL dropped for both sexes, but more so for the females (see Table 13). Since females are heavier-bodied than males in natural populations, and since the males and females are closer to this relationship when they are allowed to eat large meals, it would appear that the level of food intake in natural populations is much larger than what was available in any of the feeding regimens in this study. This same argument can be made for *N. rhombifera* since the difference between males and females in W/SVL was less when they were fed the intermediate meal size than when they were fed the small meal size (see Table 13). A summary of the results of sexual variation in growth can be found in Tables 14 and 15.

Table 13

Comparisons of the Rate of Increase in Weight Per Unit Length (W/SVL) by Sex for Three Species of *Nerodia*

| Species | Meal Size | Sex | Slope* ($\times 10^7$) | t | df | p |
|---|---|---|---|---|---|---|
| *N. fasciata* Shelby County, Tennessee | ---- | ♂ | 7.12 | 7.36 | 344 | 0.0001 |
| | | ♀ | 6.11 | | | |
| *N. fasciata* Lake County, Tennessee | Large | ♂ | 8.72 | 1.16 | 86 | 0.2504 |
| | | ♀ | 8.16 | | | |
| | Intermediate | ♂ | 7.47 | 6.65 | 101 | 0.0001 |
| | | ♀ | 6.10 | | | |
| | Small | ♂ | 6.76 | 4.14 | 41 | 0.0002 |
| | | ♀ | 5.71 | | | |
| *N. rhombifera* | Intermediate | ♂ | 8.81 | 7.13 | 116 | 0.0001 |
| | | ♀ | 7.60 | | | |
| | Small | ♂ | 9.05 | 4.07 | 73 | 0.0001 |
| | | ♀ | 6.15 | | | |
| *N. cyclopion* | Intermediate | ♂ | 6.66 | 0.75 | 116 | 0.4573 |
| | | ♀ | 6.52 | | | |

*The numbers presented here are the values of the slope of the regression of W/SVL on $SVL^2$.

Table 14

Summary of the Results of Sexual Variation in the Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), Tail Length (TL), and Weight Per Unit Length (W/SVL) in Three Species of *Nerodia*[1,2]

| Species | W | L | SVL | TL | W/SVL |
|---|---|---|---|---|---|
| *N. fasciata*<br>Shelby County, Tennessee | S***<br>(♀) | S**<br>(♀) | S***<br>(♀) | S**<br>(♂) | S***<br>(♂) |
| *N. fasciata*<br>Lake County, Tennessee<br>Large Meal Size | S***<br>(♀) | S**<br>(♂) | S**<br>(♂) | S**<br>(♂) | NS<br>(♂) |
| *N. fasciata*<br>Lake County, Tennessee<br>Intermediate Meal Size | S**<br>(♀) | NS<br>(♀) | S*<br>(♀) | NS<br>(♀) | S***<br>(♂) |
| *N. fasciata*<br>Lake County, Tennessee<br>Small Meal Size | S*<br>(♂) | NS<br>(♂) | NS<br>(♀) | S*<br>(♂) | S***<br>(♂) |
| *N. cyclopion*<br>Intermediate Meal Size | S***<br>(♀) | NS<br>(♀) | S*<br>(♀) | NS<br>(♂) | NS<br>(♂) |
| *N. rhombifera*<br>Intermediate Meal Size | S*<br>(♀) | S*<br>(♀) | S***<br>(♀) | NS<br>(♂) | S***<br>(♂) |
| *N. rhombifera*<br>Small Meal Size | S**<br>(♀) | NS<br>(♀) | S*<br>(♀) | NS<br>(♂) | S***<br>(♂) |

[1] S* = Significant difference, $p < 0.05$.
S** = Significant difference, $p < 0.005$.
S*** = Significant difference, $p < 0.0005$.
[2] NS = No significant difference, $p > 0.05$.
Symbols in parentheses represent the sex with the higher P-I ratio for that growth parameter.

Table 15

Summary of the Results of Sexual Variation in the Estimates of the Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snouth-Vent Length (SVL), and Tail Length (TL) in Three Species of *Nerodia*[1,2]

| Species | Asymptote | | | | r | | | |
|---|---|---|---|---|---|---|---|---|
| | W | L | SVL | TL | W | L | SVL | TL |
| *N. fasciata* Shelby County, Tennessee | S (♀) | S (♀) | S (♀) | NS (♀) | S (♂) | S (♂) | S (♂) | S (♂) |
| *N. fasciata* Lake County, Tennessee Intermediate Meal Size | S (♀) | S (♀) | S (♀) | NS (♀) | NS (♂) | NS (♂) | NS (♂) | NS (♂) |
| *N cyclopion* Intermediate Meal Size | S (♀) | S (♀) | S (♀) | NS (♀) | NS (♀) | NS (♂) | NS (♀) | NS (♂) |
| *N. rhombifera* Intermediate Meal Size | NS (o) | NS (♀) | NS (♀) | NS ( ) | NS (♀) | NS (♀) | NS (♀) | NS (♀) |

[1]S = Significant difference, $p < 0.05$.

[2]NS = No significant difference, $p > 0.05$.

Symbols in parentheses represent the sex with the higher estimates of the asymptote and growth constant. Data for *N. fasciata* from Shelby County, Tennessee are for four years; all others are for two years.

*Species Variation in Growth*

*Introduction.* The results of species differences in growth presented in the following sections should be considered no more than general indications of the relationships of the growth rates of these species. The comparisons among species are based on single litters of each species which may or may not be representative of the populations from which they were taken. There is also no way of knowing which individuals from these litters would have survived in the wild. The average responses of the species are therefore possibly based on data from individuals that would have been removed from natural populations. Also the snakes in this study are probably eating less than they would have in the wild (see page 110). Since these snakes are very likely to be eating different amounts of food as well as a greater variety of food items in the wild, and since the feeding regimen can have very large effects on the growth pattern (see pages 61 and 68), the differences in the growth of these species as reported here probably are not of the same magnitude as would be found in the field. The growth patterns of the species in the wild must also vary so that the snakes attain the species characteristic adult size distribution from their initial size (see Table 16). The differences reported here are, however, representative of the potentialities of the species given a particular set of circumstances.

Comparisons of all of the growth parameters are shown by species pairs in Table 17. Discussion of the results, as with feeding regimen and sexual variation in growth, are presented by growth parameter for all three species.

Table 16

Measurements at Birth for Weight (W), Total Length (L), Snout-Vent Length (SVL), Tail Length (TL), and Adult L Measurements for Three Species of *Nerodia*

| Species | Sex | W (g) | L (mm) | SVL (mm) | TL (mm) | Adult L (mm)* Average Range | Adult L (mm)* Maximum |
|---|---|---|---|---|---|---|---|
| *N. fasciata confluens* | | | | | | 560-910 | 1143 |
| Shelby County, Tennessee | ♂ | 5.8 | 276 | 208 | 68 | | |
| | ♀ | 6.0 | 274 | 211 | 63 | | |
| Lake County, Tennessee | ♂ | 4.1 | 239 | 184 | 55 | | |
| | ♀ | 4.0 | 238 | 189 | 49 | | |
| *N. c. cyclopion* | | | | | | 750-1140 | 1270 |
| | ♂ | 8.3 | 280 | 213 | 67 | | |
| | ♀ | 8.3 | 273 | 213 | 61 | | |
| *N. r. rhombifera* | | | | | | 760-1220 | 1600 |
| | ♂ | 9.9 | 316 | 240 | 76 | | |
| | ♀ | 10.8 | 314 | 247 | 67 | | |

*Conant 1975.

Table 17

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) by Species for Three Species from Lake County, Tennessee

| Groups | Parameter | Species | P-I Ratio | t | df | p |
|---|---|---|---|---|---|---|
| Intermediate Meal Size male | W | *N. fasciata* | 0.2154 | 6.24 | 108 | 0.0001 |
| | | *N. cyclopion* | 0.1679 | | | |
| | L | *N. fasciata* | 1.6158 | 3.06 | 108 | 0.0026 |
| *N. fasciata* x *N. cyclopion* (12 months) | | *N. cyclopion* | 1.3343 | | | |
| | SVL | *N. fasciata* | 1.2637 | 3.87 | 108 | 0.0002 |
| | | *N. cyclopion* | 1.0028 | | | |
| | TL | *N. fasciata* | 0.3521 | 0.66 | 108 | 0.5081 |
| | | *N. cyclopion* | 0.3316 | | | |
| *N. fasciata* x *N. rhombifera* (12 months) | W | *N. fasciata* | 0.2154 | 5.75 | 108 | 0.0001 |
| | | *N. rhombifera* | 0.1745 | | | |
| | L | *N. fasciata* | 1.6158 | 7.05 | 108 | 0.0001 |
| | | *N. rhombifera* | 0.9758 | | | |
| | SVL | *N. fasciata* | 1.2637 | 8.81 | 108 | 0.0001 |
| | | *N. rhombifera* | 0.6800 | | | |
| | TL | *N. fasciata* | 0.3521 | 1.85 | 108 | 0.0674 |
| | | *N. rhombifera* | 0.2958 | | | |
| *N. cyclopion* x *N. rhombifera* (12 months) | W | *N. cyclopion* | 0.1679 | 0.87 | 108 | 0.3864 |
| | | *N. rhombifera* | 0.1745 | | | |
| | L | *N. cyclopion* | 1.3343 | 3.89 | 108 | 0.0001 |
| | | *N. rhombifera* | 0.9758 | | | |
| | SVL | *N. cyclopion* | 1.0028 | 4.78 | 108 | 0.0001 |
| | | *N. rhombifera* | 0.6800 | | | |
| | TL | *N. cyclopion* | 0.3316 | 1.16 | 108 | 0.2483 |
| | | *N. rhombifera* | 0.2958 | | | |

Table 17 (Continued)

| Groups | Parameter | Species | P-I Ratio | t | df | p |
|---|---|---|---|---|---|---|
| Intermediate Meal Size female | W | *N. fasciata* | 0.2393 | 1.75 | 94 | 0.0817 |
| | | *N. cyclopion* | 0.2253 | | | |
| | L | *N. fasciata* | 1.8146 | 4.06 | 94 | 0.0001 |
| *N. fasciata* x *N. cyclopion* (12 months) | | *N. cyclopion* | 1.4632 | | | |
| | SVL | *N. fasciata* | 1.4605 | 4.49 | 94 | 0.0001 |
| | | *N. cyclopion* | 1.1617 | | | |
| | TL | *N. fasciata* | 0.3541 | 2.16 | 94 | 0.0322 |
| | | *N. cyclopion* | 0.3015 | | | |
| *N. fasciata* x *N. rhombifera* (12 months) | W | *N. fasciata* | 0.2393 | 5.56 | 94 | 0.0001 |
| | | *N. rhombifera* | 0.1925 | | | |
| | L | *N. fasciata* | 1.8146 | 7.48 | 94 | 0.0001 |
| | | *N. rhombifera* | 1.1507 | | | |
| | SVL | *N. fasciata* | 1.4605 | 8.80 | 94 | 0.0001 |
| | | *N. rhombifera* | 0.8666 | | | |
| | TL | *N. fasciata* | 0.3541 | 2.76 | 94 | 0.0069 |
| | | *N. rhombifera* | 0.2841 | | | |
| *N. cyclopion* x *N. rhombifera* (12 months) | W | *N. cyclopion* | 0.2253 | 4.39 | 108 | 0.0001 |
| | | *N. rhombifera* | 0.1925 | | | |
| | L | *N. cyclopion* | 1.4632 | 3.86 | 108 | 0.0002 |
| | | *N. rhombifera* | 1.1507 | | | |
| | SVL | *N. cyclopion* | 1.1617 | 4.76 | 108 | 0.0001 |
| | | *N. rhombifera* | 0.8666 | | | |
| | TL | *N. cyclopion* | 0.3015 | 0.77 | 108 | 0.4444 |
| | | *N. rhombifera* | 0.2841 | | | |

Table 17 (Continued)

| Groups | Parameter | Species | P-I Ratio | t | df | p |
|---|---|---|---|---|---|---|
| Small Meal Size male | W | *N. fasciata* | 0.2109 | 6.68 | 63 | 0.0001 |
| | | *N. rhombifera* | 0.1455 | | | |
| *N. fasciata* x *N. rhombifera* (10 months) | L | *N. fasciata* | 1.8478 | 8.71 | 63 | 0.0001 |
| | | *N. rhombifera* | 1.0411 | | | |
| | SVL | *N. fasciata* | 1.4653 | 10.81 | 63 | 0.0001 |
| | | *N. rhombifera* | 0.7279 | | | |
| | TL | *N. fasciata* | 0.3824 | 2.31 | 63 | 0.0242 |
| | | *N. rhombifera* | 0.3133 | | | |
| Small Meal Size female | W | *N. fasciata* | 0.1859 | 0.32 | 50 | 0.7523 |
| | | *N. rhombifera* | 0.1784 | | | |
| *N. fasciata* x *N. rhombifera* (8 months) | L | *N. fasciata* | 2.0563 | 2.77 | 50 | 0.0078 |
| | | *N. rhombifera* | 1.7451 | | | |
| | SVL | *N. fasciata* | 1.7451 | 3.69 | 50 | 0.0006 |
| | | *N. rhombifera* | 1.0138 | | | |
| | TL | *N. fasciata* | 0.3112 | 0.27 | 50 | 0.7876 |
| | | *N. rhombifera* | 0.2902 | | | |

*Analysis of length increases.* As would be expected from previous discussions, the differences between the species varied between the sexes and between meal size groups. Among males fed the intermediate meal size, *N. fasciata* from Lake County, Tennessee had significantly higher P-I ratios for L and SVL than *N. cyclopion* and *N. rhombifera*. *Nerodia cyclopion* in turn had higher P-I ratios for L and SVL than *N. rhombifera*. There were no significant differences in the P-I ratios for TL although the difference between *N. fasciata* and *N. rhombifera* approached significance. With the small meal size for *N. fasciata* and *N. rhombifera* the results were the same except that the P-I ratio for TL was significantly higher for *N. fasciata* (Table 17).

Among females fed the intermediate meal size, *N. fasciata* had significantly higher P-I ratios for L, SVL, and TL than the other two species. *Nerodia cyclopion* had significantly higher P-I ratios for L and SVL than *N. rhombifera*, but not for TL. With the small meal size, female *N. fasciata* had significantly higher P-I ratios for L and SVL than *N. rhombifera*, but not for TL (Table 17).

Diagrams of the relationships of the P-I ratios of both males and females of the three species are shown in Figures 36 through 38. Generally, *N. fasciata* had the highest P-I ratios for length increases followed by *N. cyclopion* than *N. rhombifera* for both males and females. Under the circumstances, these results indicate that *N. fasciata* is the fastest growing species followed by *N. cyclopion* then *N. rhombifera*. Since the linear regressions that provided the P-I ratios were based on a maximum of one year's data, the results

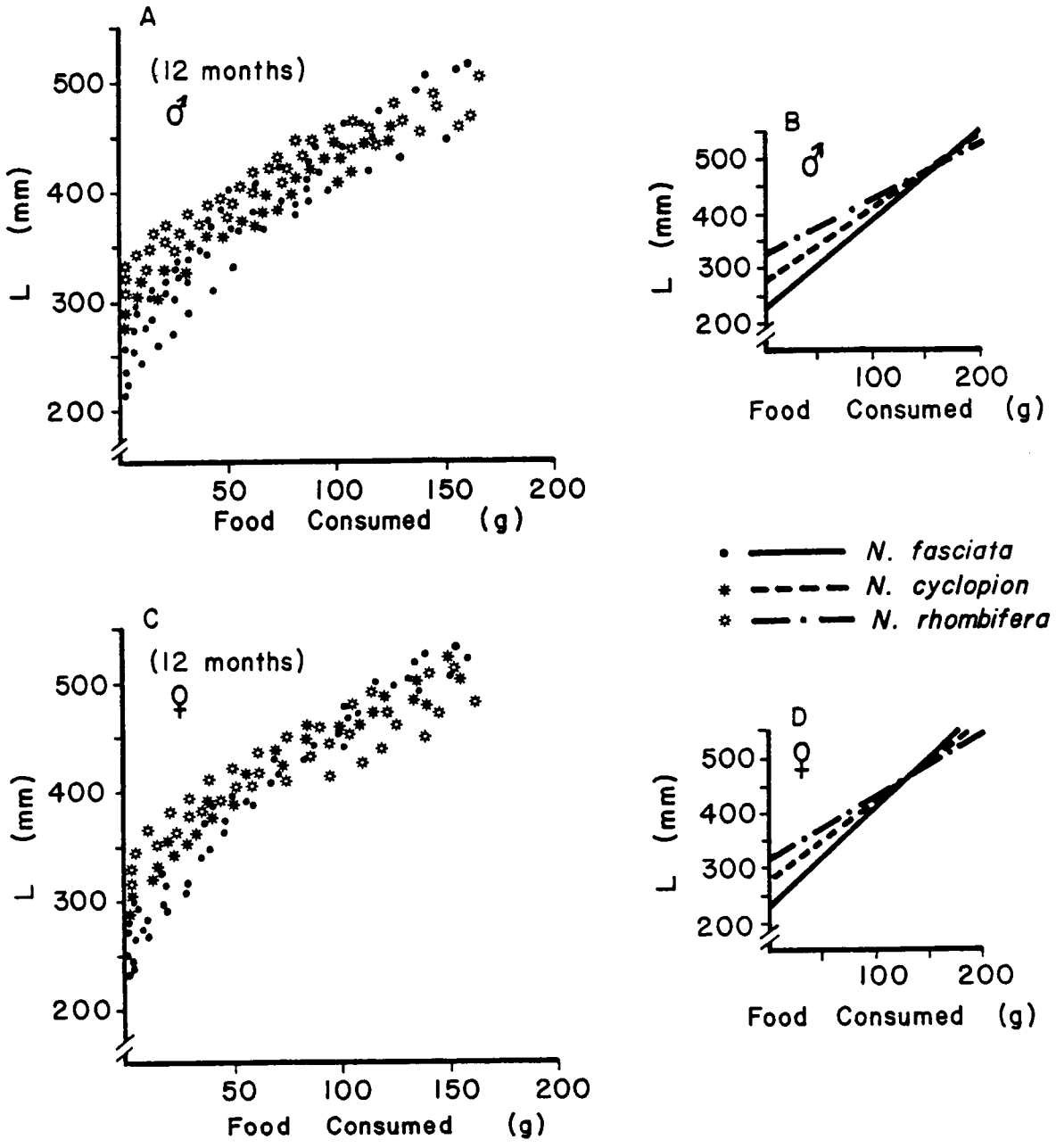



Figure 36. Variation in Growth in Total Length (L) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data for Males. B. The Regression Lines for Males. C. The Data for Females. D. The Regression Lines for Females.

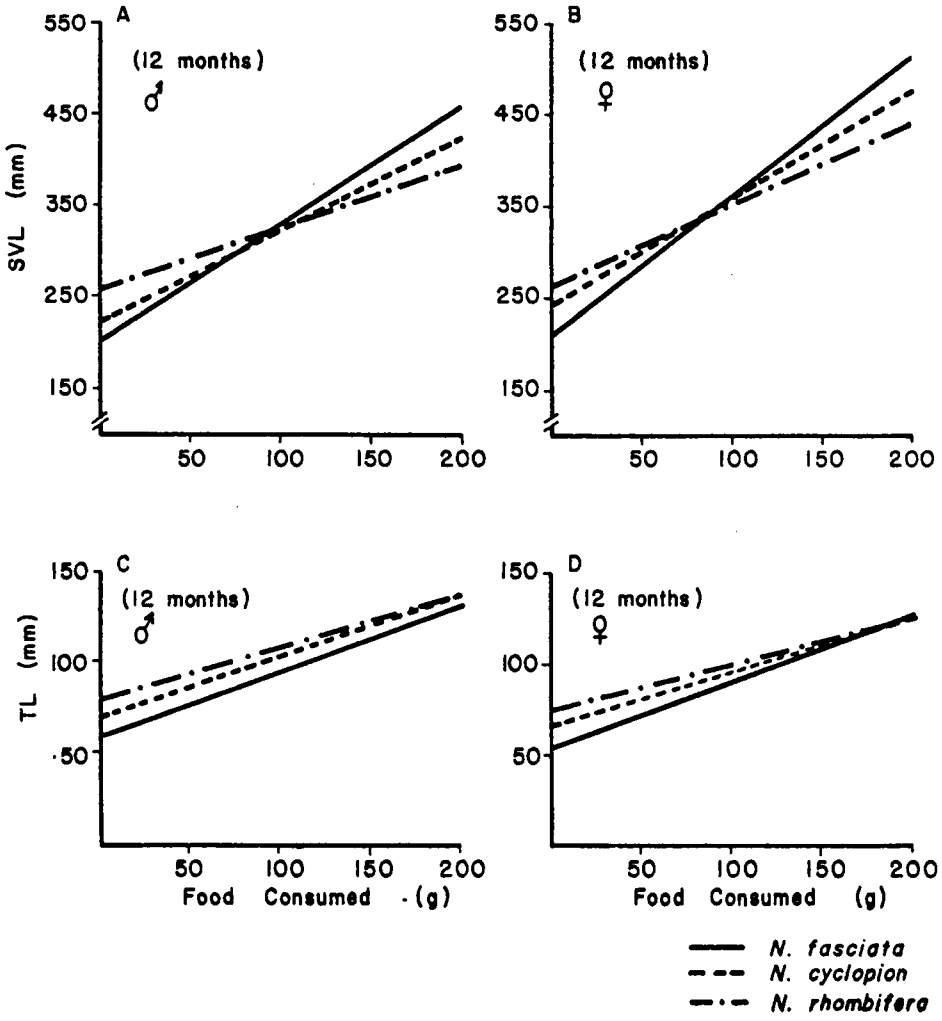



Figure 37. Variation in Growth in Snout-Vent Length (SVL) and Tail Length (TL) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. SVL for Males. B. SVL for Females. C. TL for Males. D. TL for Females.

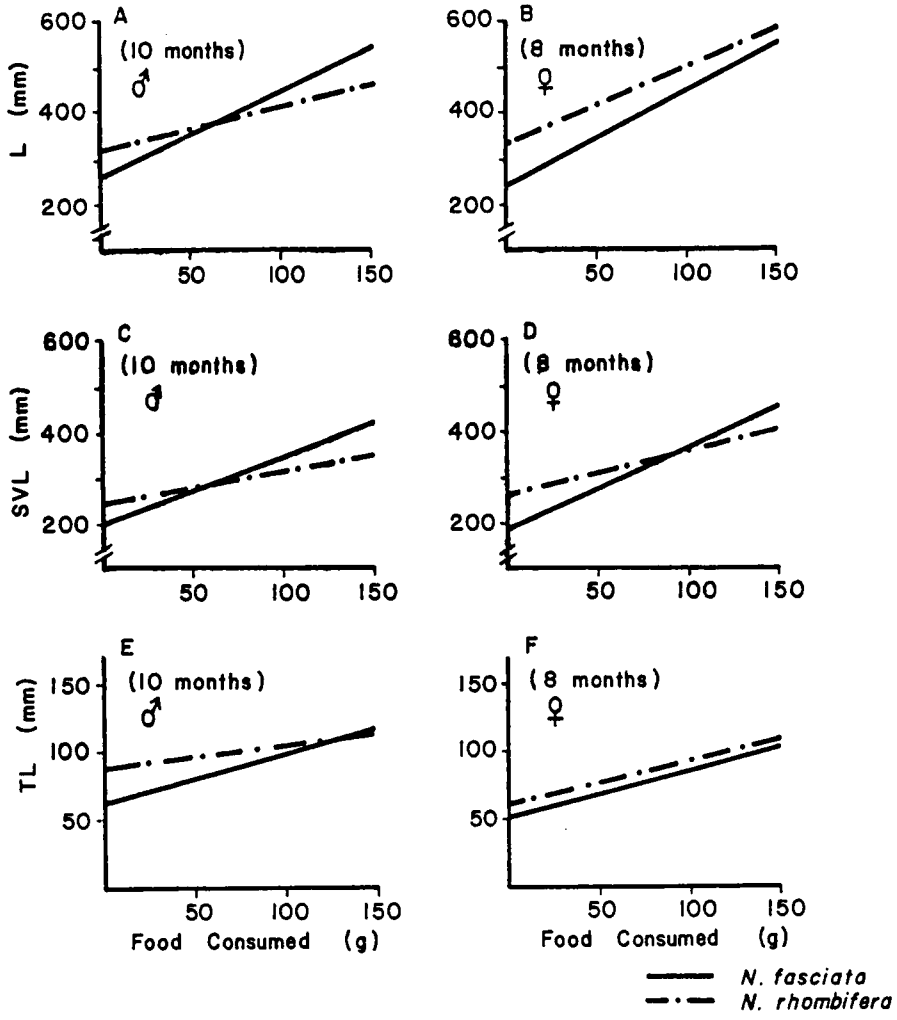



Figure 38. Variation in Growth in Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Two Species of *Nerodia* Fed the Small Meal Size. A. L for Males. B. L for Females. C. SVL for Males. D. SVL for Females. E. TL for Males. F. TL for Females.

can only apply to that time period. The P-I ratio is actually a continuously changing parameter, and these changes can be seen in the diagrams of growth for periods of longer duration than one year.

Figure 39 shows the growth curves for males of the three species of *Nerodia*. The curve of the lines indicates the changing P-I ratios of the three species, and the nature of the entire curve for each species can be described by the growth constant r. The curve for *N. fasciata* starts out with the steepest slope (highest P-I ratio), but eventually the slope of the curve diminishes as the asymptote is approached. At this point the slopes and therefore the P-I ratios of *N. cyclopion* and *N. rhombifera* exceed that of *N. fasciata*. The same changes occur with the females although the magnitude of the changes is different (Figure 40).

The change in the P-I ratios of the species can be looked at more simply by examining the values of the growth constant r (see Table 10, page 87). The r values for L for male *N. fasciata* and *N. cyclopion* were significantly larger than that for *N. rhombifera*. Although the r value for L was larger for *N. fasciata*, the 95% confidence interval for r overlaps with the 95% confidence interval for r for *N. cyclopion*. The difference in the r value for these two species was therefore probably not significant. In terms of relative growth rates, the r values indicate that generally *N. fasciata* was the fastest growing species followed by *N. cyclopion* then *N. rhombifera*. The same generalization can be made for growth in SVL and TL (see Figure 41).

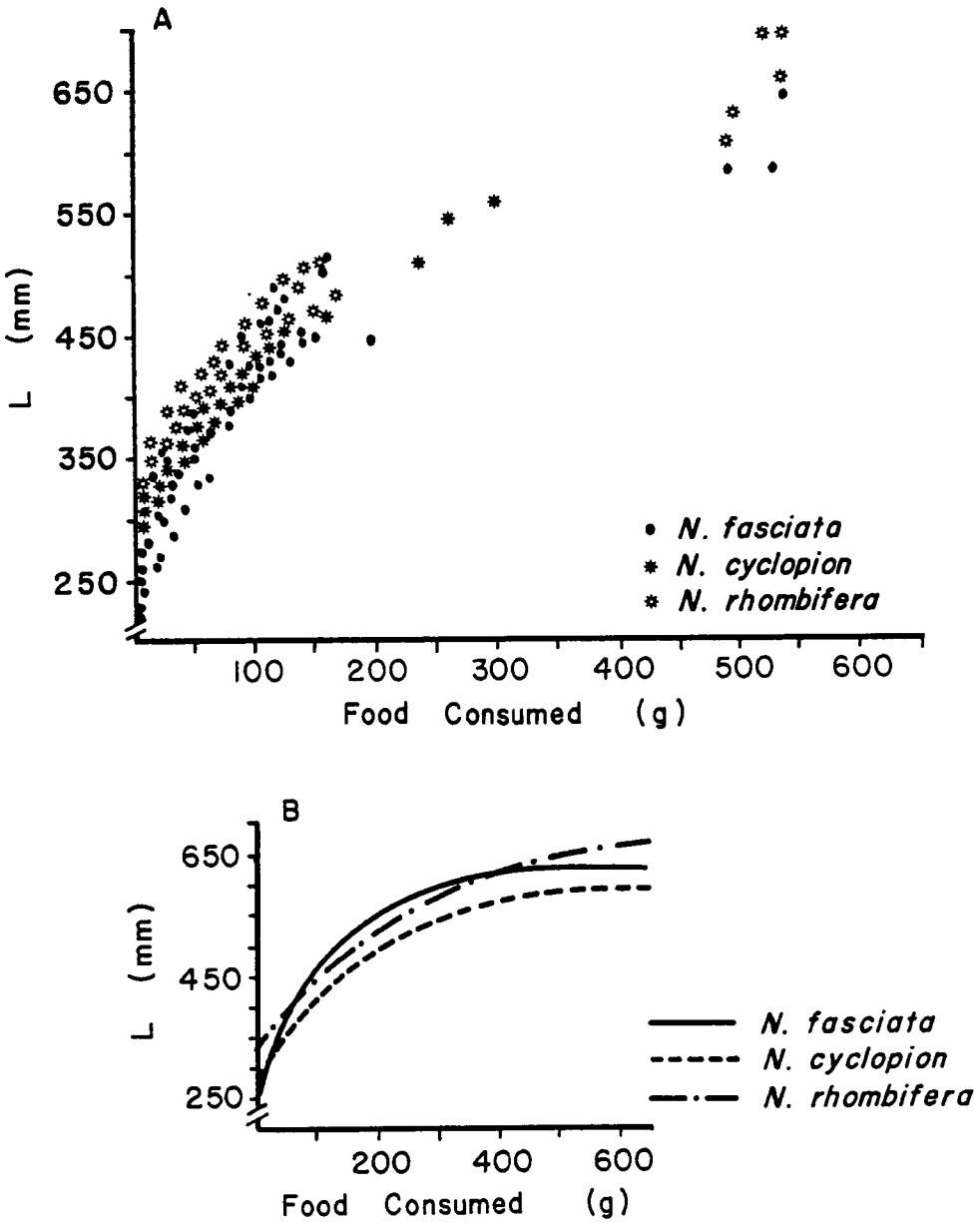



Figure 39. Growth Curves for Total Length (L) for Males of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines.

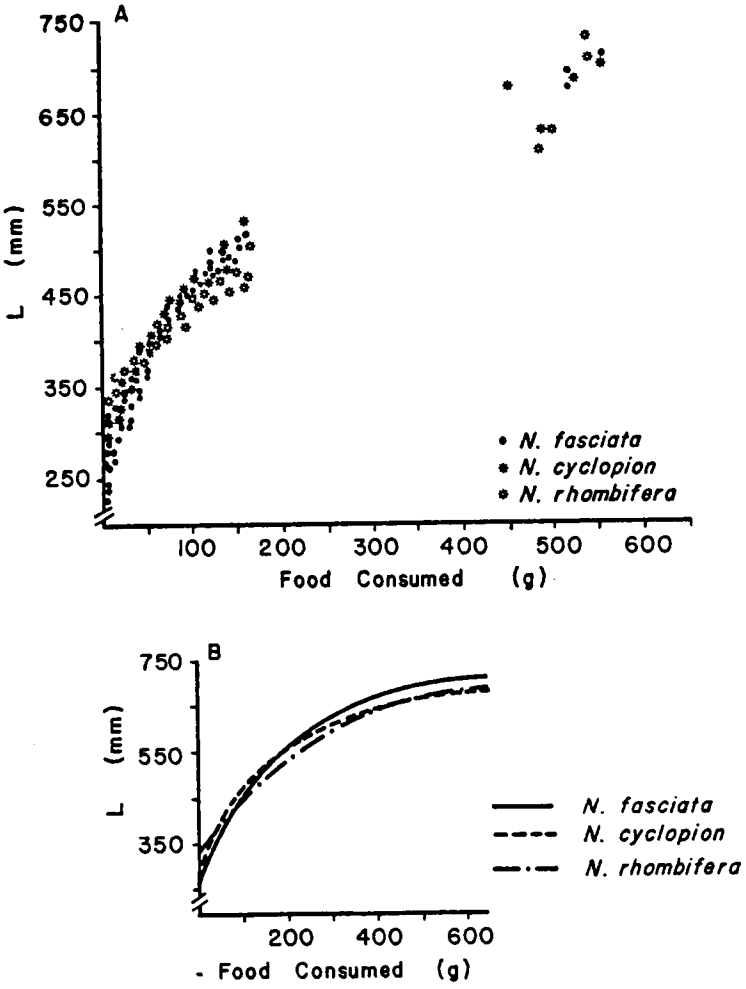



Figure 40. Growth Curves for Total Length (L) for Females of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines.

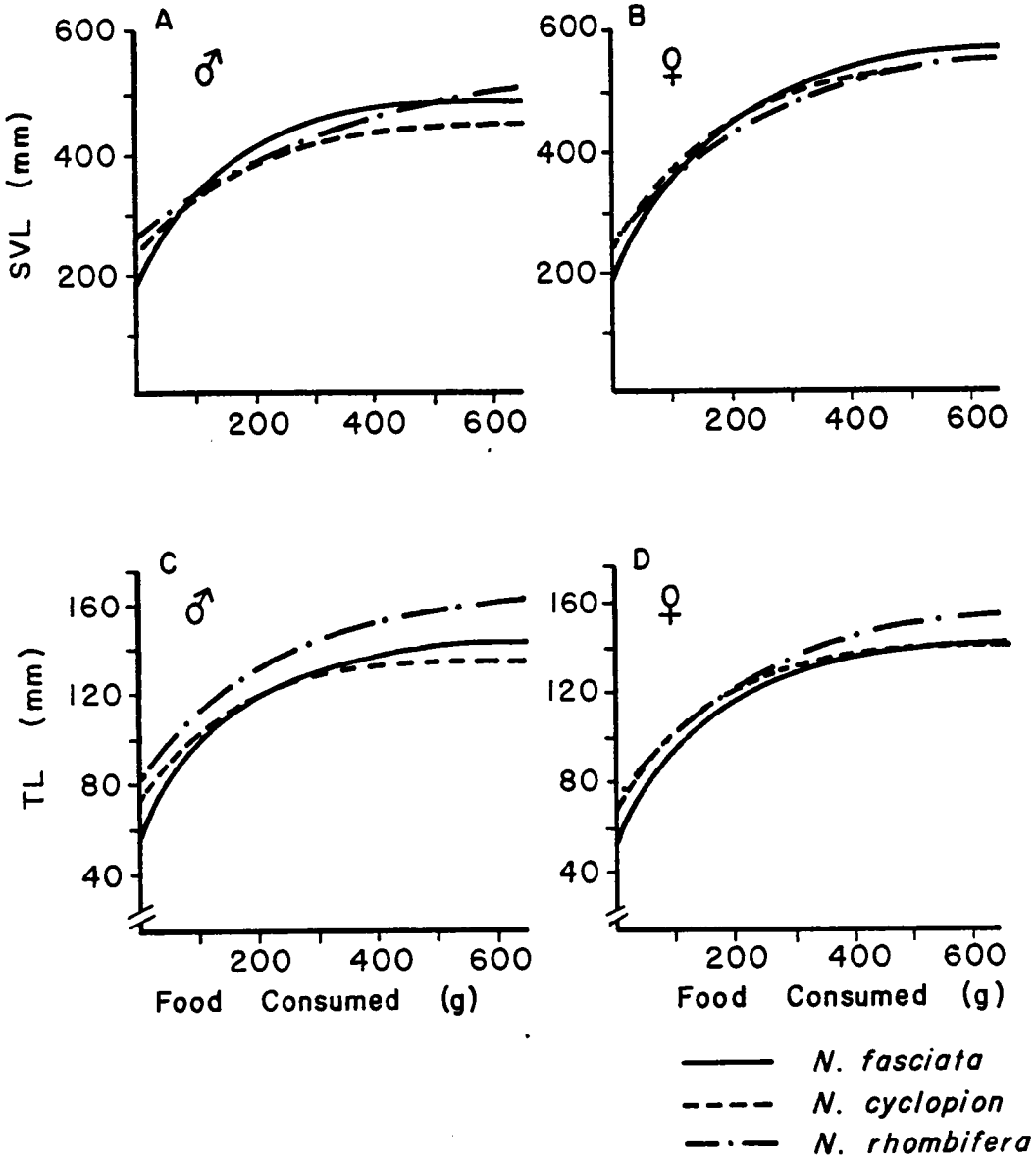



Figure 41. Growth Curves for Snout-Vent Length (SVL) and Tail Length (TL) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. SVL for Males. B. SVL for Females. C. TL for Males. D. TL for Females.

The estimated asymptotes for L, SVL, and TL are significantly greater for male *N. rhombifera* than for male *N. fasciata* and *N. cyclopion*. These results were the only significant differences for asymptotes (see Table 10, page 87). The fact that there were no significant differences among the species for most of the growth parameters is more indicative of the need to collect more data than of the similarity of the adult sizes of the species (see pages 86 and 89). Allowing the snakes more time to grow would undoubtedly change the estimates of the asymptotes.

*Analysis of weight increases*. Increases in W generally showed the same trends as increases in length (see Table 17, pages 116-118). In males fed the intermediate meal size, *N. fasciata* had a significantly higher P-I ratio than *N. cyclopion* and *N. rhombifera*. The difference in the P-I ratios for *N. cyclopion* and *N. rhombifera* were not significant (Figure 42A and 42B). Among females fed the intermediate meal size, *N. fasciata* and *N. cyclopion* had higher P-I ratios for W than *N. rhombifera*. The difference in the P-I ratios for *N. fasciata* and *N. cyclopion* only approached significance (Figure 42C and 42D). Among the small meal size groups, male *N. fasciata* had a significantly higher P-I ratio for W than male *N. rhombifera*. The difference between females of these two species was not significant (see Table 17, page 116).

As with length, the higher P-I ratio for *N. fasciata* can only be applied to the early stages of growth. The growth curves for W for males and females respectively are shown in Figures 43 and 44.

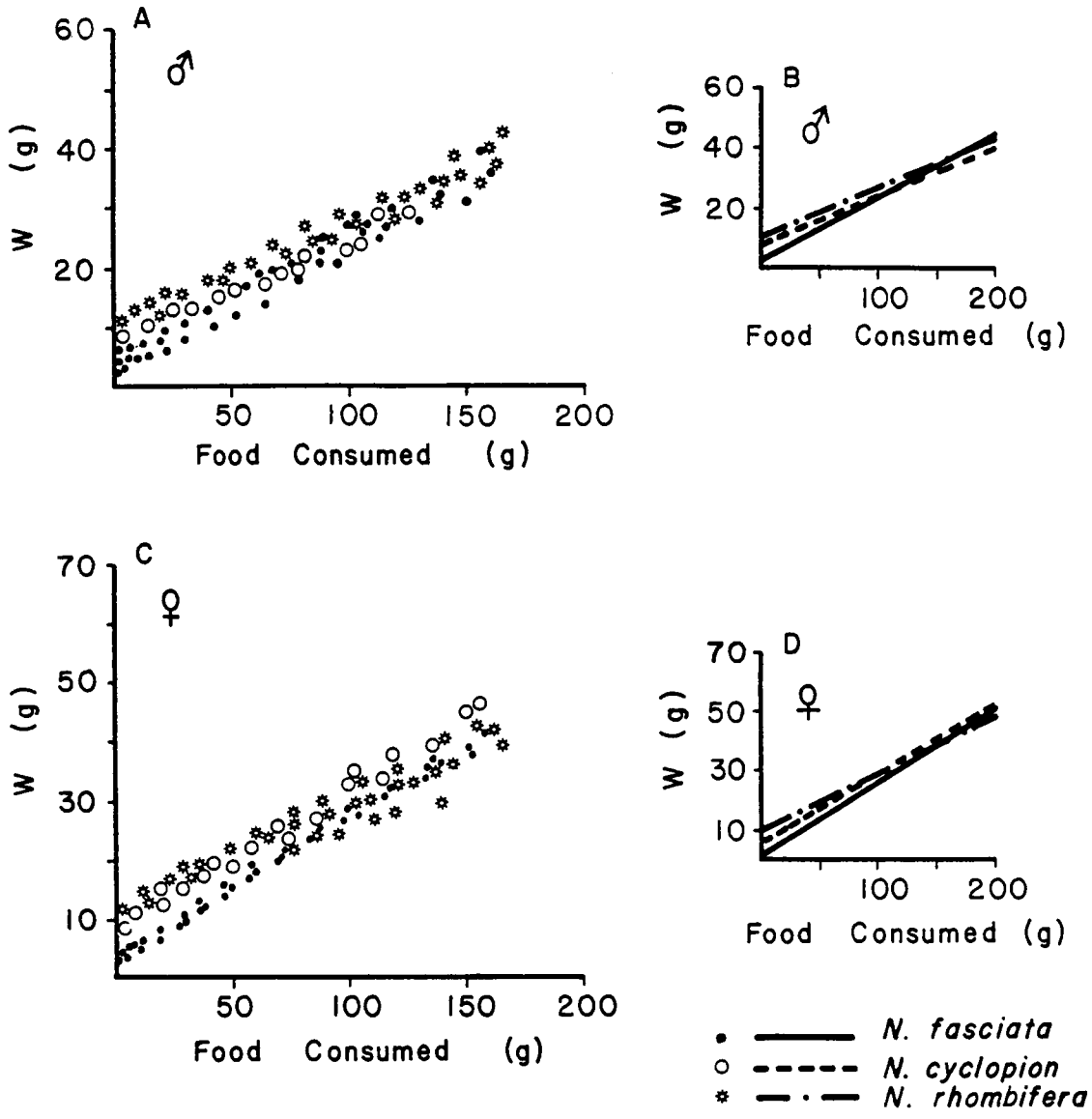



Figure 42. Variation in Growth in Weight (W) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data for Males. B. The Regression Lines for Males. C. The Data for Females. D. The Regression Lines for Females.

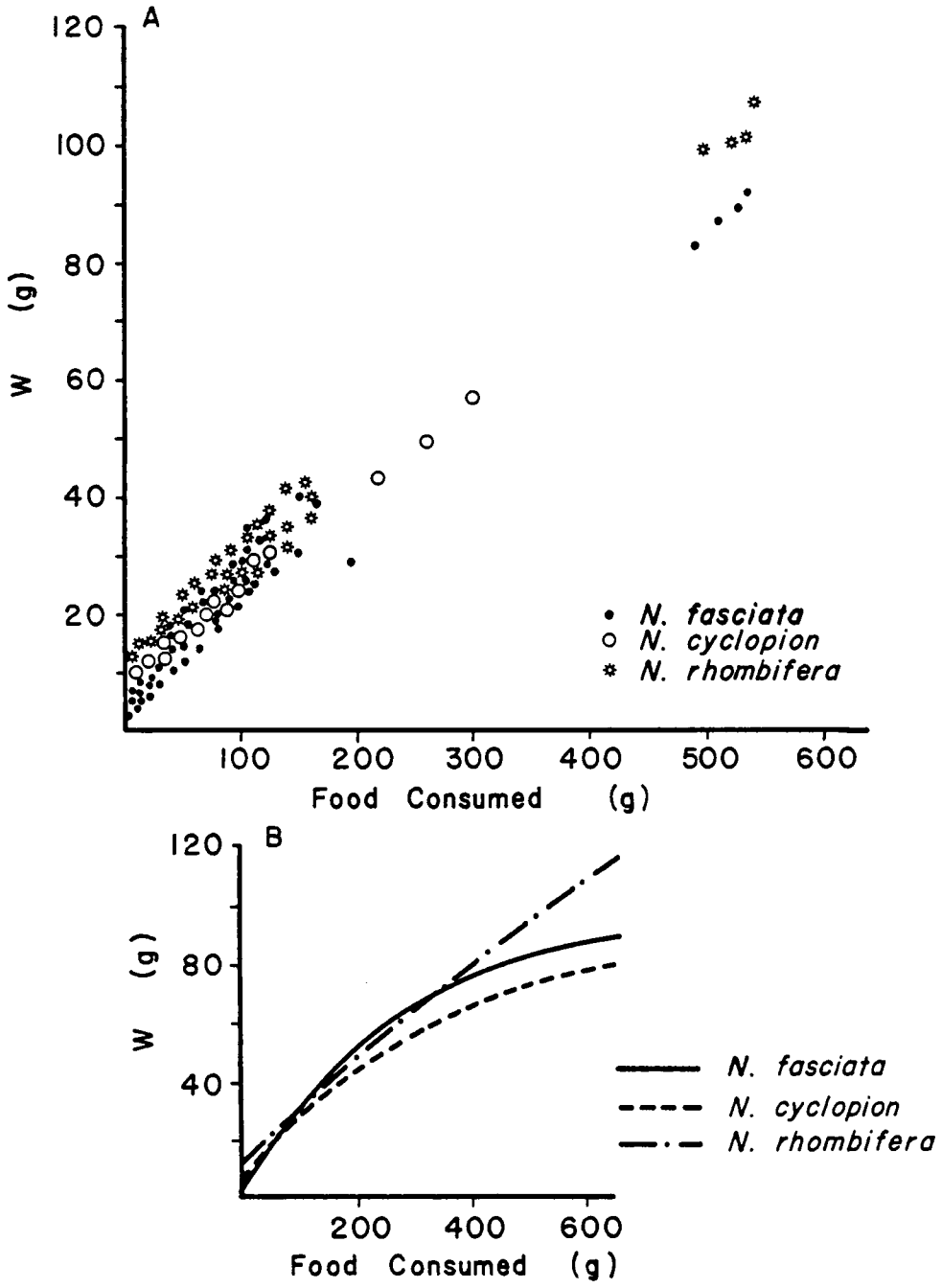



Figure 43. Growth Curves for Weight (W) for Males of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines.

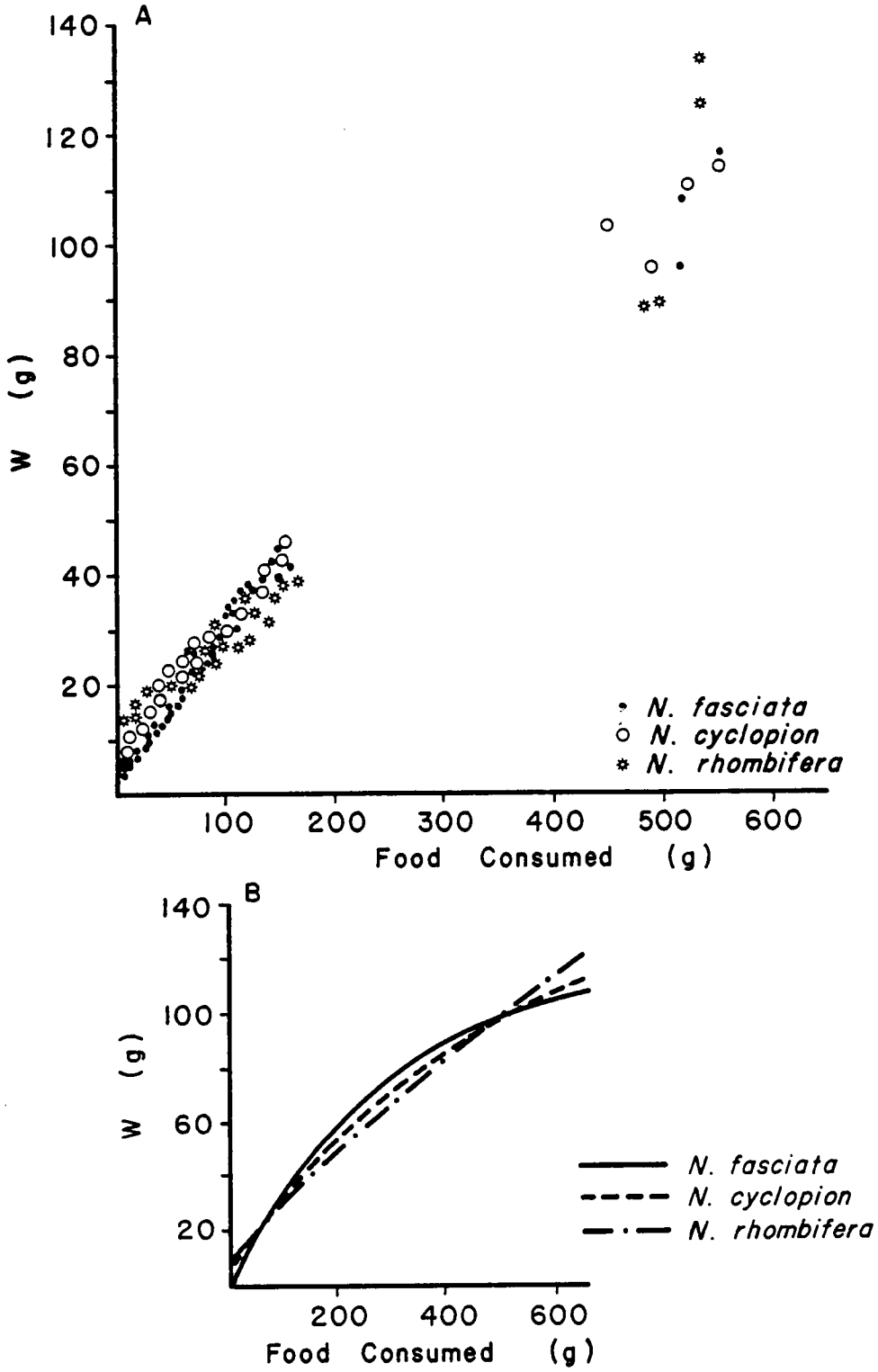



Figure 44. Growth Curves for Weight (W) for Females of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines.

The r values of the growth curves are indicative of the changing P-I ratios for W for the three species. Since the Bertalanffy growth model is based on increases in length and is modified for weight increases, the r values used for construction of the growth curve for W were those for SVL. The r values for SVL as discussed above in "Analysis of length increases" were highest for *N. fasciata* followed by *N. cyclopion* then *N. rhombifera* (see Table 10, page 87). The size of the r values indicate that *N. fasciata* will reach its asymptotic W sooner than will *N. cyclopion* and *N. rhombifera*, and consequently will show the most rapid change in the P-I ratio as the snakes grow. This greater rate of change in the P-I ratio is evident in the greater curvature in the growth curves for *N. fasciata* than for the other two species (see Figures 43 and 44). *Nerodia fasciata*, therefore, not only has a faster absolute growth rate, at least at younger ages, but also has a faster relative growth rate.

In terms of W/SVL, among snakes fed the intermediate meal size *N. rhombifera* had the largest rate of increase in both males and females (see Table 18). Males and females differed as to which species had the second largest rate of increase in W/SVL. Among males, *N. fasciata* had a significantly larger rate of increase in W/SVL than *N. cyclopion*. In females the opposite was true (Table 18). Among snakes fed the small meal size, male *N. rhombifera* had a significantly larger rate of increase in W/SVL than male *N. fasciata*. There was no difference between the females of these two species.

Graphic representations of the differences in W/SVL for snakes fed the intermediate meal size are shown in Figures 45 and 46. The

Table 18

Comparisons of the Rate of Increase in Weight Per Unit Length (W/SVL) by Species for Three Species of *Nerodia*

| Meal Size | Sex | Species | Slope* ($\times 10^7$) | t | df | p |
|---|---|---|---|---|---|---|
| Intermediate | ♂ | *N. fasciata*<br>*N. cyclopion* | 7.47<br>6.66 | 3.08 | 116 | 0.0024 |
| | | *N. fasciata*<br>*N. rhombifera* | 7.47<br>8.81 | 5.73 | 116 | 0.0001 |
| | | *N. cyclopion*<br>*N. rhombifera* | 6.66<br>8.81 | 7.72 | 116 | 0.0001 |
| | ♀ | *N. fasciata*<br>*N. cyclopion* | 6.10<br>6.52 | 3.11 | 101 | 0.0022 |
| | | *N. fasciata*<br>*N. rhombifera* | 6.10<br>7.60 | 10.26 | 101 | 0.0001 |
| | | *N. cyclopion*<br>*N. rhombifera* | 6.52<br>7.60 | 7.38 | 116 | 0.0001 |
| Small | ♂ | *N. fasciata*<br>*N. rhombifera* | 6.84<br>9.05 | 6.51 | 62 | 0.0001 |
| | ♀ | *N. fasciata*<br>*N. rhombifera* | 5.71<br>5.72 | 0.08 | 50 | 0.9356 |

*The numbers presented here are the values of the slope of the regression of W/SVL on $SVL^2$.

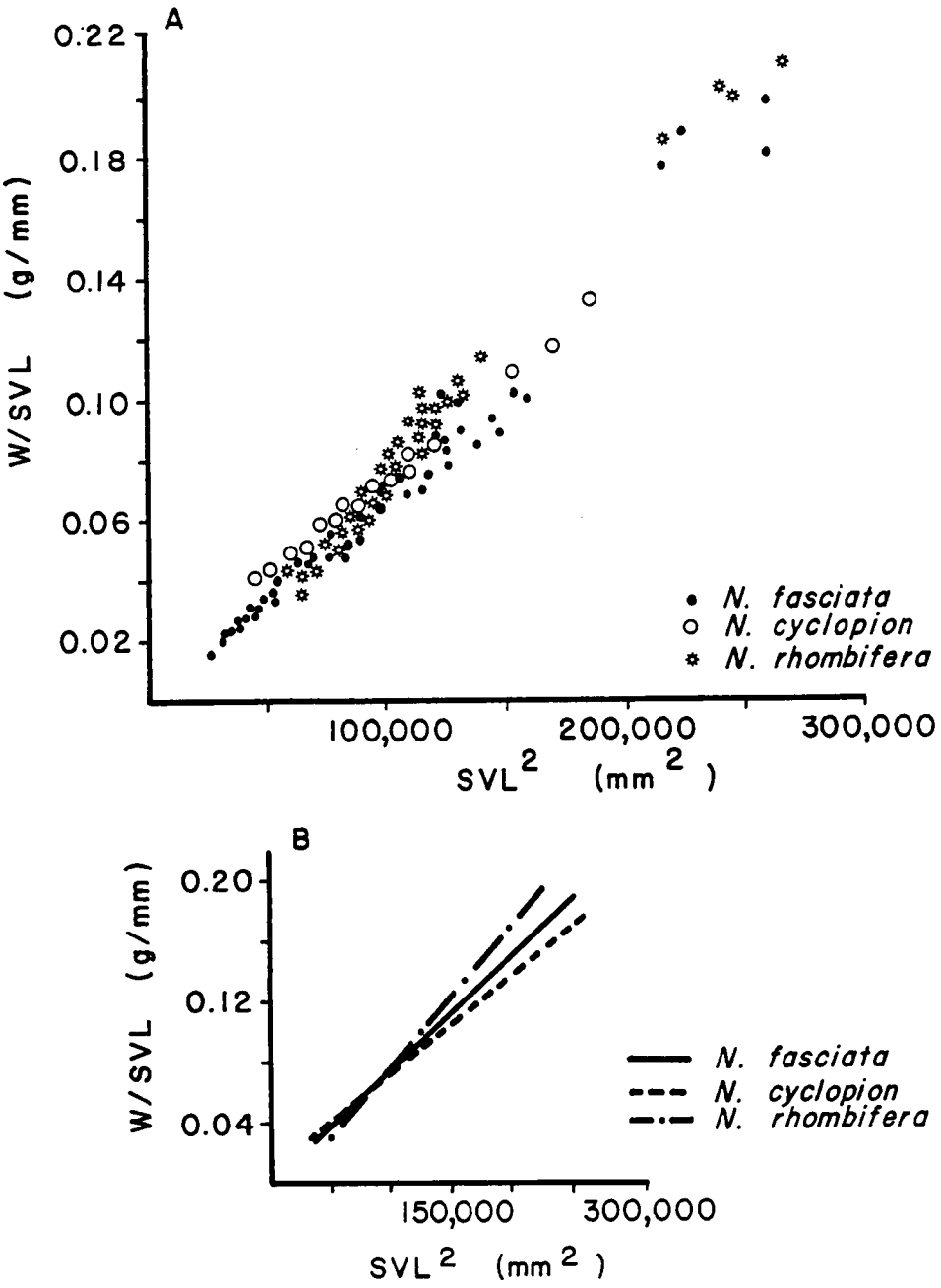



Figure 45. Variation in Growth in Weight Per Unit Length (W/SVL) for Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines.

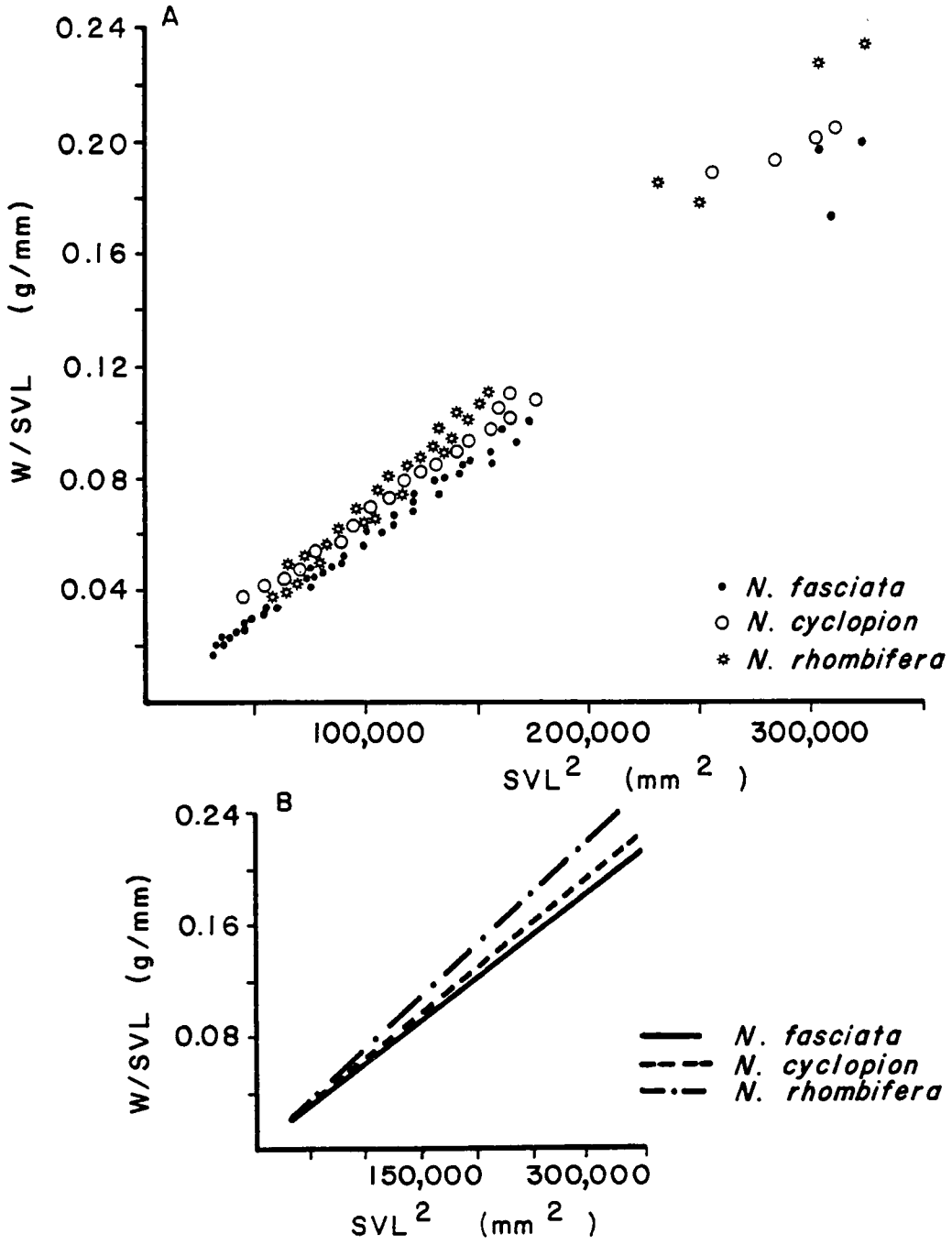



Figure 46. Variation in Growth in Weight Per Unit Length (W/SVL) for Females of Three Species of *Nerodia* Fed the Intermediate Meal Size. A. The Data. B. The Regression Lines.

figures show that as the snakes increased in size, *N. rhombifera* became heavier-bodied than the other two species. They also show that among the males, *N. fasciata* was heavier-bodied than *N. cyclopion* at larger SVLs, and that the reverse was true for females. A summary of the results of species variation in growth can be found in Tables 19 and 20.

*Dietary Assimilation Efficiency*

The results up to this point have dealt with increases in body proportions in relation to the amount of food consumed. The amount of food consumed, however, is only a crude measure of the amount of energy available for growth. A more accurate measure is obtained by comparing the food intake with the fecal output in terms of weight and calories. The possibility that shifts in P-I ratios with changing meal size were due to drops in the assimilation efficiency was discussed earlier (page 61). The differences in the P-I ratios between the sexes and among the species could also be due to differences in the assimilation efficiencies of the snakes. Values for weight and caloric assimilation efficiencies for the experimental groups can be found in Table 21. Probably the most salient characteristic of the assimilation efficiency values is their lack of correspondence with the P-I ratios discussed earlier. Where before there were very large differences between groups in their P-I ratios, there are only very small differences in their assimilation efficiencies. (Compare the P-I ratios for *N. fasciata* males and females from Shelby County, Tennessee, Table 8, page 74 with their assimilation

Table 19

Summary of the Results of Species Variation in the Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), Tail Length (TL), and Weight Per Unit Length (W/SVL) in Three Species of *Nerodia* from Lake County, Tennessee[1,2]

| Meal Size | Sex | W | L | SVL | TL | W/SVL |
|---|---|---|---|---|---|---|
| Intermediate Meal Size | | | | | | |
| *N. fasciata* x *N. cyclopion* | ♂ | S*** (f) | S** (f) | S*** (f) | NS (f) | S** (f) |
| *N. fasciata* x *N. rhombifera* | ♂ | S*** (f) | S*** (f) | S*** (f) | NS (f) | S*** (r) |
| *N. cyclopion* x *N. rhombifera* | ♂ | NS (r) | S*** (c) | S*** (c) | NS (c) | S*** (r) |
| *N. fasciata* x *N. cyclopion* | ♀ | NS (f) | S*** (f) | S*** (f) | S* (f) | S** (c) |
| *N. fasciata* x *N. rhombifera* | ♀ | S*** (f) | S*** (f) | S*** (f) | S* (f) | S*** (r) |
| *N. cyclopion* x *N. rhombifera* | ♀ | S*** (c) | S*** (c) | S*** (c) | NS (c) | S*** (c) |
| Small Meal Size | | | | | | |
| *N. fasciata* x *N. rhombifera* | ♂ | S*** (f) | S*** (f) | S*** (f) | S* (f) | S*** (r) |
| *N. fasciata* x *N. rhombifera* | ♀ | NS (f) | S* (f) | S** (f) | NS (f) | NS (r) |

[1] S* = Significant difference, $P < 0.05$.
S** = Significant difference, $P < 0.005$.
S*** = Significant difference, $P < 0.0005$.

[2] NS = No significant difference, $P > 0.05$.
Symbols in parentheses represent the species with the higher P-I ratio for that growth parameter: f = *N. fasciata*; c = *N. cyclopion*; r = *N. rhombifera*.

Table 20

Summary of the Results of Species Variation in the Estimates of the Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) in Three Species of *Nerodia* from Lake County, Tennessee Fed the Intermediate Meal Size[1,2]

| Species | Sex | Asymptote | | | | r | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | W | L | SVL | TL | W | L | SVL | TL |
| *N. fasciata* x *N. cyclopion* | ♂ | S (f) | NS (f) | NS (f) | NS (c) | NS (f) | NS (f) | NS (f) | NS (f) |
| *N. fasciata* x *N. rhombifera* | ♂ | S (r) | S (r) | S (r) | S (r) | S (f) | S (f) | S (f) | S (f) |
| *N. cyclopion* x *N. rhombifera* | ♂ | S (r) | S (r) | S (r) | S (r) | S (c) | S (c) | S (c) | NS (c) |
| *N. fasciata* x *No cyclopion* | ♀ | NS (c) | NS (f) | NS (f) | NS (f) | NS (f) | NS (f) | NS (f) | NS (f) |
| *N. fasciata* x *N. rhombifera* | ♀ | S (r) | NS (r) | NS (r) | NS (r) | S (f) | S (f) | S (f) | NS (f) |
| *No cyclopion* x *No rhombifera* | ♀ | S (r) | NS (r) | NS (r) | NS (r) | S (c) | S (c) | S (c) | NS (c) |

[1] S = Significant difference, $p < 0.05$.

[2] NS = No significant difference, $p > 0.05$.

Symbols in parentheses represent the species with the higher estimates of the asymptote and growth constant: f = *N. fasciata*; c = *N. cyclopion*; r = *N. rhombifera*. All data are for two years.

Table 21

Weight and Caloric Assimilation Efficiencies
for Three Species of *Nerodia*

| Species | Sex | Date[1] | % Assimilation | |
|---|---|---|---|---|
| | | | Weight | Calories |
| *N. fasciata* (Shelby County, Tennessee) | ♂ | Fall 1980 | 80.2 | 94.0 |
| | | Summer 1981 | 85.5 | 97.1 |
| | | Fall 1981 | 77.3 | 94.6 |
| *N. fasciata* (Shelby County, Tennessee) | ♀ | Fall 1980 | 83.7 | 95.4 |
| | | Summer 1981 | 96.2 | 96.9 |
| | | Fall 1981 | 75.9 | 93.1 |
| *N. fasciata* (Lake County, Tennessee) Intermediate Meal Size | Both | Fall 1980 | 82.0 | 92.8 |
| | | Summer 1981 | 85.3 | 94.3 |
| | | Fall 1981 | 80.2 | 91.8 |
| *N. cyclopion* Intermediate Meal Size | Both | Fall 1980 | 86.9 | 94.5 |
| | | Summer 1981 | 83.1 | 95.0 |
| | | Fall 1981 | 81.2 | 94.0 |
| *N. rhombifera* | Both | Fall 1980[2] | 90.4 | 96.2 |
| | | Summer 1981 | 82.3 | 94.1 |
| | | Fall 1981 | 78.7 | 94.1 |
| *N. fasciata* Small Meal Size | Both | Fall 1980 | 84.6 | 96.2 |
| | | Summer 1981 | 89.2 | 96.5 |
| *N. rhombifera* Small Meal Size | Both | Fall 1980[2] | 86.8 | 95.4 |
| | | Summer 1981 | 91.7 | 97.2 |

[1]Fall 1980 = September 12 to October 10.
Summer 1981 = May 8 to June 5.
Fall 1981 = September 25 to October 23.
[2]October 16 to November 14.

efficiencies). This result certainly indicates that the differences in growth among groups do not occur at the level of digestion and absorption of nutrients, but at the level of the use of these materials for maintenance and growth. The caloric assimilation efficiency was also always larger than the assimilation efficiency for weight. This result is not surprising since it is expected that the snakes would extract as much usable energy (proteins, carbohydrates, and fats) as possible from their food and discard the less digestible portions (scales, bones).

*Discussion*

Analysis of the results of these experiments involved a large number of comparisons. By itself, any one of the comparisons has little meaning, but as a group they present a fairly clear picture of the growth potentialities of these snakes. Of primary importance with regard to meal size is the shift in the allocation of energy for growth. Under conditions of readily available resources (large meal size), the snakes allocated more energy to increases in W than when resource availability was restricted (intermediate and small meal sizes). In contrast more energy was allocated to increases in length when resource availability was restricted than when resources were readily available. This phenomenon has some important implications with regard to reproduction, particularly in females. Clutch size in female snakes increases with SVL (Klauber 1956, Feaver 1977, Semlitsch and Gibbons 1982), and whether or not a female reproduces in a given year is very much dependent on its energy reserves since

undernourished or injured females may require a longer gestation period (Feaver 1977) or may not reproduce at all (Smith 1976). With this information in mind, the shift in energy allocation between growth in weight and growth in length can be seen as a possible means of optimizing reproductive output. In years with high resource availability, it would be advantageous to gain weight as efficiently as possible to ensure enough energy reserves for successful completion of gestation and parturition. In years when resource availability is low, it may be more advantageous to forego reproduction entirely because of the possibility of losing a brood due to low energy reserves. In this situation, allocating more energy for increases in length would allow more young to be produced in subsequent years when resource availability was again high. Such a strategy is speculative and may not be used in natural populations, but it is intriguing and appears possible, especially since females seem to be more highly sensitive to changes in the feeding regimen.

Sexual and species variations in growth patterns demonstrate some of the variety in ways of attaining different body sizes. Females attain larger body sizes than their male conspecifics by initially having a higher P-I ratio for all of the growth parameters except TL, having a slower decline in the P-I ratio with time, and continuing to grow for a longer period of time. *Nerodia rhombifera* attains a larger body size than *N. fasciata* and *N. cyclopion* by having a slower decline in the P-I ratio with time, and possibly by growing for a longer period of time. The P-I ratios for *N. rhombifera*, however, were initially smaller than those for the other species.

The probable explanations for the growth pattern of females in relation to males are largely reproductive. Larger size in both weight and length means larger, and in all probability, more successful clutches. The explanations for the growth pattern of males are far more problematic since to a large extent it is not known how size affects the reproductive success of males. From the data collected here it would seem that the relative size of the tail is important to reproductive success in males, but in what specific way is largely a matter of conjecture.

Explanations for the differences in the growth patterns among the species are also largely a matter of conjecture. To understand the differences in the growth patterns requires detailed ecological information of the species at all stages of life. There are some things that can be considered at this time, however. The first consideration is predation. The individual *N. fasciata* from Lake County, Tennessee were all between 2 and 5 g in weight at birth. The *N. cyclopion* and *N. rhombifera* were between 6 and 10 g and 8 and 12 g respectively. The small size of *N. fasciata* at birth means that it will be subject to predation by a number of predators that are not a threat to larger snakes for a longer period of time (Feaver 1977). Since the three litters examined are from the same area, they may be subject to similar predation pressure. The initial rapid growth of *N. fasciata* may be a means of escaping from predators that can only take small individuals.

Another consideration is competition. Mushinsky et al. (1982) observed that young of *N. fasciata*, *N. erythrogaster*, *N. cyclopion*,

and *N. rhombifera* form a single feeding unit eating the same prey species in the same areas until a certain size is attained. The rapid growth of *N. fasciata* would serve to remove it from this common feeding pool where competition may be high if resource availability is restricted. There are certainly many other considerations that shape the growth patterns of these species, but as yet not enough details of the ecological requirements of each species are known to discuss them with any confidence.

# CHAPTER 5

# INDIVIDUAL VARIATION IN GROWTH

## *Introduction*

In previous discussions the data were analyzed collectively for animals with similar backgrounds (e.g., *N. fasciata* males from Lake County, Tennessee fed the intermediate meal size). Although it is certainly desirable to summarize the results for a group of animals that have been treated similarly, a great deal of information can be lost in the process. In this case, a look at the variation between individuals provides a glimpse of the raw material available for selection and consequently for evolution.

The following discussion was drawn from the data for *N. fasciata* from Shelby County, Tennessee because the greatest number of individuals and growth data of the longest duration were available for comparisons in this group. The emphasis is on the variation among males in this group. Most of the information concerning variation among the females and the information concerning the other experimental groups can be found in the Appendix.

## *Individual Variation in N. fasciata*

A comparison of some of the phenomena associated with increases in W and SVL gives some idea of the amount of individual variation that exists. After four years of growth, W in male *N. fasciata* ranged from 67.7 to 129.6 g (see Figure 6, page 38) and SVL ranged

from 475 to 558 mm (see Figure 8, page 40). It may be guessed, and rightly so, that the differences in W and SVL reflect the amount of food that each individual had consumed during the four years. The amount of food consumed, however, is only a partial explanation for this phenomenon. Figure 47 shows the plots of W and SVL on the weight of food consumed for the first year of growth. The regression lines for these data sets explain a very large proportion of the variation in the data points and appear to be reasonable summarizations of the data sets. The data for individuals can be extracted from these data sets and the individual regression lines thus generated can be compared for differences in slope (P-I ratio). The individual regression lines are shown in Figures 48 and 49.

The extent of the variation in the individual P-I ratios for W, SVL, L, and TL is shown in Tables 22-25. The values in Tables 22-25 are the P-I ratios for each individual for the first year of growth. More specific information concerning individual differences in the P-I ratios for all of the growth parameters for males and females can be found in Tables A-1 and A-2 respectively in the Appendix.

The possibility exists that there is a relationship between the P-I ratios and the amount of food consumed so that the higher P-I ratios are due, to a large extent, to the fact that a particular snake consumed more food. There could also be an inverse relationship between the P-I ratios and the weight of food consumed. Figure 50 shows the P-I ratios for W and SVL for individual males plotted on the total weight of food consumed for the first year of

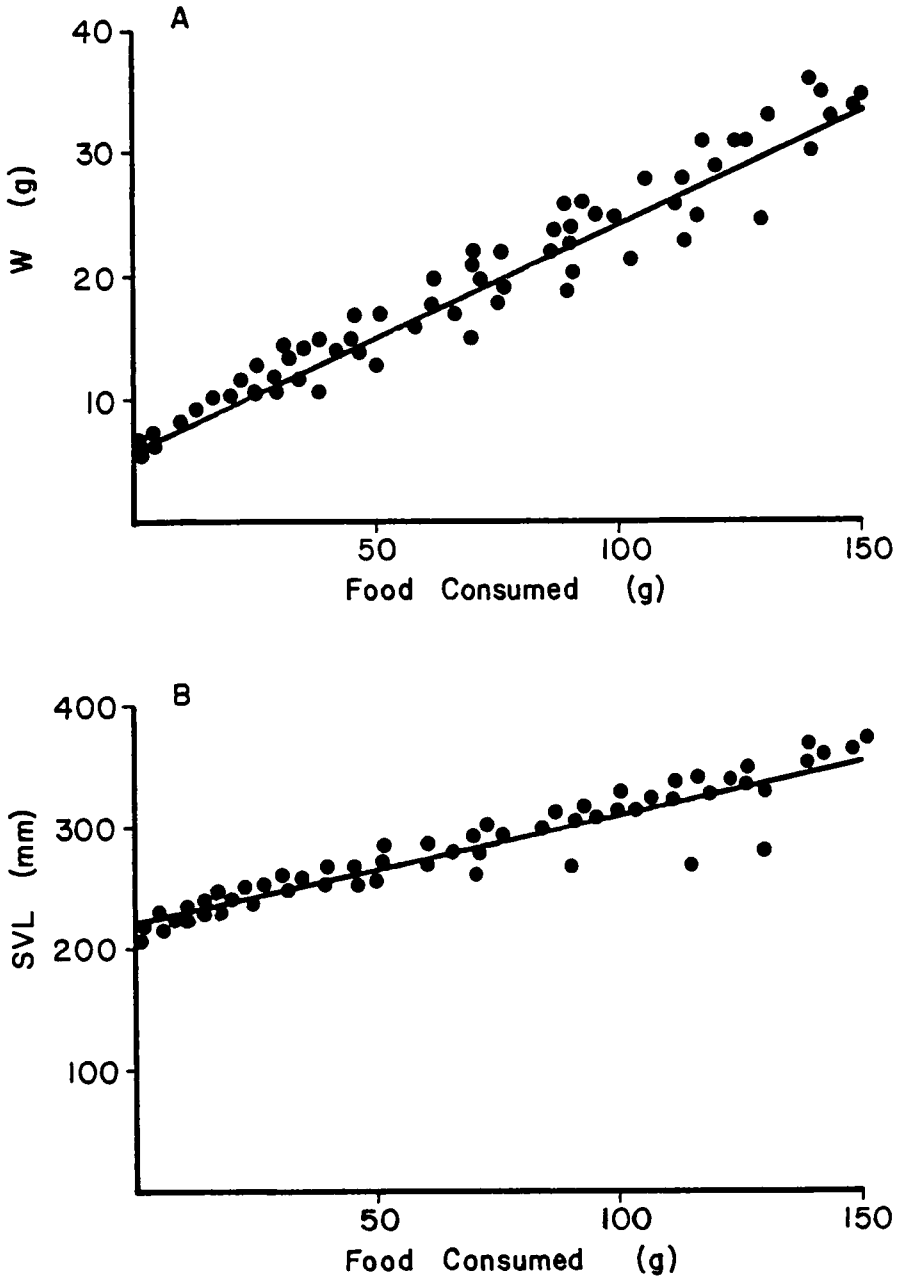



Figure 47. Weight (W) and Snout-Vent Length (SVL) as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee. A. Weight. B. Snout-Vent Length. Data Represent 12 Months of Growth.

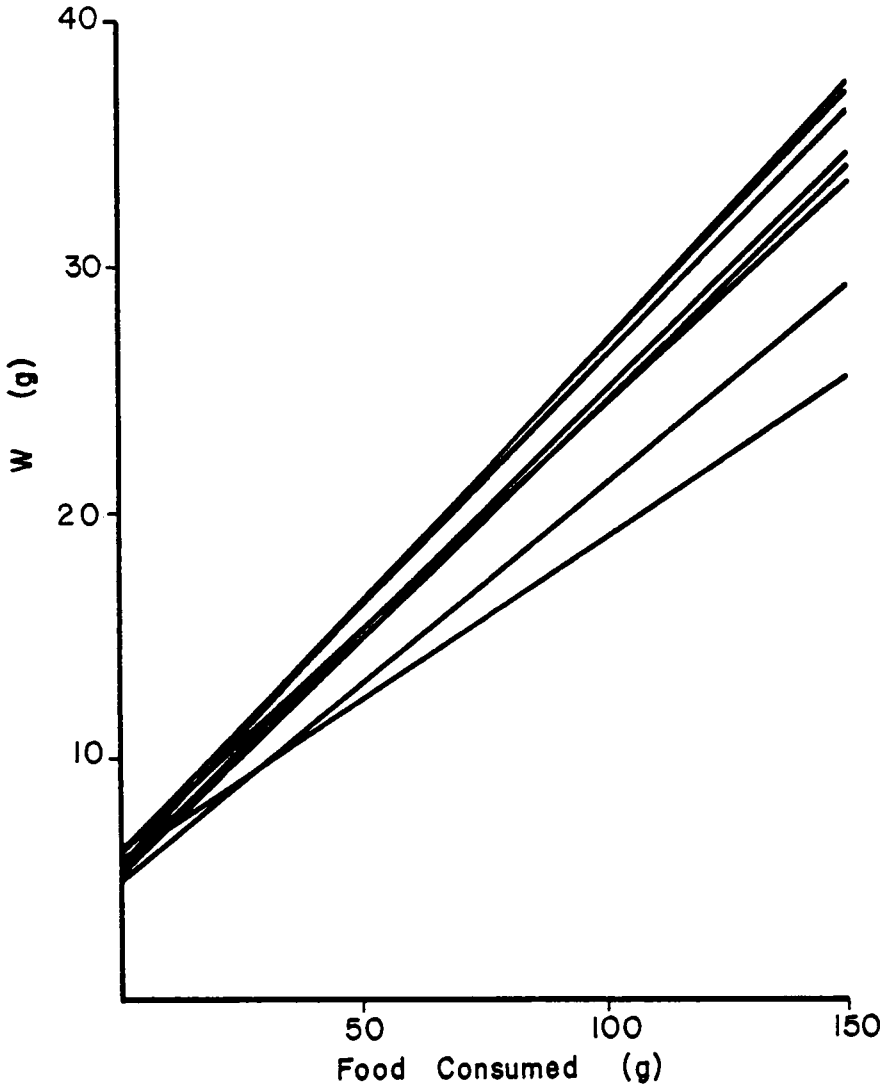



Figure 48. Individual Regression Lines for Weight (W) as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee.

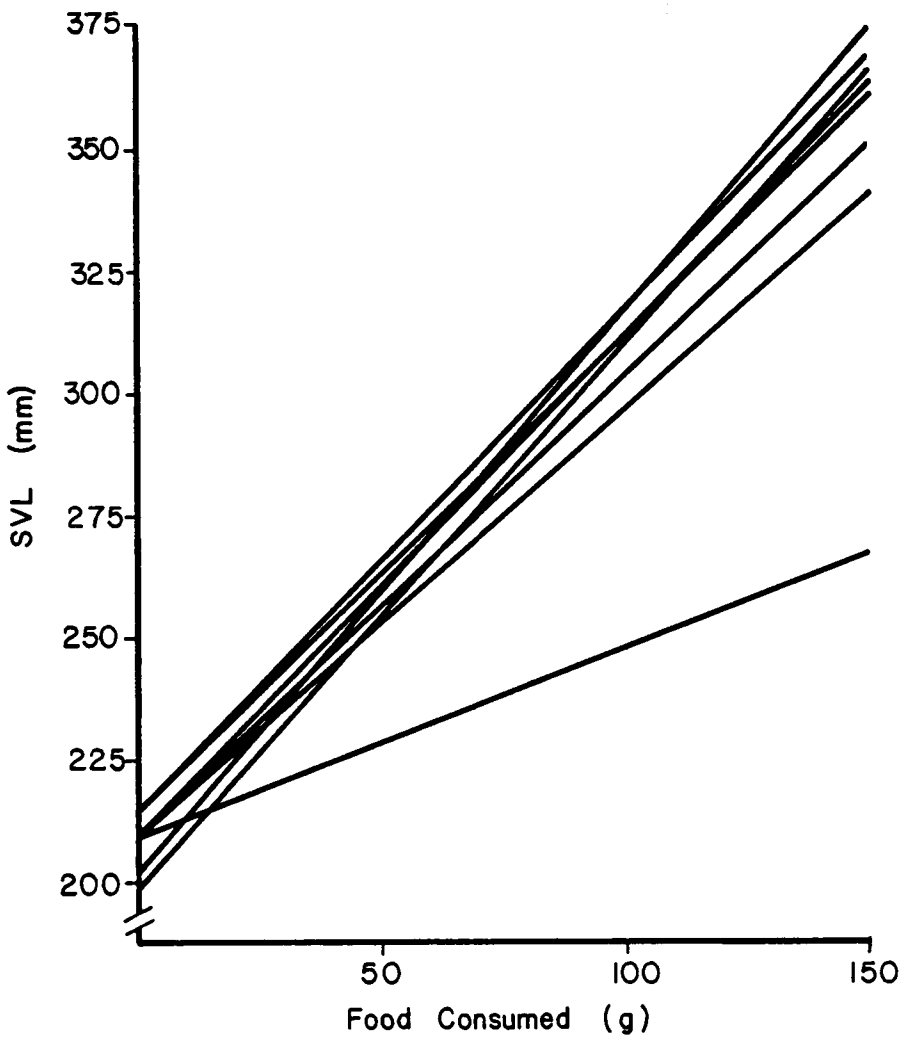



Figure 49. Individual Regression Lines for Snout-Vent Length (SVL) as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee.

Table 22

Individual Variation in the Production-Ingestion (P-I) Ratios for Weight (W) in Male *Nerodia fasciata* from Shelby County, Tennessee[1,2]

| Individual | P-I Ratio | Individuals | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 20/2 | 20/7 | 20/12 | 20/5 | 20/6 | 20/1 | 20/4 | 20/3 |
| 20/2 | 0.21 | ---- | | | | | | | |
| 20/7 | 0.21 | NS | ---- | | | | | | |
| 20/12 | 0.20 | NS | NS | ---- | | | | | |
| 20/5 | 0.19 | S | NS | NS | ---- | | | | |
| 20/6 | 0.19 | S | S | NS | NS | ---- | | | |
| 20/1 | 0.18 | S | S | S | NS | NS | ---- | | |
| 20/4 | 0.16 | S | S | S | S | S | NS | ---- | |
| 20/3 | 0.13 | S | S | S | S | S | S | S | ---- |

[1]NS = Not significant, $p > 0.05$.
[2]S = Significant, $p < 0.05$.
[2]Data represent 12 months of growth.

Table 23

Individual Variation in the Production-Ingestion (P-I) Ratios for Snout-Vent Length (SVL) in Male *Nerodia fasciata* from Shelby County, Tennessee[1,2]

| Individual | P-I Ratio | Individuals | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 20/7 | 20/4 | 20/12 | 20/2 | 20/1 | 20/5 | 20/6 | 20/3 |
| 20/7 | 1.15 | ---- | | | | | | | |
| 20/4 | 1.12 | NS | ---- | | | | | | |
| 20/12 | 1.03 | NS | NS | ---- | | | | | |
| 20/2 | 1.02 | S | NS | NS | ---- | | | | |
| 20/1 | 0.99 | S | NS | NS | NS | ---- | | | |
| 20/5 | 0.94 | S | S | NS | NS | NS | ---- | | |
| 20/6 | 0.89 | S | S | S | S | NS | NS | ---- | |
| 20/3 | 0.39 | S | S | S | S | S | S | S | ---- |

[1]NS = Not significant, $p > 0.05$.
[2]S = Significant, $p < 0.05$.
[2]Data represent 12 months of growth.

Table 24

Individual Variation in the Production-Ingestion (P-I) Ratios for Total Length (L) in Male *Nerodia fasciata* from Shelby County, Tennessee[1,2]

| Individual | P-I Ratio | Individuals | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 20/7 | 20/4 | 20/2 | 20/12 | 20/1 | 20/6 | 20/5 |
| 20/7 | 1.52 | ---- | | | | | | |
| 20/4 | 2.45 | NS | ---- | | | | | |
| 20/2 | 1.37 | S | NS | ---- | | | | |
| 20/12 | 1.36 | S | NS | NS | ---- | | | |
| 20/1 | 1.33 | S | NS | NS | NS | ---- | | |
| 20/6 | 1.21 | S | S | S | S | NS | ---- | |
| 20/5 | 1.21 | S | S | S | S | NS | NS | ---- |

[1]NS = Not significant, $p > 0.05$.
[2]S = Significant, $p < 0.05$.
[2]Data represent 12 months of growth.

Table 25

Individual Variation in the Production-Ingestion (P-I) Ratios for Tail Length (TL) in Male *Nerodia fasciata* from Shelby County, Tennessee[1,2]

| Individual | P-I Ratio | Individuals | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 20/7 | 20/2 | 20/1 | 20/12 | 20/4 | 20/6 | 20/5 |
| 20/7 | 0.37 | ---- | | | | | | |
| 20/2 | 0.35 | NS | ---- | | | | | |
| 20/1 | 0.35 | NS | NS | ---- | | | | |
| 20/12 | 0.33 | NS | NS | NS | ---- | | | |
| 20/4 | 0.33 | NS | NS | NS | NS | ---- | | |
| 20/6 | 0.33 | NS | NS | NS | NS | NS | ---- | |
| 20/5 | 0.26 | S | S | S | S | S | S | ---- |

[1]NS = Not significant, $p > 0.05$.
[2]S = Significant, $p < 0.05$.
[2]Data represent 12 months of growth.

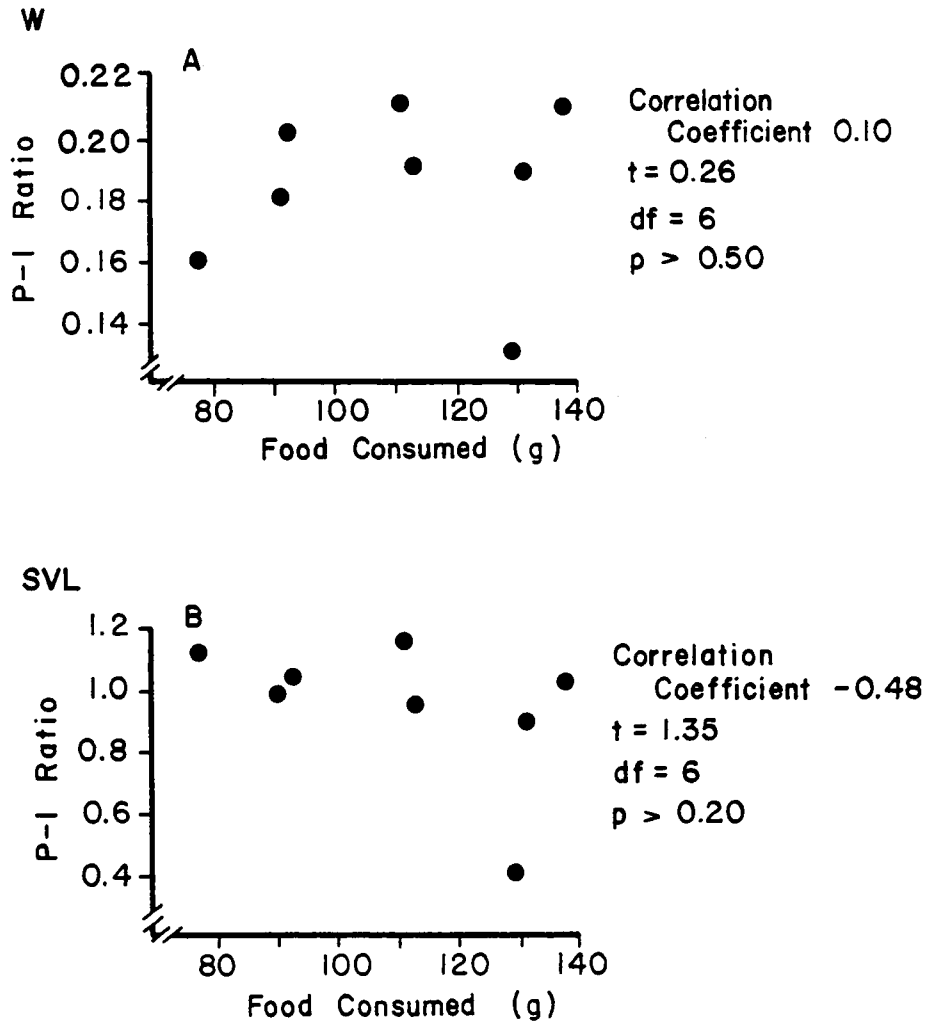



Figure 50. Production-Ingestion (P-I) Ratios as a Function of Food Consumed for Male *Nerodia fasciata* from Shelby County, Tennessee. A. P-I Ratios for Weight (W). B. P-I Ratios for Snout-Vent Length (SVL).

growth. There was no significant relationship between the P-I ratios and food consumption for either sex (Table 26). There seem, therefore, to be reliable differences between individuals in their P-I ratios for all of the growth parameters. Any growth effects due to external factors are superimposed on these basic differences.

An interesting fact that goes along with the idea that individuals are different in their use of food for growth is that the P-I ratios for increases in weight and length are not correlated. Table 27 shows the correlation coefficients for L, SVL, and TL in association with W. Since the P-I ratios for W and the other growth parameters are not correlated, an individual can have a low P-I ratio for W and a high P-I ratio for L (see individual 20/4, Tables 22 and 23). All other combinations of high and low P-I ratios for W and the other growth parameters are also possible.

Differences in the levels of the P-I ratios for W and SVL result in differences in the rate of increase in W/SVL. Values for the rate of increase in W/SVL are shown in Table 28. As would be expected, individual 20/4 with its low P-I ratio for W and high P-I ratio for SVL (see Tables 22 and 23, pages 148 and 149) has a low value for the increase in W/SVL.

Individuals not only differ in their P-I ratios and the rate of increase in W/SVL, but they also differed in the estimates of their maximum sizes and growth constant values (r). Table 29 shows the estimated asymptotes and r values for individual male and female *N. fasciata* for four years of growth along with the 95% confidence intervals for these values. Individuals 20/7 and 20/9 were omitted

Table 26

Correlation of the Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) and the Weight of Food Consumed for *Nerodia fasciata* from Shelby County, Tennessee[1,2]

| Sex | Parameter | Correlation Coefficient | t | df | p |
|---|---|---|---|---|---|
| ♂ | W | 0.10 | 0.26 | 6 | >0.50 |
| | L | -0.38 | 0.92 | 5 | >0.20 |
| | SVL | -0.48 | 1.35 | 6 | >0.20 |
| | TL | 0.01 | 0.02 | 5 | >0.90 |
| ♀ | W | 0.75 | 2.27 | 4 | >0.05 |
| | L | 0.20 | 0.41 | 4 | >0.50 |
| | SVL | 0.05 | 0.10 | 4 | >0.90 |
| | TL | 0.38 | 0.82 | 4 | >0.40 |

Table 27

Correlation of the Production-Ingestion (P-I) Ratios for Weight (W), with the P-I Ratios for Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for *Nerodia fasciata* from Shelby County, Tennessee[1,2]

| Sex | Parameter | Correlation Coefficient | t | df | p |
|---|---|---|---|---|---|
| ♂ | L | 0.02 | 0.04 | 5 | >0.90 |
| | SVL | -0.05 | 0.12 | 6 | >0.90 |
| | TL | 0.22 | 0.50 | 5 | >0.50 |
| ♀ | L | 0.45 | 1.01 | 4 | >0.20 |
| | SVL | 0.39 | 0.85 | 4 | >0.40 |
| | TL | 0.09 | 0.18 | 4 | >0.50 |

Table 28

Individual Variation in the Rate of Increase in Weight Per Unit Length (W/SVL) in Male *Nerodia fasciata* from Shelby County, Tennessee[1,2]

| Individual | Rate of Increase in W/SVL ($\times 10^7$) | Individuals | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 20/6 | 20/2 | 20/1 | 20/12 | 20/3 | 20/5 | 20/4 |
| 20/6 | 7.80 | ---- | | | | | | |
| 20/2 | 7.47 | NS | ---- | | | | | |
| 20/1 | 7.25 | NS | NS | ---- | | | | |
| 20/12 | 7.19 | S | NS | NS | ---- | | | |
| 20/3 | 6.78 | S | S | NS | NS | ---- | | |
| 20/5 | 6.34 | S | S | S | S | NS | ---- | |
| 20/4 | 6.10 | S | S | S | S | S | NS | ---- |

[1]NS = Not significant, $p > 0.05$.
[2]S = Significant, $p < 0.05$.
[2]W/SVL is in units of grams per millimeter.

Table 29

Individual Estimates of Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) from the Bertalanffy Growth Model for *Nerodia fasciata* from Shelby County, Tennessee

| | | | Estimate of Asymptote | | Estimate of r | |
|---|---|---|---|---|---|---|
| Individual | Sex | Parameter | Value | 95% Confidence Interval | Value | 95% Confidence Interval |
| 20/1 | ♂ | W (g) | 98.2 | 95.6-100.8 | 0.0053 | 0.0047-0.0058 |
| | | L (mm) | 633 | 619 -648 | 0.0054 | 0.0049-0.0060 |
| | | SVL (mm) | 479 | 467 -490 | 0.0053 | 0.0047-0.0058 |
| | | TL (mm) | 155 | 151 -159 | 0.0058 | 0.0051-0.0065 |
| 20/2 | ♂ | W (g) | 108.7 | 105.7-112.7 | 0.0044 | 0.0041-0.0048 |
| | | L (mm) | 721 | 709 -733 | 0.0045 | 0.0042-0.0048 |
| | | SVL (mm) | 550 | 540 -560 | 0.0044 | 0.0041-0.0048 |
| | | TL (mm) | 171 | 167 -176 | 0.0047 | 0.0042-0.0053 |
| 20/3 | ♂ | W (g) | 138.1 | 134.8-142.4 | 0.0026 | 0.0018-0.0034 |
| | | L (mm) | ---- | ---- | ---- | ---- |
| | | SVL (mm) | 576 | 521 -632 | 0.0026 | 0.0018-0.0034 |
| | | TL (mm) | ---- | ---- | ---- | ---- |
| 20/4 | ♂ | W (g) | 73.3 | 72.0-74.5 | 0.0057 | 0.0052-0.0063 |
| | | L (mm) | 627 | 612 -642 | 0.0058 | 0.0053-0.0064 |
| | | SVL (mm) | 480 | 469 -492 | 0.0057 | 0.0052-0.0063 |
| | | TL (mm) | 147 | 141 -153 | 0.0061 | 0.0051-0.0071 |

Table 29 (Continued)

| Individual | Sex | Parameter | Estimate of Asymptote | | Estimate of r | |
|---|---|---|---|---|---|---|
| | | | Value | 95% Confidence Interval | Value | 95% Confidence Interval |
| 20/5 | ♂ | W (g) | 122.3 | 120.1-124.6 | 0.0038 | 0.0035-0.0041 |
| | | L (mm) | 741 | 723 -759 | 0.0037 | 0.0034-0.0040 |
| | | SVL (mm) | 563 | 549 -576 | 0.0038 | 0.0035-0.0041 |
| | | TL (mm) | 178 | 170 -186 | 0.0036 | 0.0031-0.0041 |
| 20/6 | ♂ | W (g) | 123.7 | 121.2-126.1 | 0.0035 | 0.0032-0.0037 |
| | | L (mm) | 715 | 703 -727 | 0.0035 | 0.0033-0.0038 |
| | | SVL (mm) | 540 | 529 -550 | 0.0035 | 0.0032-0.0037 |
| | | TL (mm) | 176 | 172 -180 | 0.0037 | 0.0034-0.0040 |
| 20/12 | ♂ | W (g) | 98.6 | 96.7-100.5 | 0.0046 | 0.0042-0.0050 |
| | | L (mm) | 670 | 658 -682 | 0.0047 | 0.0043-0.0050 |
| | | SVL (mm) | 507 | 497 -517 | 0.0046 | 0.0042-0.0050 |
| | | TL (mm) | 163 | 159 -167 | 0.0048 | 0.0043-0.0052 |
| 20/8 | ♀ | W (g) | 120.5 | 116.1-125.0 | 0.0045 | 0.0041-0.0049 |
| | | L (mm) | ---- | ---- | ---- | ---- |
| | | SVL (mm) | 571 | 560 -583 | 0.0045 | 0.0041-0.0049 |
| | | TL (mm) | ---- | ---- | ---- | ---- |
| 20/10 | ♀ | W (g) | 177.4 | 167.8-186.9 | 0.0030 | 0.0025-0.0035 |
| | | L (mm) | ---- | ---- | ---- | ---- |
| | | SVL (mm) | 618 | 589 -647 | 0.0030 | 0.0025-0.0035 |
| | | TL (mm) | ---- | ---- | ---- | ---- |

Table 29 (Continued)

| Individual | Sex | Parameter | Estimate of Asymptote | | Estimate of r | |
|---|---|---|---|---|---|---|
| | | | Value | 95% Confidence Interval | Value | 95% Confidence Interval |
| 20/11 | ♀ | W (g) | 175.0 | 167.9-182.0 | 0.0033 | 0.0029-0.0036 |
| | | L (mm) | 837 | 813 -861 | 0.0032 | 0.0029-0.0036 |
| | | SVL (mm) | 658 | 638 -679 | 0.0033 | 0.0029-0.0036 |
| | | TL (mm) | 179 | 174 -183 | 0.0032 | 0.0029-0.0035 |
| 20/13 | ♀ | W (g) | 199.5 | 191.6-207.5 | 0.0029 | 0.0026-0.0031 |
| | | L (mm) | 846 | 828 -864 | 0.0028 | 0.0026-0.0030 |
| | | SVL (mm) | 657 | 641 -673 | 0.0029 | 0.0026-0.0031 |
| | | TL (mm) | 189 | 185 -193 | 0.0028 | 0.0026-0.0029 |
| 20/14 | ♀ | W (g) | 156.0 | 149.1-163.0 | 0.0033 | 0.0029-0.0037 |
| | | L (mm) | ---- | ---- | ---- | ---- |
| | | SVL (mm) | 634 | 614 -654 | 0.0033 | 0.0029-0.0037 |
| | | TL (mm) | ---- | ---- | ---- | ---- |

from the table due to insufficient data that did not cover the full four years. Those individuals with non-overlapping confidence intervals are significantly different from one another ($p < 0.05$). It is apparent that each individual was approaching its own set of maximum sizes for the growth parameters. There were also differences in the estimated r values.

As discussed in Chapter 3, pages 41 and 47, the r value is a measure of how rapidly the snakes approach their estimated asymptotes. The larger the value of r, the more rapidly the individual will approach its estimated asymptote and consequently the more rapid will be the decline in its growth rate as it matures. Snakes with smaller values of r will approach their estimated asymptotes at a slower rate and consequently will show a more gradual decline in growth rate as they mature. Knowing this information, it is not surprising that the r values were inversely correlated with the estimated asymptotes for males (correlation coefficient = -0.91, $t = 4.91$, $df = 5$, $p < 0.01$), and nearly inversely correlated for females (correlation coefficient = -0.84, $t = 2.68$, $df = 3$, $p > 0.05$). The lack of a significant correlation in the females was apparently due to the small sample size since they showed the same trend as the males. The inverse condition between the estimated asymptote and the growth constant indicates that, at least within a litter, the larger the estimated asymptote, the longer an individual will take in reaching it.

*Discussion*

The amount of variation in growth among members of the same litter is certainly only a small indication of the variation that exists among juveniles of an entire population. Of course, there is no guarantee that the amount of variation measured in a single litter is indicative of the variation that exists in the population as a whole. Survivorship is low in juvenile snakes and increases as the animals get older (Feaver 1977). There is the distinct possibility that individuals displaying certain growth patterns are systematically eliminated from the population. This selective process would tend to lower the total amount of variation in the population so that the variation among older snakes is much less than among juveniles. There is no way of knowing at this time which of the growth patterns would be favored or eliminated under any particular set of circumstances, but there is certainly enough variation available to allow selection to push a population in a number of different directions.

Given the amount of individual variation displayed under the present feeding regimen, it is not hard to imagine that the magnitude of the response to a change in the feeding regimen would vary among individuals. Variation in the response to a change in the feeding regimen would certainly cause variation in the reproductive output among individuals. Little is known about size in relation to reproductive success in males so not much can be said about changes in their reproductive output with a change in the feeding regimen. Females, however, that were better able to maintain their P-I ratios for W at a high level when resources were not readily available would

be more likely to produce successful broods during that year when females whose P-I ratios dropped drastically. Prolonged periods of low resource availability would certainly increase the proportion of snakes in the population displaying small changes in the P-I ratio with changing resource availability. On the other hand, females that have a large change in their P-I ratios for W may be able to increase their reproductive output beyond that of females that do not during long periods of high resource availability. The population would consequently show an increase in the proportion of individuals displaying large fluctuations in the P-I ratio with changing resource availability. Speculation could certainly come up with other scenarios that would favor certain growth patterns. Without more information about selection in natural populations, this process would do little more than create many possibilities with no way of choosing which ones were actually operating in the wild.

# CHAPTER 6

# GENERAL DISCUSSION

*Introduction*

This chapter is divided into two major parts. The first part deals with the relationship of the findings in this study with those reported in the literature. The second part deals with questions that have arisen as a result of this work and some possibilities for addressing them in the future.

*Growth Studies in the Literature*

*Energetics.* Assimilation efficiency values were reported for a number of species of reptiles in Chapter 1. Caloric assimilation efficiency values for the species in this study range from 91.8% to 97.2% (see Table 21, page 138). These values are slightly higher than those reported by Smith (1976) for *Elaphe guttata* and *Heterodon platyrhinos* and by Gehrmann (1971) for *Natrix* (=*Nerodia*) *erythrogaster transversa* (see Table 1, pages 9 and 10). The values reported certainly fall within the range reported for insectivorous and carnivorous reptile species (Skoczylas 1978). The differences between the caloric assimilation efficiencies reported here and those for *E. guttata* and *H. platyrhinos* certainly can be attributed to the species differences as well as to the differences in their diet. The difference in the caloric assimilation efficiencies for *N. erythrogaster* and the three species in this study is at least 10 percentage

points. This difference is of interest since not only are all of the species in the same genus, but they were all maintained on a diet of minnows. The difference between the assimilation efficiencies also includes the magnitude of the change in the values with time. The largest drop in the caloric assimilation efficiency between one month of age and 12 months of age was 2.1% for *N. rhombifera* fed the intermediate meal size. The drops reported by Gehrmann (1971) were 2.7% for females and 2.8% for males between the ages of three and one-half and seven months. The apparent disparity in these values can be explained in a number of ways. Although the species are related, *N. erythrogaster* is from a different geographic location than the species in this study and it would not be surprising if the particular set of circumstances under which the populations evolved caused disparities in their assimilation efficiencies. It is more intriguing, however, to attribute the disparity to seasonal fluctuation in the caloric assimilation efficiencies. With only one exception, the highest caloric assimilation efficiencies were measured during the summer months. It would not be surprising to discover that assimilation efficiencies were highest in the summer and lowest in the winter in reptiles that normally hibernate during the colder months of the year. Although there is much variation, some reptiles do show a reduced metabolism during the winter months (see Bennett and Dawson 1976 for a review), and quite possibly could display reduced assimilation efficiencies during that time. The *N. erythrogaster* in Gehrmann's (1971) study were born on September 4th and 10th, and within hours were introduced into the experiment. The initial measurement of the

assimilation efficiency would involve data produced from September through late December. The second measurement would involve data produced from late December through late March or early April. If there is a seasonal fluctuation in the caloric assimilation efficiency, the first measurement would have been taken on data produced when assimilation efficiency was on the downswing, and the second measurement would have been taken on data produced when assimilation efficiency was at its lowest point. The measurements in the present study would have been taken during periods when the assimilation efficiency would be at a relatively high level. The argument presented above is entirely speculative, but it is certainly one that can be tested.

*Growth Rates*

There are two patterns of sexual dimorphism in adult size reported for snakes: one in which males are larger, and one in which females are larger (Feaver 1977). There are also two patterns of sexual dimorphism in growth: one in which juveniles grow at similar rates until individuals of the smaller sex reach maturity, and one in which juveniles grow at different rates (Andrews 1982). Species that follow the former growth pattern include *Elaphe o. obsoleta* (Fitch 1963), and *E. g. guttata* (Barnard et al. 1979). Species that follow the latter growth pattern include *Spalerosophis cliffordi* (Dmi'el 1967), and *Natrix* (=*Nerodia*) *sipedon* and *Natrix* (=*Regina*) *septemvittata* (Raney and Roecker 1947). The snakes in this study of course follow the latter growth pattern.

As with assimilation efficiencies, the P-I ratios for *N. fasciata*, *N. cyclopion*, and *N. rhombifera* are directly comparable with those for *N. erythrogaster*. P-I ratios for W for *N. erythrogaster* females were 28% for the first three and one-half months and 20% for the second three and one-half months. Values for males were 27% and 20% respectively (Gehrmann 1971). These values are certainly within the range of values reported for this study (see Table 8, pages 74 and 76). There is also the expected drop in the P-I ratio for *N. erythrogaster* as the snakes get older.

There are several pieces of information in the literature that are pertinent to explaining some of the results in this study. In those cases where adequate data are available, females generally have been found to have lower metabolic rates than males (Bennett and Dawson 1976). Lower metabolic rates indicate lower maintenance costs and frees more of the ingested energy for other uses (e.g., growth). As a result females can grow more rapidly than males. This explanation works well in this situation, but what happens in situations where males grow more rapidly than females? Unfortunately the metabolic data are not available for enough species to ascertain whether the situation is reversed in such cases (Bennett and Dawson (1976).

In the lizard *Anolis carolinensis*, the percent of energy expended as metabolism increased at higher feeding levels (Kitchell and Windell 1972). This fact certainly goes along with the idea of a shift in the allocation of energy for various purposes with a change in the feeding regimen. A possible mechanism for the shift in

the amount of energy allocated to increases in weight and length involves a change in hormone levels. Licht and Jones (1967) found that when energy intake exceeded demand, prolactin treated *Anolis carolinensis* elongated while the controls fattened. This result was found in spite of the fact that the caloric assimilation was similar in the two groups. The shift from fattening to elongation is exactly what happened when the feeding regimen was changed for *N. fasciata*. Whether or not a hormone change is involved in the present study is not important at this time, but the change in *Anolis carolinensis* certainly shows that a mechanism is available for such a shift.

Differences in growth rates among species are much more difficult to attribute to any particular influence. Growth rates are adapted to certain features of an animal's environment including the feeding requirements of the young, the infant mortality rate, and the availability of food for adults (Case 1978b). Adaptation to a particular lifestyle can certainly affect the growth rate of a species. Slow growth may represent an adaptive trait for species with secretive habits and low frequencies of prey encounter (Andrews 1982).

There are also examples in the literature of intraspecific selection among individuals that vary in growth rate. In the lizard genus *Sceloporus*, fast-growing individuals are favored under conditions of high food availability because they reach the largest size prior to the breeding season and dominate the smaller individuals for breeding territories. Slow-growing individuals are favored under

conditions of low predation and a stable food supply. These individuals store a higher proportion of the ingested energy as glycogen and fat and consequently have less somatic tissue to support during the winter. This fact results in higher winter-spring survivorship for these animals (Ferguson and Brockman 1980).

In *Amphibolurus ornata*, an agamid lizard, fast-growing individuals mature at one year and slow growing individuals at two years. Slow-growing individuals are cold-sensitive, but drought-resistant. Fast-growing individuals are cold-hardy, but drought-sensitive. At sites with a variable climate, both growth types persist because of the differential mortality of the types with shifts in the climate. Fast-growing individuals are unable to tolerate high levels of electrolytes in their body fluids during periods of water deprivation, and slow-growing individuals are intolerant of cold (Bradshaw 1971). While the exact selective pressures for the species in this study are unknown, the variety in growth patterns is certainly sufficient to allow differential mortality to push a population in a number of directions.

*Problems for Future Research*

While individual variation is far from being a new idea, close examination of the subject has been neglected in favor of making generalizations about groups of organisms. Probably the most important contribution of this study is in revealing some of the variation that exists in growth rates even among individuals from the same litter. This information opens up a number of avenues of

research in natural selection. What is of particular interest is the effect that differences in individual growth rates may have on fecundity in females and reproductive success in males.

There are obviously fast and slow-growing individuals in any population. Regression lines showing the increase in reproductive output with increases in SVL for snakes are constructed from individuals that probably have different growth rates. This situation is very much like the group regression lines in this study which were constructed from individuals that were later shown to have significantly different growth rates. By knowing the individual growth rates of captive animals, it would be an easy matter to conduct breeding experiments to ascertain whether there truly is a difference in the relationship between SVL and fecundity in snakes with different growth rates.

Although it could not be addressed in this study, differential shifts in the P-I ratios with changing meal size should be as likely among individuals as it was between the sexes. Under these circumstances the question arises as to the effect these differential shifts would have on fecundity. In years with low resource availability, would there be some individuals whose P-I ratio for W still allowed them to accumulate enough energy reserve to successfully reproduce? If there were such individuals, how would they compare with the snakes that could not reproduce during that time when resource availability was again high?

In connection with high and low resource availability, increases in L and SVL were much greater when resources were not

readily available. The idea that individuals forego reproduction during unfavorable years and increase in L and SVL as rapidly as possible in order to increase their reproductive output in the future when conditions are again favorable is intriguing. Although it may not be possible to show for certain that this reproductive strategy is employed, the possibility of its existence can certainly be addressed in the lab. Controlled breeding experiments with snakes maintained on diets that can be changed to fit the demands of simulating changing resource availability can provide the information needed to evaluate this possibility.

One more question that needs to be addressed is the relationship among growth rate, size, and reproductive success in males. This information is particularly needed in species that do not have male-male combat. Addressing this question has been difficult because it is not readily apparent which male sired which litter. Under controlled conditions in the lab, this problem can be overcome, although finding a solution to the problem may still be difficult.

All of the questions presented above require long term investigation which may entail producing multiple generations from snakes with known growth rates. These experiments, however, would be a first step in the direction of a more full understanding of the selective process and how it works to shape certain growth patterns and strategies of reproduction.

# LITERATURE CITED

## LITERATURE CITED


Alpatov, W. W. 1929. Biometrical studies on variation and races of the honey bee (*Apis mellifera* L.). *Quart. Rev. Biol.* 4:1-58.

Andrews, R. M. 1976. Growth rate in island and mainland anoline lizards. *Copeia* 1976:477-482.

Andrews, R. M. 1982. Patterns of growth in reptiles. pp. 273-320 *in* C. Gans and F. H. Pough eds., *Biology of the Reptilla*, vol. 13, Physiology D, Physiological Ecology. Academic Press, London, 345 pp.

Avery, R. 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *J. Animal Ecol.* 40:351-365.

Barnard, E. A. 1973. Comparative biochemistry and physiology of digestion. III. Biochemical adaptations to diet. *in* C. L. Prosser ed., *Comparative Animal Physiology*. W. B. Saunders Co., Phila.

Barnard, S. M., T. G. Hollinger, and T. A. Romaine. 1979. Growth and food consumption in the corn snake, *Elaphe guttata guttata* (Serpentes: Colubridae). *Copeia* 1979:739-741.

Bennett, A. F. and W. R. Dawson. 1976. Metabolism. pp. 127-223 *in* C. Gans and W. R. Dawson eds., *Biology of the Reptilia*, vol. 5, Physiology A. Academic Press, London.

Bertalanffy, L. von. 1957. Quantitative laws in metabolism and growth. *Quart. Rev. Biol.* 32:217-231.

Bradshaw, S. D. 1971. Growth and maturity in a field population of *Amphibolurus* lizards exposed to seasonal cold and aridity. *J. Zool.* 165:1-25.

Carpenter, C. C. 1952. Growth and maturity of the three species of *Thamnophis* in Michigan. *Copeia* 1952:237-243.

Case, T. J. 1978a. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59:1-18.

Case, T. J. 1978b. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quart. Rev. Biol.* 53:243-282.

Chabreck, R. H. and T. Joanen. 1979. Growth rates of American alligators in Louisiana. *Herpetologica* 35:51-57.

Conant, R. 1969. A review of the water snakes of the genus *Natrix* in Mexico. *Bull. Amer. Mus. Nat. Hist.* 142:1-140.

Conant, R. 1975. *A Field Guide to Reptiles and Amphibians of Eastern and Central North America*, Houghton Mifflin Co., Boston, 429 pp.

Dmi'el, R. 1967. Studies on reproduction, growth, and feeding in the snake *Spalerosophis cliffordi*. *Copeia* 1967:332-346.

Dunham, A. E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology* 59:770-778.

Dunham, A. E., D. W. Tinkle, and J. W. Gibbons. 1978. Body size in island lizards: A cautionary tale. *Ecology* 59:1230-1238.

Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265-289.

Feaver, P. 1977. The demography of a Michigan population of *Natrix sipedon* with discussions of ophidian growth and reproduction. Ph.D. dissertation, The University of Michigan, Ann Arbor, Michigan.

Ferguson, G. W. and T. Brockman. 1980. Geographic differences of growth rate of *Sceloporus* lizards (Sauria: Iguanidae). *Copeia* 1980:259-264.

Fitch, H. S. 1963. Natural history of the black rat snake *Elaphe o. obsoleta* in Kansas. *Copeia* 1963:649-658.

Ford, N. B. 1974. Growth and food consumption in the yellow rat snake, *Elaphe obsoleta quadrivittata*. *Herpetologica* 30:102-104.

Fukada, H. 1961. Biological studies on the snakes. VIII. On the growth formulae of snakes and their applications to other reptiles. *Bull. Kyoto Gakugei Univ.*, Ser. B, No. 17.

Gehrmann, W. H. 1971. Food consumption and growth in the immature water snake. *Natrix erythrogaster transversa*. *Growth* 35:127-136.

Gibbons, J. W. 1972. Reproduction, growth, and sexual dimorphism in the canebrake rattlesnake (*Crotalus horridus atricaudatus*). *Copeia* 1972:222-226.

Gibbons, J. W., R. D. Semlitsch, J. L. Greene, and J. P. Schubauer. 1981. Variation in age and size at maturity of the slider turtle (*Pseudemys scripta*). *Amer. Nat.* 117:841-845.

Grant, P. R. 1965. The adaptive significance of some size trends in island birds. *Evolution* 19:355-367.

Heaney, L. R. 1978. Island area and body size of insular mammals: Evidence from the tri-colored squirrel (*Callosciurus prevosti*) of southeast Asia. *Evolution* 32:29-44.

Hebrard, J. J. and H. R. Mushinsky. 1978. Habitat use by five sympatric water snakes in a Louisiana swamp. *Herpetologica* 34: 306-311.

Hellmich, W. C. 1951. On ecotypic and autotypic characters, a contribution to the knowledge of the evolution of the genus *Liolaemus* (Iguanidae). *Evolution* 5:359-369.

Hovanitz, W. 1942. Genetic and ecologic analyses of wild populations in Lepidoptera. I. Pupal size and weight variation in some California populations of *Melitaea chalcedona*. *Ecology* 23:175-188.

Johnston, D. W. and R. W. McFarlane. 1967. Migration and biogeneratics of flight in the Pacific Golden Plover. *Condor* 69:156-168.

Kaufmann, K. W. 1981. Fitting and using growth curves. *Oecologia* 49:293-299.

Kitchell, J. F. and J. T. Windell. 1972. Energy budget for the lizard, *Anolis carolinensis*. *Physiol. Zool.* 45:178-188.

Klauber, L. M. 1956. *Rattlesnakes. Their Habits, Life Histories, and Influence on Mankind.* Univ. of Calif. Press, Berkeley, 2 vol., 1476 pp.

Kramer, G. 1951. Body proportions of mainland and island lizards. *Evolution* 5:193-206.

Licht, P. and R. E. Jones. 1967. Effects of exogenous prolactin on reproduction and growth in adult males of the lizard *Anolis carolinensis*. *Gen. and Comp. Endocrinology* 8:228-244.

Lister, B. C. 1975. The nature of niche expansion in West Indian *Anolis* lizards: I. Ecological consequences of reduced competition. *Evolution* 30:659-676.

Mayr, E. 1970. *Populations, Species, and Evolution.* The Belknap Press of Harvard University Press, Cambridge, MA, 453 pp.

Minnich, J. 1970. Water and electrolyte balance of the desert iguana, *Dipsosaurus dorsalis*, in its natural habitat. *Comp. Biochem. Physiol.* 35:921-933.

Mount, R. H. 1975. *The Reptiles and Amphibians of Alabama*. Auburn University Agricultural Experiment Station, Auburn, Alabama, 347 pp.

Mueller, C. F. 1970. Energy utilization in the lizards *Sceloporus graciousus* and *S. occidentalis*. *J. Herp.* 4:131-134.

Mushinsky, H. R. and J. J. Hebrard. 1977a. Food partitioning by five species of water snakes in Louisiana. *Herpetologica* 33:162-166.

Mushinsky, H. R. and J. J. Hebrard. 1977b. The use of time by sympatric water snakes. *Can. J. Zool.* 55:1545-1550.

Mushinsky, H. R., J. J. Hebrard, and D. S. Vodopich. 1982. Ontogeny of water snake foraging ecology. *Ecology* 63:1624-1629.

Myer, J. S. and A. P. Kowell. 1971. Eating patterns and body weight change of snakes when eating and when food deprived. *Physiology and Behavior* 6:71-74.

Myer, J. S. and A. P. Kowell. 1973. Effects of feeding schedule and food deprivation on the growth of neonatal garter snakes (*Thamnophis sirtalis*). *J. Herp.* 7:225-229.

Nagy, K. and V. Shoemaker. 1975. Energy and nitrogen budgets of the free-living desert lizard *Sauromalus obesus*. *Physiol. Zool.* 48:252-262.

Park, O. 1949. Application of the converse Bergmann principle to the carabid beetle. *Dicaelus purpuratus*. *Physiol. Zool.* 22:359-372.

Pianka, E. 1974. *Evolutionary Ecology*. Harper and Row, New York, 356 pp.

Porter, K. R. 1972. *Herpetology*. W. B. Saunders Co., Phila., 524 pp.

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

Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *J. Morph.* 106:85-108.

Ricklefs, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419-451.

Schoener, T. W. 1969. Size patterns in West Indiana *Anolis* lizards: I. Size and species diversity. *Syst. Zool.* 18:386-401.

Schoener, T. W. and A. Schoener. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. *Copeia* 1978:390-405.

Semlitsch, R. D. and J. W. Gibbons. 1982. Body size dimorphism and sexual selection in two species of water snakes. *Copeia* 1982:974-976.

Shine, R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia* 33:269-277.

Skoczylas, R. 1978. PTysiology of the digestive tract. pp. 589-717 *in* C. Gans and K. A. Gans eds., *Biology of the Reptilia*, vol. 8, Physiology B. Academic Press, London, 782 pp.

Soule, M. 1966. Trends in the insular radiation of a lizard. *Amer. Nat.* 100:47-64.

Smith, G. C. 1976. Ecological energetics of three species of ectothermic vertebrates. *Ecology* 57:252-264.

Taylor, C. R. 1969. The eland and the oryx. *Sci. Amer.* 220:88-95.

Taylor, C. R., S. L. Caldwell, and V. J. Rowntree. 1972. Running up and down hills: Some consequences of size. *Science* 178:1096-1097.

Throckmorton, G. 1973. Digestive efficiency in the herbivorous lizard *Ctenosaura pectinata*. *Copeia* 1973:431-434.

Van Devender, R. W. 1978. Growth ecology of a tropical lizard, *Basiliscus basiliscus*. *Ecology* 59:1031-1038.

Van Devender, R. W. 1982. Growth and ecology of spiny-tailed and green iguanas in Costa Rica, with comments on the evoluation of herbivory and large body size. pp. 162-183 *in* G. M. Burghardt and A. S. Rand eds., *Iguanas of the World. Their Behavior, Ecology, and Conservation*. Noyes Publications, Park Ridge, New Jersey, 472 pp.

Wharton, C. H. 1966. Reproduction and growth in the cottonmouths, *Agkistrodon piscivorus* Lacepede, of Cedar Keys, Florida. *Copeia* 1966:149-161.

Wilbur, H. M. 1975. A growth model for the turtle *Chrysemys picta*. *Copeia* 1975:337-343.

# APPENDIX

# COMPARISON OF INDIVIDUAL GROWTH PARAMETERS

# APPENDIX

## COMPARISON OF INDIVIDUAL GROWTH PARAMETERS

### Table A-1

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia fasciata* from Shelby County, Tennessee*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 20/1 | 20/2 | 20/3 | 20/4 | 20/5 | 20/6 | 20/7 | 20/12 |
| 20/3 | W | 0.13 | t | 5.61 | 11.37 | ---- | 3.73 | 9.15 | 9.52 | 10.91 | 9.70 |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | 0.0001 | 0.0001 | ---- | 0.0005 | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| | L | ---- | t | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- |
| | | | df | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- |
| | | | p | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- |
| | SVL | 0.39 | t | 7.71 | 9.83 | ---- | 9.18 | 9.29 | 8.81 | 12.64 | 10.12 |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | 0.0001 | 0.0001 | ---- | 0.0001 | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| | TL | ---- | t | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- |
| | | | df | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- |
| | | | p | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- |
| 20/4 | W | 0.16 | t | 1.51 | 5.36 | -3.73 | ---- | 3.36 | 3.38 | 4.89 | 4.29 |
| | | | df | 24 | 24 | 24 | ---- | 24 | 24 | 24 | 24 |
| | | | p | 0.1381 | 0.0001 | 0.0005 | | 0.0014 | 0.0012 | 0.0001 | 0.0001 |
| | L | 1.45 | t | -1.35 | -1.05 | ---- | ---- | -3.23 | -2.99 | 0.82 | -1.70 |
| | | | df | 24 | 24 | ---- | ---- | 24 | 24 | 24 | 24 |
| | | | p | 0.1853 | 0.2993 | ---- | ---- | 0.0022 | 0.0041 | 0.4177 | 0.2880 |
| | SVL | 1.13 | t | -1.55 | -1.36 | -9.18 | ---- | -2.36 | -3.22 | 0.38 | -1.17 |
| | | | df | 24 | 24 | 24 | ---- | 24 | 24 | 24 | 24 |
| | | | p | 0.1288 | 0.1804 | 0.0001 | ---- | 0.0215 | 0.0019 | 0.0705 | 0.2439 |
| | TL | 0.33 | t | 0.69 | 1.04 | ---- | ---- | -2.70 | -0.12 | 1.28 | 0.12 |
| | | | df | 24 | 24 | ---- | ---- | 24 | 24 | 24 | 24 |
| | | | p | 0.4926 | 0.3055 | ---- | ---- | 0.0095 | 0.9043 | 0.2038 | 0.9042 |

Table A-1 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 20/1 | 20/2 | 20/3 | 20/4 | 20/5 | 20/6 | 20/7 | 20/12 |
| 20/5 | W | 0.19 | t | -1.80 | 2.66 | -9.15 | -3.36 | ---- | -0.02 | 1.96 | 1.33 |
| | | | df | 24 | 24 | 24 | 24 | ---- | 24 | 24 | 24 |
| | | | p | 0.0768 | 0.0100 | 0.0001 | 0.0014 | ---- | 0.9812 | 0.0528 | 0.1860 |
| | L | 1.21 | t | 1.84 | 2.81 | ---- | 3.23 | ---- | 0.09 | 4.67 | 2.28 |
| | | | df | 24 | 24 | ---- | 24 | ---- | 24 | 24 | 24 |
| | | | p | 0.0715 | 0.0071 | ---- | 0.0022 | ---- | 0.9257 | 0.0001 | 0.0251 |
| | SVL | 0.94 | t | 0.61 | 1.24 | -9.29 | 2.36 | ---- | -3.22 | 3.28 | 1.33 |
| | | | df | 24 | 24 | 24 | 24 | ---- | 24 | 24 | 24 |
| | | | p | 0.5468 | 0.2215 | 0.0001 | 0.0215 | ---- | 0.0019 | 0.0015 | 0.1872 |
| | TL | 0.26 | t | 3.79 | 4.83 | ---- | 2.70 | ---- | 3.07 | 4.38 | 2.85 |
| | | | df | 24 | 24 | ---- | 24 | ---- | 24 | 24 | 24 |
| | | | p | 0.0004 | 0.0001 | ---- | 0.0095 | ---- | 0.0032 | 0.0001 | 0.0056 |
| 20/6 | W | 0.19 | t | -1.82 | 2.81 | -9.52 | -3.38 | 0.02 | ---- | 2.12 | 1.43 |
| | | | df | 24 | 24 | 24 | 24 | 24 | ---- | 24 | 24 |
| | | | p | 0.0733 | 0.0064 | 0.0001 | 0.0012 | 0.9812 | ---- | 0.0370 | 0.1562 |
| | L | 1.21 | t | 1.68 | 2.65 | ---- | 2.99 | -0.09 | ---- | 4.89 | 2.32 |
| | | | df | 24 | 24 | ---- | 24 | 24 | ---- | 24 | 24 |
| | | | p | 0.0984 | 0.0103 | ---- | 0.0041 | 0.9257 | ---- | 0.0001 | 0.0230 |
| | SVL | 0.89 | t | 1.50 | 2.37 | -8.81 | 3.22 | 0.98 | ---- | 4.48 | 2.33 |
| | | | df | 24 | 24 | 24 | 24 | 24 | ---- | 24 | 24 |
| | | | p | 0.1379 | 0.0203 | 0.0001 | 0.0019 | 0.3323 | ---- | 0.0001 | 0.0217 |
| | TL | 0.33 | t | 0.94 | 1.47 | ---- | 0.12 | -3.07 | ---- | 1.79 | 0.28 |
| | | | df | 24 | 24 | ---- | 24 | 24 | ---- | 24 | 24 |
| | | | p | 0.3494 | 0.1455 | ---- | 0.9043 | 0.0032 | ---- | 0.0778 | 0.7784 |

Table A-1 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 20/1 | 20/2 | 20/3 | 20/4 | 20/5 | 20/6 | 20/7 | 20/12 |
| 20/1 | W | 0.18 | t | ---- | 5.03 | -5.61 | -1.51 | 1.80 | 1.82 | 3.52 | 2.90 |
| | | | df | ---- | 24 | 24 | 24 | 24 | 24 | 24 | 24 |
| | | | p | ---- | 0.0001 | 0.0001 | 0.1381 | 0.0768 | 0.0733 | 0.0007 | 0.0047 |
| | L | 1.33 | t | ---- | 0.51 | ---- | -1.35 | -1.84 | -1.68 | 2.49 | 0.40 |
| | | | df | ---- | 24 | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | ---- | 0.6114 | ---- | 0.1853 | 0.0715 | 0.0984 | 0.0151 | 0.6903 |
| | SVL | 0.99 | t | ---- | 0.55 | -7.71 | 1.55 | -0.61 | -1.50 | 2.37 | 0.64 |
| | | | df | ---- | 24 | 24 | 24 | 24 | 24 | 24 | 24 |
| | | | p | ---- | 0.5895 | 0.0001 | 0.1288 | 0.5468 | 0.1379 | 0.0202 | 0.5261 |
| | TL | 0.35 | t | ---- | 0.29 | ---- | -0.69 | -3.79 | -0.94 | 0.68 | -0.57 |
| | | | df | ---- | 24 | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | ---- | 0.7764 | ---- | 0.4926 | 0.0004 | 0.3494 | 0.5002 | 0.5707 |
| 20/2 | W | 0.21 | t | -5.03 | ---- | -11.37 | -5.36 | -2.66 | -2.81 | -0.46 | -0.99 |
| | | | df | 24 | ---- | 24 | 24 | 24 | 24 | 24 | 24 |
| | | | p | 0.0001 | ---- | 0.0001 | 0.0001 | 0.0100 | 0.0064 | 0.6490 | 0.3249 |
| | L | 1.37 | t | -0.51 | ---- | ---- | 1.05 | -2.81 | -2.65 | 2.7 | -0.09 |
| | | | df | 24 | ---- | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | 0.6114 | ---- | ---- | 0.2993 | 0.0071 | 0.0103 | 0.0206 | 0.9273 |
| | SVL | 1.02 | t | -0.55 | ---- | -9.83 | 1.36 | -1.24 | -2.37 | 2.30 | 0.25 |
| | | | df | 24 | ---- | 24 | 24 | 24 | 24 | 24 | 24 |
| | | | p | 0.5895 | ---- | 0.0001 | 0.1804 | 0.2215 | 0.0203 | 0.0241 | 0.8008 |
| | TL | 0.35 | t | -0.29 | ---- | ---- | -1.04 | -4.83 | -1.47 | 0.52 | -0.93 |
| | | | df | 24 | ---- | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | 0.7764 | ---- | ---- | 0.3055 | 0.0001 | 0.1455 | 0.6049 | 0.3572 |

Table A-1 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 20/1 | 20/2 | 20/3 | 20/4 | 20/5 | 20/6 | 20/7 | 20/12 |
| 20/7 | W | 0.21 | t | -3.52 | 0.46 | -10.91 | -4.89 | -1.96 | -2.12 | ---- | -0.53 |
| | | | df | 24 | 24 | 24 | 24 | 24 | 24 | ---- | 24 |
| | | | p | 0.0007 | 0.6490 | 0.0001 | 0.0001 | 0.0528 | 0.0370 | ---- | 0.6008 |
| | L | 1.52 | t | -2.49 | -2.37 | ---- | -0.82 | -4.67 | -4.89 | ---- | -2.18 |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 | ---- | 24 |
| | | | p | 0.0151 | 0.0206 | ---- | 0.4177 | 0.0001 | 0.0001 | ---- | 0.0318 |
| | SVL | 1.15 | t | -2.37 | -2.30 | -12.64 | -0.38 | -3.28 | -4.48 | ---- | -1.80 |
| | | | df | 24 | 24 | 24 | 24 | 24 | 24 | ---- | 24 |
| | | | p | 0.0202 | 0.0241 | 0.0001 | 0.7075 | 0.0015 | 0.0001 | ---- | 0.0748 |
| | TL | 0.37 | t | -0.68 | -0.52 | ---- | -1.28 | -4.38 | -1.79 | ---- | -1.32 |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 | ---- | 24 |
| | | | p | 0.5002 | 0.6049 | ---- | 0.2038 | 0.0001 | 0.0778 | ---- | 0.1889 |
| 20/12 | W | 0.20 | t | -2.90 | 0.99 | -9.70 | -4.29 | -1.33 | -1.43 | 0.53 | ---- |
| | | | df | 24 | 24 | 24 | 24 | 24 | 24 | 24 | ---- |
| | | | p | 0.0047 | 0.3249 | 0.0001 | 0.0001 | 0.1860 | 0.1562 | 0.6008 | |
| | L | 1.36 | t | -0.40 | 0.09 | ---- | 1.70 | -2.28 | -2.32 | 2.18 | ---- |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 | 24 | ---- |
| | | | p | 0.6903 | 0.9273 | ---- | 0.2880 | 0.0251 | 0.0230 | 0.0318 | ---- |
| | SVL | 1.03 | t | -0.64 | -0.25 | -10.12 | 1.17 | -1.33 | -2.33 | 1.80 | ---- |
| | | | df | 24 | 24 | 24 | 24 | 24 | 24 | 24 | ---- |
| | | | p | 0.5261 | 0.8008 | 0.0001 | 0.2439 | 0.1872 | 0.0217 | 0.0748 | ---- |
| | TL | 0.33 | t | 0.57 | 0.93 | ---- | -0.12 | -2.85 | -0.28 | 1.32 | ---- |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 | 24 | ---- |
| | | | p | 0.5707 | 0.3572 | ---- | 0.9042 | 0.0056 | 0.7784 | 0.1889 | ---- |

*Data represent 12 months of growth.

Table A-2

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia fasciata* from Shelby County, Tennessee*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | 20/8 | 20/9 | 20/10 | 20/11 | 20/13 | 20/14 |
| 20/8 | W | 0.22 | t | ---- | -1.53 | -0.48 | -0.44 | -2.30 | -0.80 |
| | | | df | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | ---- | 0.1345 | 0.6387 | 0.6596 | 0.0251 | 0.4251 |
| | L | 1.44 | t | ---- | -0.08 | -0.13 | 1.93 | -0.61 | 1.05 |
| | | | df | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | ---- | 0.9400 | 0.8979 | 0.0597 | 0.5430 | 0.2960 |
| | SVL | 1.14 | t | ---- | 0.38 | -0.45 | 2.01 | -0.52 | 2.08 |
| | | | df | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | ---- | 0.7042 | 0.6557 | 0.0505 | 0.6072 | 0.0411 |
| | TL | 0.30 | t | ---- | -1.80 | 1.13 | 1.08 | -0.73 | -2.31 |
| | | | df | ---- | 24 | 24 | 24 | 24 | 24 |
| | | | p | ---- | 0.0797 | 0.2693 | 0.2854 | 0.4671 | 0.0240 |
| 20/9 | W | 0.21 | t | 1.53 | ---- | 2.04 | 1.17 | -0.64 | 2.52 |
| | | | df | 24 | ---- | 24 | 24 | 24 | 24 |
| | | | p | 0.1345 | ---- | 0.0492 | 0.2468 | 0.5225 | 0.0140 |

Table A-2 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | 20/8 | 20/9 | 20/10 | 20/11 | 20/13 | 20/14 |
| | L | 1.44 | t | 0.08 | ---- | -0.07 | 2.00 | -0.53 | 1.12 |
| | | | df | 24 | ---- | 24 | 24 | 24 | 24 |
| | | | p | 0.9400 | ---- | 0.9413 | 0.0514 | 0.5947 | 0.2673 |
| | SVL | 1.16 | t | -0.38 | ---- | -0.91 | 1.62 | -0.90 | 1.71 |
| | | | df | 24 | ---- | 24 | 24 | 24 | 24 |
| | | | p | 0.7042 | ---- | 0.3697 | 0.1108 | 0.3696 | 0.0911 |
| | TL | 0.27 | t | 1.80 | ---- | 3.14 | 2.74 | 0.92 | -0.94 |
| | | | df | 24 | ---- | 24 | 24 | 24 | 24 |
| | | | p | 0.0797 | ---- | 0.0034 | 0.0086 | 0.3600 | 0.3501 |
| 20/10 | W | 0.22 | t | -0.48 | -2.04 | ---- | -0.96 | -2.85 | 0.27 |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 |
| | | | p | 0.6387 | 0.0492 | ---- | 0.3423 | 0.0060 | 0.7877 |
| | L | 1.43 | t | 0.13 | 0.07 | ---- | 2.10 | -0.47 | 1.20 |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 |
| | | | p | 0.8979 | 0.9413 | ---- | 0.0409 | 0.6412 | 0.2337 |
| | SVL | 1.11 | t | 0.45 | 0.91 | ---- | 2.55 | -0.00 | 2.60 |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 |
| | | | p | 0.6557 | 0.3697 | ---- | 0.0141 | 0.9965 | 0.0113 |

Table A-2 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | 20/8 | 20/9 | 20/10 | 20/11 | 20/13 | 20/14 |
| | TL | 0.32 | t | -1.13 | -3.14 | ---- | -0.12 | -1.94 | -3.33 |
| | | | df | 24 | 24 | ---- | 24 | 24 | 24 |
| | | | p | 0.2693 | 0.0034 | ---- | 0.9087 | 0.0567 | 0.0014 |
| 20/11 | W | 0.21 | t | 0.44 | -1.17 | 0.96 | ---- | -1.81 | 1.25 |
| | | | df | 24 | 24 | 24 | ---- | 24 | 24 |
| | | | p | 0.6596 | 0.2468 | 0.3423 | ---- | 0.0755 | 0.2161 |
| | L | 1.57 | t | -1.93 | -2.00 | -2.10 | ---- | -2.55 | -0.70 |
| | | | df | 24 | 24 | 24 | ---- | 24 | 24 |
| | | | p | 0.0597 | 0.0514 | 0.0409 | ---- | 0.0133 | 0.4878 |
| | SVL | 1.25 | t | -2.01 | -1.62 | -2.55 | ---- | -2.53 | 0.15 |
| | | | df | 24 | 24 | 24 | ---- | 24 | 24 |
| | | | p | 0.0505 | 0.1108 | 0.0141 | ---- | 0.0142 | 0.8801 |
| | TL | 0.32 | t | -1.08 | -2.74 | 0.12 | ---- | -1.77 | -3.13 |
| | | | df | 24 | 24 | 24 | ---- | 24 | 24 |
| | | | p | 0.2854 | 0.0086 | 0.9087 | ---- | 0.0817 | 0.0026 |
| 20/13 | W | 0.20 | t | 2.30 | 0.64 | 2.85 | 1.81 | ---- | 3.04 |
| | | | df | 24 | 24 | 24 | 24 | ---- | 24 |
| | | | p | 0.0251 | 0.5225 | 0.0060 | 0.0755 | ---- | 0.0033 |

Table A-2 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | 20/8 | 20/9 | 20/10 | 20/11 | 20/13 | 20/14 |
| | L | 1.40 | t | 0.61 | 0.53 | 0.47 | 2.55 | ---- | 1.52 |
| | | | df | 24 | 24 | 24 | 24 | ---- | 24 |
| | | | p | 0.5430 | 0.5947 | 0.6412 | 0.0133 | ---- | 0.1340 |
| | SVL | 1.11 | t | 0.52 | 0.90 | -0.00 | 2.53 | ---- | 2.43 |
| | | | df | 24 | 24 | 24 | 24 | ---- | 24 |
| | | | p | 0.6072 | 0.3696 | 0.9965 | 0.0142 | ---- | 0.0174 |
| | TL | 0.29 | t | 0.73 | -0.92 | 1.94 | 1.77 | ---- | -1.62 |
| | | | df | 24 | 24 | 24 | 24 | ---- | 24 |
| | | | p | 0.4671 | 0.3600 | 0.0567 | 0.0817 | ---- | 0.1100 |
| 20/14 | W | 0.22 | t | -0.80 | -2.52 | -0.27 | -1.25 | -3.04 | ---- |
| | | | df | 24 | 24 | 24 | 24 | 24 | ---- |
| | | | p | 0.4251 | 0.0140 | 0.7877 | 0.2161 | 0.0033 | ---- |
| | L | 1.52 | t | -1.05 | -1.12 | -1.20 | 0.70 | -1.52 | ---- |
| | | | df | 24 | 24 | 24 | 24 | 24 | ---- |
| | | | p | 0.2960 | 0.2673 | 0.2337 | 0.4878 | 0.1340 | ---- |
| | SVL | 1.26 | t | -2.08 | -1.71 | -2.60 | -0.15 | -2.43 | ---- |
| | | | df | 24 | 24 | 24 | 24 | 24 | ---- |
| | | | p | 0.0411 | 0.0911 | 0.0113 | 0.8801 | 0.0174 | ---- |
| | TL | 0.26 | t | 2.31 | 0.94 | 3.33 | 3.13 | 1.62 | ---- |
| | | | df | 24 | 24 | 24 | 24 | 24 | ---- |
| | | | p | 0.0240 | 0.3501 | 0.0014 | 0.0026 | 0.1100 | ---- |

*Data represent 12 months of growth.

Table A-3

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia fasciata* from Lake County, Tennessee Fed the Large Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | |
|---|---|---|---|---|---|---|
| | | | | 20/107 | 20/108 | 20/110 |
| 20/107 | W | 0.22 | t | ---- | 0.89 | 0.39 |
| | | | df | ---- | 26 | 26 |
| | | | p | ---- | 0.3804 | 0.6973 |
| | L | 1.07 | t | ---- | 1.76 | 3.38 |
| | | | df | ---- | 26 | 26 |
| | | | p | ---- | 0.0863 | 0.0023 |
| | SVL | 0.89 | t | ---- | 1.68 | 3.22 |
| | | | df | ---- | 26 | 26 |
| | | | p | ---- | 0.1015 | 0.0034 |
| | TL | 0.19 | t | ---- | 1.94 | 3.74 |
| | | | df | ---- | 26 | 26 |
| | | | p | ---- | 0.0593 | 0.0009 |
| 20/108 | W | 0.22 | t | -0.89 | ---- | -0.45 |
| | | | df | 26 | ---- | 26 |
| | | | p | 0.3804 | ---- | 0.6571 |
| | L | 1.26 | t | -1.76 | ---- | 1.46 |
| | | | df | 26 | ---- | 26 |
| | | | p | 0.0863 | ---- | 0.1525 |
| | SVL | 1.03 | t | -1.68 | ---- | 1.37 |
| | | | df | 26 | ---- | 26 |
| | | | p | 0.1015 | ---- | 0.1789 |
| | TL | 0.24 | t | -1.94 | ---- | 1.68 |
| | | | df | 26 | ---- | 26 |
| | | | p | 0.0593 | ---- | 0.1008 |

Table A-3 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals 20/107 | 20/108 | 20/110 |
|---|---|---|---|---|---|---|
| 20/110 | W | 0.22 | t | -0.39 | 0.45 | ---- |
| | | | df | 26 | 26 | ---- |
| | | | p | 0.6973 | 0.6571 | ---- |
| | L | 1.44 | t | -3.38 | -1.46 | ---- |
| | | | df | 26 | 26 | ---- |
| | | | p | 0.0023 | 0.1525 | ---- |
| | SVL | 1.15 | t | -3.22 | -1.37 | ---- |
| | | | df | 26 | 26 | ---- |
| | | | p | 0.0034 | 0.1789 | ---- |
| | TL | 0.29 | t | -3.74 | -1.68 | ---- |
| | | | df | 26 | 26 | ---- |
| | | | p | 0.0009 | 0.1008 | |

*Data represent 12 months of growth.

Table A-4

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia fasciata* from Lake County, Tennessee Fed the Large Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals 20/107 | 20/108 | 20/110 |
|---|---|---|---|---|---|---|
| 20/101 | W | 0.28 | t | ---- | -4.15 | -7.30 |
| | | | df | ---- | 26 | 26 |
| | | | p | ---- | 0.0003 | 0.0001 |
| | L | 0.96 | t | ---- | -0.26 | 0.75 |
| | | | df | ---- | 26 | 26 |
| | | | p | ---- | 0.7980 | 0.4604 |
| | SVL | 0.77 | t | ---- | 0.67 | 1.45 |
| | | | df | ---- | 26 | 26 |
| | | | p | ---- | 0.5102 | 0.1544 |
| | TL | 0.18 | t | ---- | -4.28 | -2.34 |
| | | | df | ---- | 26 | 26 |
| | | | p | ---- | 0.0002 | 0.0243 |
| 20/102 | W | 0.25 | t | 4.15 | ---- | -2.56 |
| | | | df | 26 | ---- | 26 |
| | | | p | 0.0003 | ---- | 0.0145 |
| | L | 0.93 | t | 0.26 | ---- | 0.92 |
| | | | df | 26 | ---- | 26 |
| | | | p | 0.7980 | ---- | 0.3654 |
| | SVL | 0.82 | t | -0.67 | ---- | 0.69 |
| | | | df | 26 | ---- | 26 |
| | | | p | 0.5102 | ---- | 0.4965 |
| | TL | 0.11 | t | 4.28 | ---- | -2.34 |
| | | | df | 26 | ---- | 26 |
| | | | p | 0.0002 | ---- | 0.0243 |

Table A-4 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals 20/107 | 20/108 | 20/109 |
|---|---|---|---|---|---|---|
| 20/104 | W | 0.24 | t | 7.30 | 2.56 | ---- |
| | | | df | 26 | 26 | ---- |
| | | | p | 0.0001 | 0.0145 | ---- |
| | L | 1.02 | t | -0.75 | -0.92 | ---- |
| | | | df | 26 | 26 | ---- |
| | | | p | 0.4604 | 0.3654 | ---- |
| | SVL | 0.88 | t | -1.45 | -0.69 | ---- |
| | | | df | 26 | 26 | ---- |
| | | | p | 0.1544 | 0.4965 | |
| | TL | 0.14 | t | 2.34 | -1.84 | ---- |
| | | | df | 26 | 26 | ---- |
| | | | p | 0.0243 | 0.0729 | ---- |

*Data represent 12 months of growth.

Table A-5

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 20/113 | 20/114 | 20/117 | 20/119 |
| 20/113 | W | 0.20 | t | ---- | -1.54 | 5.57 | 2.54 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.1375 | 0.0001 | 0.0144 |
| | L | 1.43 | t | ---- | 1.31 | 2.16 | 0.92 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.2019 | 0.0377 | 0.3638 |
| | SVL | 1.12 | t | ---- | 1.46 | 1.80 | 0.91 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.1578 | 0.0801 | 0.3695 |
| | TL | 0.30 | t | ---- | 0.63 | 3.25 | 0.88 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.5362 | 0.0025 | 0.3827 |
| 20/114 | W | 0.19 | t | 1.54 | ---- | 6.92 | 4.08 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.1375 | ---- | 0.0001 | 0.0002 |

Table A-5 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 20/113 | 20/114 | 20/117 | 20/119 |
| | L | 1.62 | t | -1.31 | ---- | 0.94 | -0.30 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.2019 | ---- | 0.3553 | 0.7630 |
| | SVL | 1.29 | t | -1.46 | ---- | 1.80 | -0.46 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.1578 | ---- | 0.0801 | 0.6469 |
| | TL | 0.32 | t | -0.63 | ---- | 2.62 | 0.29 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.5362 | ---- | 0.0129 | 0.7735 |
| 20/117 | W | 0.24 | t | -5.57 | -6.92 | ---- | -3.47 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0001 | 0.0001 | ---- | 0.0011 |
| | L | 1.177 | t | -2.16 | -0.94 | ---- | -1.28 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0377 | 0.3553 | ---- | 0.2063 |
| | SVL | 1.35 | t | -1.80 | -0.45 | ---- | -0.93 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0801 | 0.6589 | ---- | 0.3563 |
| | TL | 0.42 | t | -3.25 | -2.62 | ---- | -2.43 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0025 | 0.0129 | ---- | 0.0187 |

Table A-5 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 20/113 | 20/114 | 20/117 | 20/119 |
| 20/119 | W | 0.22 | t | -2.54 | -4.08 | 3.47 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.0144 | 0.0002 | 0.0011 | ---- |
| | L | 1.57 | t | -0.92 | 0.30 | 1.28 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.3638 | 0.7630 | 0.2063 | ---- |
| | SVL | 1.23 | t | -0.91 | 0.46 | 0.93 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.3695 | 0.6469 | 0.3563 | ---- |
| | TL | 0.33 | t | -0.88 | -0.29 | 2.43 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.3827 | 0.7735 | 0.0187 | |

*Data represent 12 months of growth.

Table A-6

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | |
|---|---|---|---|---|---|---|
| | | | | 20/105 | 20/106 | 20/118 |
| 20/105 | W | 0.24 | t | ---- | -0.08 | 0.77 |
| | | | df | ---- | 24 | 24 |
| | | | p | ---- | 0.9383 | 0.4446 |
| | L | 1.72 | t | ---- | 1.29 | 0.52 |
| | | | df | ---- | 24 | 24 |
| | | | p | ---- | 0.2097 | 0.6071 |
| | SVL | 1.39 | t | ---- | 1.11 | 0.50 |
| | | | df | ---- | 24 | 24 |
| | | | p | ---- | 0.2768 | 0.6204 |
| | TL | 0.33 | t | ---- | 1.97 | 0.55 |
| | | | df | ---- | 24 | 24 |
| | | | p | ---- | 0.0604 | 0.5873 |
| 20/106 | W | 0.24 | t | 0.08 | ---- | 0.85 |
| | | | df | 24 | ---- | 24 |
| | | | p | 0.9383 | ---- | 0.4014 |
| | L | 1.93 | t | -1.29 | ---- | -0.78 |
| | | | df | 24 | ---- | 24 |
| | | | p | 0.2097 | ---- | 0.4402 |
| | SVL | 1.54 | t | -1.11 | ---- | -0.64 |
| | | | df | 24 | ---- | 24 |
| | | | p | 0.2768 | ---- | 0.5275 |
| | TL | 0.39 | t | -1.97 | ---- | -1.38 |
| | | | df | 24 | ---- | 24 |
| | | | p | 0.0604 | ---- | 0.1750 |
| 20/118 | W | 0.24 | t | -0.77 | -0.85 | ---- |
| | | | df | 24 | 24 | ---- |
| | | | p | 0.4446 | 0.4014 | ---- |

Table A-6 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | |
|---|---|---|---|---|---|---|
| | | | | 20/105 | 20/106 | 20/118 |
| | L | 1.80 | t | -0.52 | 0.78 | ---- |
| | | | df | 24 | 24 | ---- |
| | | | p | 0.6071 | 0.4402 | ---- |
| | SVL | 1.45 | t | -0.50 | 0.64 | ---- |
| | | | df | 24 | 24 | ---- |
| | | | p | 0.6204 | 0.5275 | ---- |
| | TL | 0.35 | t | -0.55 | 1.38 | ---- |
| | | | df | 24 | 24 | ---- |
| | | | p | 0.5873 | 0.1750 | ---- |

*Data represent 12 months of growth.

Table A-7

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia cyclopion* Fed the Intermediate Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 21/104 | 21/106 | 21/108 | 21/110 |
| 21/104 | W | 0.18 | t | ---- | -8.19 | -8.99 | 1.39 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.0001 | 0.0001 | 0.1765 |
| | L | 1.40 | t | ---- | -2.23 | -2.47 | 0.82 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.0320 | 0.0173 | 0.4197 |
| | SVL | 1.07 | t | ---- | -2.92 | -3.30 | 0.72 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.0061 | 0.0018 | 0.4755 |
| | TL | 0.34 | t | ---- | -0.72 | -0.60 | 0.89 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.4746 | 0.5505 | 0.3798 |
| 21/106 | W | 0.13 | t | 8.19 | ---- | 1.07 | 9.41 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.0001 | ---- | 0.2880 | 0.0001 |

Table A-7 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 21/104 | 21/106 | 21/108 | 21/110 |
| | L | 1.13 | t | 2.23 | ---- | 0.28 | 2.87 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.0320 | ---- | 0.7836 | 0.0068 |
| | SVL | 0.83 | t | 2.92 | ---- | 0.26 | 3.51 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.0061 | ---- | 0.7925 | 0.0012 |
| | TL | 0.31 | t | 0.72 | ---- | 0.26 | 1.37 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.4746 | ---- | 0.7944 | 0.1805 |
| 21/108 | W | 0.14 | t | 8.99 | -1.07 | ---- | 10.54 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0001 | 0.2880 | ---- | 0.0001 |
| | L | 1.16 | t | 2.47 | -0.28 | ---- | 3.28 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0173 | 0.7836 | ---- | 0.0020 |
| | SVL | 0.85 | t | 3.30 | -0.26 | ---- | 4.05 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0018 | 0.7925 | ---- | 0.0002 |

Table A-7 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 21/104 | 21/106 | 21/108 | 21/110 |
| | TL | 0.32 | t | 0.60 | -0.26 | ---- | 1.42 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.5505 | 0.7944 | ---- | 0.1618 |
| 21/110 | W | 0.19 | t | -1.39 | -9.41 | -10.54 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.1765 | 0.0001 | 0.0001 | ---- |
| | L | 1.48 | t | -0.82 | -2.87 | -3.28 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.4197 | 0.0068 | 0.0020 | ---- |
| | SVL | 1.11 | t | -0.72 | -3.51 | -4.05 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.4755 | 0.0012 | 0.0002 | ---- |
| | TL | 0.37 | t | -0.89 | -1.37 | -1.42 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.3798 | 0.1805 | 0.1618 | ---- |

*Data represent 12 months of growth.

Table A-8

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia cyclopion* Fed the Intermediate Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 21/101 | 21/105 | 21/107 | 21/114 |
| 21/101 | W | 0.23 | t | ---- | -3.33 | -4.67 | 3.08 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.0028 | 0.0001 | 0.0034 |
| | L | 1.53 | t | ---- | -0.95 | -1.35 | 0.40 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.3522 | 0.1865 | 0.6924 |
| | SVL | 1.22 | t | ---- | -0.92 | -1.34 | 0.29 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.3643 | 0.1897 | 0.7724 |
| | TL | 0.31 | t | ---- | -0.94 | -1.19 | 0.70 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.3546 | 0.2406 | 0.4859 |
| 21/105 | W | 0.21 | t | 3.33 | ---- | -1.13 | 6.59 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.0028 | ---- | 0.2643 | 0.0001 |

Table A-8 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 21/101 | 21/105 | 21/107 | 21/114 |
| | L | 1.40 | t | 0.95 | ---- | -0.38 | 1.31 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.3522 | ---- | 0.7052 | 0.1952 |
| | SVL | 1.12 | t | 0.92 | ---- | -0.40 | 1.19 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.3643 | ---- | 0.6887 | 0.2403 |
| | TL | 0.28 | t | 0.94 | ---- | -0.25 | 1.55 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.3546 | ---- | 0.8064 | 0.1277 |
| 21/107 | W | 0.20 | t | 4.67 | 1.13 | ---- | 7.88 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0001 | 0.2643 | ---- | 0.0001 |
| | L | 1.35 | t | 1.35 | 0.38 | ---- | 1.71 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.1865 | 0.7052 | ---- | 0.0932 |
| | SVL | 1.07 | t | 1.34 | 0.40 | ---- | 1.61 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.1897 | 0.6887 | ---- | 0.1131 |

Table A-8 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 21/101 | 21/105 | 21/107 | 21/114 |
| | TL | 0.28 | t | 1.19 | 0.25 | ---- | 1.81 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.2406 | 0.8064 | ---- | 0.0768 |
| 21/114 | W | 0.25 | t | -3.08 | -6.59 | -7.88 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.0034 | 0.0001 | 0.0001 | ---- |
| | L | 1.58 | t | -0.40 | -1.31 | -1.71 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.6924 | 0.1952 | 0.0932 | ---- |
| | SVL | 1.25 | t | -0.29 | -1.19 | -1.61 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.7724 | 0.2403 | 0.1131 | ---- |
| | TL | 0.34 | t | -0.70 | -1.55 | -1.81 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.4859 | 0.1277 | 0.0768 | ---- |

*Data represent 12 months of growth.

Table A-9

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia rhombifera* Fed the Intermediate Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 22/7 | 22/19 | 22/23 | 22/31 |
| 22/7 | W | 0.19 | t | ---- | -9.78 | -2.85 | -3.03 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.0001 | 0.0065 | 0.0037 |
| | L | 1.03 | t | ---- | -3.28 | 0.45 | -0.32 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.0025 | 0.6552 | 0.7508 |
| | SVL | 0.71 | t | ---- | -3.16 | -0.09 | 0.77 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.0034 | 0.9270 | 0.4459 |
| | TL | 0.32 | t | ---- | -2.44 | 1.47 | -2.85 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.0205 | 0.1481 | 0.0061 |
| 22/19 | W | 0.14 | t | 9.78 | ---- | 7.45 | 8.00 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.0001 | ---- | 0.0001 | 0.0001 |

Table A-9 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 22/7 | 22/19 | 22/23 | 22/31 |
| | L | 0.78 | t | 3.28 | ---- | 3.71 | 2.99 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.0025 | ---- | 0.0006 | 0.0041 |
| | SVL | 0.52 | t | 3.16 | ---- | 3.12 | 3.94 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.0034 | ---- | 0.0031 | 0.0002 |
| | TL | 0.26 | t | 2.44 | ---- | 3.68 | -0.35 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.0205 | ---- | 0.0006 | 0.7310 |
| 22/23 | W | 0.18 | t | 2.85 | -7.45 | ---- | 0.03 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0065 | 0.0001 | ---- | 0.9798 |
| | L | 1.06 | t | -0.45 | -3.71 | ---- | -0.75 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.6552 | 0.0006 | ---- | 0.4582 |
| | SVL | 0.70 | t | 0.09 | -3.12 | ---- | 0.83 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.9270 | 0.0031 | ---- | 0.4115 |

Table A-9 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 22/7 | 22/19 | 22/23 | 22/31 |
| | TL | 0.36 | t | -1.47 | -3.68 | ---- | -4.32 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.1481 | 0.0006 | ---- | 0.0001 |
| 22/31 | W | 0.18 | t | 3.03 | -8.00 | -0.03 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.0037 | 0.0001 | 0.9798 | ---- |
| | L | 1.01 | t | 0.32 | -2.99 | 0.75 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.7508 | 0.0041 | 0.4582 | ---- |
| | SVL | 0.75 | t | -0.77 | -3.94 | -0.83 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.4459 | 0.0002 | 0.4115 | ---- |
| | TL | 0.25 | t | 2.85 | 0.35 | 4.32 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.0061 | 0.7310 | 0.0001 | ---- |

*Data represent 12 months of growth.

Table A-10

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia rhombifera* Fed the Intermediate Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 22/9 | 22/10 | 22/27 | 22/32 |
| 22/9 | W | 0.17 | t | ---- | -2.78 | 5.26 | 9.49 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.0104 | 0.0001 | 0.0001 |
| | L | 0.97 | t | ---- | -0.46 | 2.09 | 6.36 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.6492 | 0.0420 | 0.0001 |
| | SVL | 0.73 | t | ---- | -0.15 | 1.94 | 6.19 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.8846 | 0.0591 | 0.0001 |
| | TL | 0.24 | t | ---- | -1.47 | 2.07 | 5.36 |
| | | | df | ---- | 24 | 24 | 24 |
| | | | p | ---- | 0.1558 | 0.0443 | 0.0001 |
| 22/10 | W | 0.15 | t | 2.78 | ---- | 8.03 | 12.05 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.0104 | ---- | 0.0001 | 0.0001 |

Table A-10 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 22/9 | 22/10 | 22/27 | 22/32 |
| | L | 0.93 | t | 0.46 | ---- | 2.47 | 6.54 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.6492 | ---- | 0.0173 | 0.0001 |
| | SVL | 0.72 | t | 0.15 | ---- | 2.00 | 6.06 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.8846 | ---- | 0.0519 | 0.0001 |
| | TL | 0.21 | t | 1.47 | ---- | 3.25 | 6.36 |
| | | | df | 24 | ---- | 24 | 24 |
| | | | p | 0.1558 | ---- | 0.0022 | 0.0001 |
| 22/27 | W | 0.21 | t | -5.26 | -8.03 | ---- | 4.27 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0001 | 0.0001 | ---- | 0.0001 |
| | L | 1.16 | t | -2.09 | -2.47 | ---- | 4.26 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0420 | 0.0173 | ---- | 0.0001 |
| | SVL | 0.86 | t | -1.94 | -2.00 | ---- | 4.25 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0591 | 0.0519 | ---- | 0.0001 |

Table A-10 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 22/9 | 22/10 | 22/27 | 22/32 |
| | TL | 0.29 | t | -2.07 | -3.25 | ---- | 3.31 |
| | | | df | 24 | 24 | ---- | 24 |
| | | | p | 0.0443 | 0.0022 | ---- | 0.0016 |
| 22/32 | W | 0.24 | t | -9.49 | -12.05 | -4.27 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.0001 | 0.0001 | 0.0001 | ---- |
| | L | 1.55 | t | -6.36 | -6.54 | -4.26 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.0001 | 0.0001 | 0.0001 | ---- |
| | SVL | 1.17 | t | -6.19 | -6.06 | -4.25 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.0001 | 0.0001 | 0.0001 | ---- |
| | TL | 0.38 | t | -5.36 | -6.36 | -3.31 | ---- |
| | | | df | 24 | 24 | 24 | ---- |
| | | | p | 0.0001 | 0.0001 | 0.0016 | ---- |

*Data represent 12 months of growth.

Table A-11

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia fasciata* Fed the Small Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | |
|---|---|---|---|---|---|---|
| | | | | 20/111 | 20/112 | 20/122 |
| 20/111 | W | 0.22 | t | ---- | -4.69 | -0.98 |
| | | | df | ---- | 18 | 18 |
| | | | p | ---- | 0.0002 | 0.3378 |
| | L | 1.82 | t | ---- | 0.06 | 0.35 |
| | | | df | ---- | 18 | 18 |
| | | | p | ---- | 0.9492 | 0.7324 |
| | SVL | 1.46 | t | ---- | 0.25 | -0.23 |
| | | | df | ---- | 18 | 18 |
| | | | p | ---- | 0.8028 | 0.8179 |
| | TL | 0.35 | t | ---- | -0.48 | 2.18 |
| | | | df | ---- | 18 | 18 |
| | | | p | ---- | 0.6391 | 0.0381 |
| 20/112 | W | 0.20 | t | 4.69 | ---- | -1.82 |
| | | | df | 18 | ---- | 18 |
| | | | p | 0.0002 | ---- | 0.0801 |
| | L | 1.83 | t | -0.06 | ---- | 0.29 |
| | | | df | 18 | ---- | 18 |
| | | | p | 0.9492 | ---- | 0.7770 |
| | SVL | 1.49 | t | -0.25 | ---- | -0.42 |
| | | | df | 18 | ---- | 18 |
| | | | p | 0.8028 | ---- | 0.6758 |
| | TL | 0.34 | t | 0.48 | ---- | 2.55 |
| | | | df | 18 | 18 | 18 |
| | | | p | 0.6391 | ---- | 0.0166 |
| 20/122 | W | 0.21 | t | 0.98 | -1.82 | ---- |
| | | | df | 18 | 18 | ---- |
| | | | p | 0.3378 | 0.0801 | ---- |

Table A-11 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | |
|---|---|---|---|---|---|---|
| | | | | 20/111 | 20/112 | 20/122 |
| | L | 1.87 | t | -0.35 | -0.29 | ---- |
| | | | df | 18 | 18 | ---- |
| | | | p | 0.7324 | 0.7770 | ---- |
| | SVL | 1.43 | t | 0.23 | 0.42 | ---- |
| | | | df | 18 | 18 | ---- |
| | | | p | 0.8179 | 0.6758 | ---- |
| | TL | 0.44 | t | -2.18 | -2.55 | ---- |
| | | | df | 18 | 18 | ---- |
| | | | p | 0.0381 | 0.0166 | ---- |

*Data Represent 10 months of growth.

Table A-12

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Female *Nerodia fasciata* Fed the Small Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals 20/115 | Individuals 20/121 |
|---|---|---|---|---|---|
| 20/115 | W | 0.21 | t | ---- | -4.20 |
| | | | df | ---- | 14 |
| | | | p | ---- | 0.0009 |
| | L | 2.24 | t | ---- | -2.35 |
| | | | df | ---- | 14 |
| | | | p | ---- | 0.0338 |
| | SVL | 1.88 | t | ---- | -2.18 |
| | | | df | ---- | 14 |
| | | | p | ---- | 0.0466 |
| | TL | 0.36 | t | ---- | -2.28 |
| | | | df | ---- | 14 |
| | | | p | ---- | 0.0384 |
| 20/121 | W | 0.16 | t | 4.20 | ---- |
| | | | df | 14 | ---- |
| | | | p | 0.0009 | ---- |
| | L | 1.89 | t | 2.35 | ---- |
| | | | df | 14 | ---- |
| | | | p | 0.0338 | ---- |
| | SVL | 1.63 | t | 2.18 | ---- |
| | | | df | 14 | ---- |
| | | | p | 0.0466 | ---- |
| | TL | 0.27 | t | 2.28 | ---- |
| | | | df | 14 | ---- |
| | | | p | 0.0384 | ---- |

*Data represent 8 months of growth.

Table A-13

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Individual Male *Nerodia rhombifera* Fed the Small Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals 22/25 | 22/29 | 22/30 |
|---|---|---|---|---|---|---|
| 22/25 | W | 0.15 | t | ---- | -0.14 | -0.39 |
| | | | df | ---- | 19 | 19 |
| | | | p | ---- | 0.8925 | 0.6991 |
| | L | 1.07 | t | ---- | -0.42 | -0.79 |
| | | | df | ---- | 19 | 19 |
| | | | p | ---- | 0.6795 | 0.4378 |
| | SVL | 0.74 | t | ---- | 0.05 | -0.88 |
| | | | df | ---- | 19 | 19 |
| | | | p | ---- | 0.9601 | 0.3891 |
| | TL | 0.33 | t | ---- | -1.05 | -0.46 |
| | | | df | ---- | 19 | 19 |
| | | | p | ---- | 0.3020 | 0.6493 |
| 22/29 | W | 0.15 | t | 0.14 | ---- | -0.28 |
| | | | df | 19 | 19 | 18 |
| | | | p | 0.8925 | ---- | 0.7788 |
| | L | 1.04 | t | 0.42 | ---- | -0.36 |
| | | | df | 19 | ---- | 18 |
| | | | p | 0.6795 | ---- | 0.7196 |
| | SVL | 0.74 | t | -0.05 | ---- | -0.84 |
| | | | df | 19 | ---- | 18 |
| | | | p | 0.9601 | ---- | 0.4075 |
| | TL | 0.29 | t | 1.05 | ---- | 0.52 |
| | | | df | 19 | ---- | 18 |
| | | | p | 0.3020 | ---- | 0.6064 |
| 22/30 | W | 0.14 | t | 0.39 | 0.28 | ---- |
| | | | df | 19 | 18 | ---- |
| | | | p | 0.6991 | 0.7788 | ---- |

Table A-13 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals 22/25 | 22/29 | 22/30 |
|---|---|---|---|---|---|---|
| | L | 1.01 | t | 0.79 | 0.36 | ---- |
| | | | df | 19 | 18 | ---- |
| | | | p | 0.4378 | 0.7196 | ---- |
| | SVL | 0.70 | t | 0.88 | 0.84 | ---- |
| | | | df | 19 | 18 | ---- |
| | | | p | 0.3891 | 0.4075 | ---- |
| | TL | 0.31 | t | 0.46 | -0.52 | ---- |
| | | | df | 19 | 18 | ---- |
| | | | p | 0.6493 | 0.6064 | ---- |

*Data represent 10 months of growth.

Table A-14

Comparisons of Production-Ingestion (P-I) Ratios for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL), for Individual Female *Nerodia rhombifera* Fed the Small Meal Size*

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 22/1 | 22/11 | 22/24 | 22/33 |
| 22/1 | W | 0.22 | t | ---- | -2.95 | -4.29 | -4.00 |
| | | | df | ---- | 20 | 19 | 19 |
| | | | p | ---- | 0.0080 | 0.0002 | 0.0003 |
| | L | 1.62 | t | ---- | -2.35 | -4.69 | -2.87 |
| | | | df | ---- | 20 | 19 | 19 |
| | | | p | ---- | 0.0291 | 0.0001 | 0.0067 |
| | SVL | 1.24 | t | ---- | -2.03 | -4.60 | -2.53 |
| | | | df | ---- | 20 | 19 | 19 |
| | | | p | ---- | 0.0554 | 0.0001 | 0.0157 |
| | TL | 0.38 | t | ---- | -3.05 | -4.19 | -3.39 |
| | | | df | ---- | 20 | 19 | 19 |
| | | | p | ---- | 0.0064 | 0.0002 | 0.0016 |
| 22/11 | W | 0.18 | t | 2.95 | ---- | -1.00 | -0.66 |
| | | | df | 20 | ---- | 19 | 19 |
| | | | p | 0.0080 | ---- | 0.3264 | 0.5152 |

Table A-14 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 22/1 | 22/11 | 22/24 | 22/33 |
| | L | 1.31 | t | 2.35 | ---- | -2.35 | -0.32 |
| | | | df | 20 | ---- | 19 | 19 |
| | | | p | 0.0291 | ---- | 0.0259 | 0.7491 |
| | SVL | 1.02 | t | 2.03 | ---- | -2.52 | -0.28 |
| | | | df | 20 | ---- | 19 | 19 |
| | | | p | 0.0554 | ---- | 0.0175 | 0.7782 |
| | TL | 0.29 | t | 3.05 | ---- | -1.34 | -0.38 |
| | | | df | 20 | ---- | 19 | 19 |
| | | | p | 0.0064 | ---- | 0.1900 | 0.7039 |
| 22/24 | W | 0.17 | t | 4.29 | 1.00 | ---- | 0.37 |
| | | | df | 19 | 19 | ---- | 18 |
| | | | p | 0.0002 | 0.3264 | ---- | 0.7154 |
| | L | 0.99 | t | 4.69 | 2.35 | ---- | 2.28 |
| | | | df | 19 | 19 | ---- | 18 |
| | | | p | 0.0001 | 0.0259 | ---- | 0.0281 |
| | SVL | 0.74 | t | 4.60 | 2.52 | ---- | 2.49 |
| | | | df | 19 | 19 | ---- | 18 |
| | | | p | 0.0001 | 0.0175 | ---- | 0.0171 |

Table A-14 (Continued)

| Focal Individual | Parameter | P-I Ratio | Statistics | Individuals | | | |
|---|---|---|---|---|---|---|---|
| | | | | 22/1 | 22/11 | 22/24 | 22/33 |
| | TL | 0.25 | t | 4.19 | 1.34 | ---- | 1.06 |
| | | | df | 19 | 19 | ---- | 18 |
| | | | p | 0.0002 | 0.1900 | ---- | 0.2963 |
| 22/33 | W | 0.18 | t | 4.00 | 0.66 | -0.37 | ---- |
| | | | df | 19 | 19 | 18 | ---- |
| | | | p | 0.0003 | 0.5152 | 0.7154 | ---- |
| | L | 1.27 | t | 2.87 | 0.32 | -2.28 | ---- |
| | | | df | 19 | 19 | 18 | ---- |
| | | | p | 0.0067 | 0.7491 | 0.0281 | ---- |
| | SVL | 0.99 | t | 2.53 | 0.28 | -2.49 | ---- |
| | | | df | 19 | 19 | 18 | ---- |
| | | | p | 0.0157 | 0.7782 | 0.0171 | ---- |
| | TL | 0.28 | t | 3.39 | 0.38 | -1.06 | ---- |
| | | | df | 19 | 19 | 18 | ---- |
| | | | p | 0.0016 | 0.7039 | 0.2963 | ---- |

*Data represent 10 months of growth.

Table A-15

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia fasciata* from Shelby County, Tennessee

| Focal Individual | *Slope ($\times 10^7$) | Statis-tics | Individuals | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | 20/1 | 20/2 | 20/3 | 20/4 | 20/5 | 20/6 | 20/12 |
| 20/1 | 7.25 | t | ---- | | | | | | |
| | | df | ---- | | | | | | |
| | | p | ---- | | | | | | |
| 20/2 | 7.47 | t | -0.70 | ---- | | | | | |
| | | df | 54 | ---- | | | | | |
| | | p | 0.4886 | ---- | | | | | |
| 20/3 | 6.78 | t | 1.27 | 2.41 | ---- | | | | |
| | | df | 54 | 54 | ---- | | | | |
| | | p | 0.2080 | 0.0182 | ---- | | | | |
| 20/4 | 6.10 | t | 3.05 | 4.38 | 2.06 | ---- | | | |
| | | df | 54 | 54 | 54 | ---- | | | |
| | | p | 0.0029 | 0.0001 | 0.0420 | ---- | | | |
| 20/5 | 6.34 | t | 2.87 | 4.69 | 1.68 | -0.75 | ---- | | |
| | | df | 54 | 54 | 54 | 54 | ---- | | |
| | | p | 0.0047 | 0.0001 | 0.0949 | 0.4564 | ---- | | |
| 20/6 | 7.80 | t | -1.72 | -1.35 | -3.85 | -5.40 | -5.71 | ---- | |
| | | df | 54 | 54 | 54 | 54 | 54 | ---- | |
| | | p | 0.0873 | 0.1785 | 0.0002 | 0.0001 | 0.0001 | ---- | |

Table A-15 (Continued)

| Focal Individual | *Slope ($\times 10^7$) | Statis-tics | Individuals | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | 20/1 | 20/2 | 20/3 | 20/4 | 20/5 | 20/6 | 20/12 |
| 20/12 | 7.19 | t | 0.19 | 1.05 | -1.41 | -3.27 | -3.03 | 2.12 | ---- |
| | | df | 54 | 54 | 54 | 54 | 54 | 54 | ---- |
| | | p | 0.8461 | 0.2966 | 0.1603 | 0.0013 | 0.0028 | 0.0350 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-16

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia fasciata* from Shelby County, Tennessee

| Focal Individual | *Slope ($\times 10^7$) | Statistics | Individuals | | | | |
|---|---|---|---|---|---|---|---|
| | | | 20/8 | 20/10 | 20/11 | 20/13 | 20/14 |
| 20/8 | 5.81 | t | ---- | | | | |
| | | df | ---- | | | | |
| | | p | ---- | | | | |
| 20/10 | 7.34 | t | -6.27 | ---- | | | |
| | | df | 54 | ---- | | | |
| | | p | 0.0001 | ---- | | | |
| 20/11 | 5.82 | t | -0.06 | 7.55 | ---- | | |
| | | df | 54 | 54 | ---- | | |
| | | p | 0.9535 | 0.0001 | ---- | | |
| 20/13 | 6.68 | t | -3.77 | 2.80 | -4.05 | ---- | |
| | | df | 54 | 54 | 54 | ---- | |
| | | p | 0.0003 | 0.0061 | 0.0001 | ---- | |
| 20/14 | 5.42 | t | 1.78 | 8.82 | 2.01 | 5.90 | ---- |
| | | df | 54 | 54 | 54 | 54 | ---- |
| | | p | 0.0768 | 0.0001 | 0.0469 | 0.0001 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-17

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia fasciata* from Lake County, Tennessee Fed the Large Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 20/107 | 20/108 | 20/110 |
|---|---|---|---|---|---|
| 20/107 | 11.06 | t | ---- | | |
| | | df | ---- | | |
| | | p | ---- | | |
| 20/108 | 8.66 | t | 5.59 | ---- | |
| | | df | 26 | ---- | |
| | | p | 0.0001 | ---- | |
| 20/110 | 7.69 | t | 7.78 | -2.38 | ---- |
| | | df | 26 | 26 | ---- |
| | | p | 0.0001 | 0.0225 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-18

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia fasciata* from Lake County, Tennessee Fed the Large Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 20/101 | 20/102 | 20/104 |
|---|---|---|---|---|---|
| 20/101 | 8.27 | t | ---- | | |
| | | df | ---- | | |
| | | p | ---- | | |
| 20/102 | 8.86 | t | -1.16 | ---- | |
| | | df | 26 | ---- | |
| | | p | 0.2564 | ---- | |
| 20/104 | 7.42 | t | 1.85 | 2.78 | ---- |
| | | df | 26 | 26 | ---- |
| | | p | 0.0714 | 0.0084 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-19

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 20/113 | 20/114 | 20/117 | 20/119 |
|---|---|---|---|---|---|---|
| 20/113 | 8.22 | t | ---- | | | |
| | | df | ---- | | | |
| | | p | ---- | | | |
| 20/114 | 8.30 | t | -0.23 | ---- | | |
| | | df | 26 | ---- | | |
| | | p | 0.8203 | ---- | | |
| 20/117 | 7.45 | t | 2.29 | 2.64 | ---- | |
| | | df | 26 | 26 | ---- | |
| | | p | 0.0276 | 0.0119 | ---- | |
| 20/119 | 6.89 | t | 3.93 | 4.36 | 1.85 | ---- |
| | | df | 26 | 26 | 26 | ---- |
| | | p | 0.0003 | 0.0001 | 0.0706 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-20

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia fasciata* from Lake County, Tennessee Fed the Intermediate Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 20/105 | 20/106 | 20/118 |
|---|---|---|---|---|---|
| 20/105 | 6.35 | t | ---- | | |
| | | df | ---- | | |
| | | p | ---- | | |
| 20/106 | 5.54 | t | 7.26 | ---- | |
| | | df | 26 | ---- | |
| | | p | 0.0001 | ---- | |
| 20/118 | 6.40 | t | -0.29 | -5.56 | ---- |
| | | df | 26 | 26 | ---- |
| | | p | 0.7767 | 0.0001 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-21

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia cyclopion* Fed the Intermediate Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 21/104 | 21/106 | 21/108 | 21/110 |
|---|---|---|---|---|---|---|
| 21/104 | 6.64 | t | ---- | | | |
| | | df | ---- | | | |
| | | p | ---- | | | |
| 21/106 | 6.82 | t | -0.50 | ---- | | |
| | | df | 26 | ---- | | |
| | | p | 0.6200 | ---- | | |
| 21/108 | 6.66 | t | -0.07 | 0.40 | ---- | |
| | | df | 26 | 26 | ---- | |
| | | p | 0.9422 | 0.6942 | ---- | |
| 21/110 | 6.87 | t | -1.17 | -0.14 | -0.75 | ---- |
| | | df | 26 | 26 | 26 | ---- |
| | | p | 0.2514 | 0.8916 | 0.4565 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-22

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia cyclopion* Fed the Intermediate Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 20/101 | 21/105 | 21/107 | 21/114 |
|---|---|---|---|---|---|---|
| 21/101 | 6.16 | t | ---- | | | |
| | | df | ---- | | | |
| | | p | ---- | | | |
| 21/105 | 7.03 | t | -2.68 | ---- | | |
| | | df | 26 | ---- | | |
| | | p | 0.0127 | ---- | | |
| 21/107 | 6.42 | t | -1.02 | 2.11 | ---- | |
| | | df | 26 | 26 | ---- | |
| | | p | 0.3145 | 0.0415 | ---- | |
| 21/114 | 6.74 | t | -2.46 | 1.12 | -1.32 | ---- |
| | | df | 26 | 26 | 26 | ---- |
| | | p | 0.0173 | 0.2660 | 0.1931 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-23

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia rhombifera* Fed the Intermediate Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 22/7 | 22/19 | 22/23 | 22/31 |
|---|---|---|---|---|---|---|
| 22/7 | 8.64 | t | ---- | | | |
| | | df | ---- | | | |
| | | p | ---- | | | |
| 22/19 | 9.28 | t | -1.99 | ---- | | |
| | | df | 26 | ---- | | |
| | | p | 0.0577 | ---- | | |
| 22/23 | 8.73 | t | -0.28 | 1.65 | ---- | |
| | | df | 26 | 26 | ---- | |
| | | p | 0.7814 | 0.1061 | ---- | |
| 22/31 | 9.02 | t | -1.34 | 0.80 | -1.02 | ---- |
| | | df | 26 | 26 | 26 | ---- |
| | | p | 0.1855 | 0.4276 | 0.3138 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-24

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia rhombifera* Fed the Intermediate Meal Size

| Focal Individual | Score* ($\times 10^7$) | Statistics | Individuals 22/9 | 22/10 | 22/27 | 22/32 |
|---|---|---|---|---|---|---|
| 22/9 | 7.38 | t | ---- | | | |
| | | df | ---- | | | |
| | | p | ---- | | | |
| 22/10 | 8.51 | t | -4.74 | ---- | | |
| | | df | 26 | ---- | | |
| | | p | 0.0001 | ---- | | |
| 22/27 | 7.84 | t | -2.27 | 3.10 | ---- | |
| | | df | 26 | 26 | ---- | |
| | | p | 0.0289 | 0.0036 | ---- | |
| 22/32 | 7.32 | t | 0.23 | 4.83 | 2.58 | ---- |
| | | df | 26 | 26 | 26 | ---- |
| | | p | 0.8180 | 0.0001 | 0.0128 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-25

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia fasciata* from Lake County, Tennessee Fed the Small Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 20/111 | 20/112 | 20/122 |
|---|---|---|---|---|---|
| 20/111 | 7.12 | t | ---- | | |
| | | df | ---- | | |
| | | p | ---- | | |
| 20/112 | 6.70 | t | 2.85 | ---- | |
| | | df | 18 | ---- | |
| | | p | 0.0107 | ---- | |
| 20/122 | 6.78 | t | 1.61 | -0.38 | ---- |
| | | df | 18 | 18 | ---- |
| | | p | 0.1194 | 0.7106 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-26

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia fasciata* from Lake County, Tennessee Fed the Small Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 20/115 | Individuals 20/121 |
|---|---|---|---|---|
| 20/115 | 5.49 | t | ---- | |
| | | df | ---- | |
| | | p | ---- | |
| 20/121 | 6.42 | t | -4.44 | ---- |
| | | df | 14 | ---- |
| | | p | 0.0006 | ---- |

*Of regression grams per millimeter of SVL and $SVL^2$.

Table A-27

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Male *Nerodia rhombifera* Fed the Small Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 22/25 | 22/29 | 22/30 |
|---|---|---|---|---|---|
| 22/25 | 8.30 | t | ---- | | |
| | | df | ---- | | |
| | | p | ---- | | |
| 22/29 | 9.20 | t | -1.23 | ---- | |
| | | df | 19 | ---- | |
| | | p | 0.2281 | ---- | |
| 22/30 | 10.04 | t | -2.15 | -1.08 | ---- |
| | | df | 19 | 18 | ---- |
| | | p | 0.0447 | 0.2892 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-28

Comparisons of Individual Rates of Increase in Weight Per Unit Length (W/SVL) for Female *Nerodia rhombifera* Fed the Small Meal Size

| Focal Individual | Slope* ($\times 10^7$) | Statistics | Individuals 22/1 | 22/11 | 22/24 | 22/33 |
|---|---|---|---|---|---|---|
| 22/1 | 5.68 | t | ---- | | | |
| | | df | ---- | | | |
| | | p | ---- | | | |
| 22/11 | 5.76 | t | -0.14 | ---- | | |
| | | df | 20 | ---- | | |
| | | p | 0.8928 | ---- | | |
| 22/24 | 9.03 | t | -4.61 | -4.20 | ---- | |
| | | df | 19 | 19 | ---- | |
| | | p | 0.0001 | 0.0002 | ---- | |
| 22/33 | 7.55 | t | -3.24 | -2.83 | 2.01 | ---- |
| | | df | 19 | 19 | 18 | ---- |
| | | p | 0.0025 | 0.0073 | 0.0518 | ---- |

*Of regression grams per millimeter of SVL on $SVL^2$.

Table A-29

Estimates of the Asymptotes and Growth Constant Values (r) for Weight (W), Total Length (L), Snout-Vent Length (SVL), and Tail Length (TL) for Three Species of *Nerodia* from Lake County, Tennessee from the Bertalanffy Growth Model

| Individual | Species | Sex | Age (Years) | Parameter | Predicted Asymptote | | Predicted r | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Value (mm) | 95% Confidence Interval (mm) | Value | 95% Confidence Interval |
| 20/113 | *N. fasciata* | ♂ | 2 | W (g) | 80.6 | 77.3-83.9 | 0.0067 | 0.0055-0.0079 |
| | | | | L (mm) | 586 | 560 -613 | 0.0073 | 0.0061-0.0085 |
| | | | | SVL (mm) | 470 | 446 -494 | 0.0067 | 0.0055-0.0079 |
| | | | | TL (mm) | 118 | 112 -124 | 0.0103 | 0.0081-0.0125 |
| 20/114 | *N. fasciata* | ♂ | 2 | W (g) | 87.0 | 82.9-91.0 | 0.0063 | 0.0058-0.0069 |
| | | | | L (mm) | 594 | 581 -606 | 0.0067 | 0.0063-0.0072 |
| | | | | SVL (mm) | 483 | 470 -495 | 0.0063 | 0.0058-0.0069 |
| | | | | TL (mm) | 112 | 109 -116 | 0.0086 | 0.0075-0.0097 |
| 20/117 | *N. fasciata* | ♂ | 2 | W (g) | 94.1 | 89.1-99.0 | 0.0071 | 0.0061-0.0082 |
| | | | | L (mm) | 662 | 634 -689 | 0.0072 | 0.0062-0.0082 |
| | | | | SVL (mm) | 511 | 488 -534 | 0.0071 | 0.0061-0.0082 |
| | | | | TL (mm) | 151 | 144 -157 | 0.0074 | 0.0064-0.0085 |
| 20/119 | *N. fasciata* | ♂ | 2 | W (g) | 89.1 | 85.5-92.7 | 0.0065 | 0.0056-0.0075 |
| | | | | L (mm) | 652 | 627 -677 | 0.0068 | 0.0059-0.0078 |
| | | | | SVL (mm) | 516 | 493 -537 | 0.0065 | 0.0056-0.0075 |
| | | | | TL (mm) | 137 | 132 -142 | 0.0081 | 0.0069-0.0093 |

Table A-29 (Continued)

| Individual | Species | Sex | Age (Years) | Parameter | Predicted Asymptote | | Predicted r | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Value (mm) | 95% Confidence Interval (mm) | Value | 95% Confidence Interval |
| 20/105 | *N. fasciata* | ♀ | 2 | W (g) | 122.3 | 118.7-125.9 | 0.0055 | 0.0047-0.0064 |
| | | | | L (mm) | 733 | 698 -768 | 0.0054 | 0.0046-0.0062 |
| | | | | SVL (mm) | 581 | 553 -610 | 0.0055 | 0.0047-0.0064 |
| | | | | TL (mm) | 152 | 144 -159 | 0.0051 | 0.0043-0.0059 |
| 20/106 | *N. fasciata* | ♀ | 2 | W (g) | 100.7 | 98.2-103.2 | 0.0065 | 0.0057-0.0072 |
| | | | | L (mm) | 709 | 686 -731 | 0.0063 | 0.0057-0.0069 |
| | | | | SVL (mm) | 563 | 542 -585 | 0.0065 | 0.0057-0.0072 |
| | | | | TL (mm) | 145 | 138 -152 | 0.0057 | 0.0049-0.0065 |
| 20/118 | *N. fasciata* | ♀ | 2 | W (g) | 108.4 | 104.1-110.7 | 0.0063 | 0.0055-0.0071 |
| | | | | L (mm) | 689 | 663 -715 | 0.0064 | 0.0056-0.0071 |
| | | | | SVL (mm) | 561 | 539 -583 | 0.0063 | 0.0055-0.0071 |
| | | | | TL (mm) | 129 | 124 -134 | 0.0068 | 0.0059-0.0077 |
| 21/104 | *N. cyclopion* | ♂ | 2 | W (g) | 77.4 | 75.8-79.0 | 0.0061 | 0.0053-0.0070 |
| | | | | L (mm) | 602 | 574 -630 | 0.0066 | 0.0055-0.0076 |
| | | | | SVL (mm) | 469 | 448 -489 | 0.0061 | 0.0053-0.0070 |
| | | | | TL (mm) | 135 | 125 -144 | 0.0082 | 0.0060-0.0104 |
| 21/106 | *N. cyclopion* | ♂ | 2 | W (g) | 37.4 | 36.7-38.1 | 0.0090 | 0.0051-0.0128 |
| | | | | L (mm) | 462 | 425 -500 | 0.0111 | 0.0063-0.0160 |
| | | | | SVL (mm) | 362 | 328 -395 | 0.0090 | 0.0051-0.0128 |
| | | | | TL (mm) | 105 | 98 -111 | 0.0227 | 0.0111-0.0343 |

Table A-29 (Continued)

| Individual | Species | Sex | Age (Years) | Parameter | Predicted Asymptote | | Predicted r | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Value (mm) | 95% Confidence Interval (mm) | Value | 95% Confidence Interval |
| 21/108 | *N. cyclopion* | ♂ | 2 | W (g) | 110.8 | 108.9-112.6 | 0.0034 | 0.0020-0.0048 |
| | | | | L (mm) | 624 | 556 -693 | 0.0045 | 0.0031-0.0059 |
| | | | | SVL (mm) | 525 | 437 -613 | 0.0034 | 0.0020-0.0048 |
| | | | | TL (mm) | 129 | 120 -137 | 0.0081 | 0.0059-0.0102 |
| 21/110 | *N. cyclopion* | ♂ | 2 | W (g) | 69.9 | 69.0-70.9 | 0.0064 | 0.0057-0.0071 |
| | | | | L (mm) | 611 | 594 -628 | 0.0064 | 0.0059-0.0070 |
| | | | | SVL (mm) | 461 | 445 -478 | 0.0064 | 0.0057-0.0071 |
| | | | | TL (mm) | 150 | 139 -160 | 0.0066 | 0.0051-0.0081 |
| 21/101 | *N. cyclopion* | ♀ | 2 | W (g) | 120.1 | 116.9-123.3 | 0.0055 | 0.0048-0.0061 |
| | | | | L (mm) | 720 | 697 -745 | 0.0054 | 0.0048-0.0061 |
| | | | | SVL (mm) | 570 | 550 -590 | 0.0055 | 0.0048-0.0061 |
| | | | | TL (mm) | 151 | 145 -157 | 0.0053 | 0.0045-0.0061 |
| 21/105 | *N. cyclopion* | ♀ | 2 | W (g) | 94.6 | 90.8-98.4 | 0.0063 | 0.0052-0.0074 |
| | | | | L (mm) | 637 | 611 -664 | 0.0067 | 0.0056-0.0077 |
| | | | | SVL (mm) | 514 | 490 -537 | 0.0063 | 0.0052-0.0074 |
| | | | | TL (mm) | 125 | 120 -130 | 0.0084 | 0.0069-0.0098 |
| 21/107 | *N. cyclopion* | ♀ | 2 | W (g) | 135.0 | 132.5-137.4 | 0.0042 | 0.0032-0.0053 |
| | | | | L (mm) | 724 | 676 -772 | 0.0044 | 0.0035-0.0054 |
| | | | | SVL (mm) | 586 | 542 -629 | 0.0042 | 0.0032-0.0053 |
| | | | | TL (mm) | 139 | 130 -149 | 0.0052 | 0.0039-0.0064 |

Table A-29 (Continued)

| Individual | Species | Sex | Age (Years) | Parameter | Predicted Asymptote | | Predicted r | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Value (mm) | 95% Confidence Interval (mm) | Value | 95% Confidence Interval |
| 21/114 | *N. cyclopion* | ♀ | 2 | W (g) | 114.2 | 111.8-116.6 | 0.0058 | 0.0049-0.0066 |
| | | | | L (mm) | 699 | 668 -731 | 0.0059 | 0.0050-0.0068 |
| | | | | SVL (mm) | 553 | 527 -578 | 0.0058 | 0.0049-0.0066 |
| | | | | TL (mm) | 147 | 138 -156 | 0.0065 | 0.0051-0.0080 |
| 22/7 | *N. rhombifera* | ♂ | 2 | W (g) | 159.8 | 156.8-162.8 | 0.0027 | 0.0022-0.0033 |
| | | | | L (mm) | 714 | 685 -743 | 0.0037 | 0.0032-0.0043 |
| | | | | SVL (mm) | 588 | 550 -625 | 0.0027 | 0.0022-0.0033 |
| | | | | TL (mm) | 152 | 147 -157 | 0.0072 | 0.0058-0.0085 |
| 22/19 | *N. rhombifera* | ♂ | 2 | W (g) | 175.5 | 173.9-181 | 0.0018 | 0.0008-0.0029 |
| | | | | L (mm) | 729 | 640 -818 | 0.0025 | 0.0015-0.0035 |
| | | | | SVL (mm) | 596 | 470 -722 | 0.0018 | 0.0008-0.0029 |
| | | | | TL (mm) | 168 | 158 -177 | 0.0045 | 0.0034-0.0055 |
| 22/23 | *N. rhombifera* | ♂ | 2 | W (g) | 166.3 | 163.7-168.9 | 0.0025 | 0.0019-0.0031 |
| | | | | L (mm) | 745 | 706 -784 | 0.0032 | 0.0027-0.0038 |
| | | | | SVL (mm) | 592 | 545 -639 | 0.0025 | 0.0019-0.0031 |
| | | | | TL (mm) | 175 | 164 -186 | 0.0051 | 0.0039-0.0063 |
| 22/31 | *N. rhombifera* | ♂ | 2 | W (g) | 127.9 | 124.4-131.4 | 0.0033 | 0.0026-0.0041 |
| | | | | L (mm) | 725 | 679 -770 | 0.0032 | 0.0025-0.0038 |
| | | | | SVL (mm) | 543 | 505 -580 | 0.0033 | 0.0026-0.0041 |
| | | | | TL (mm) | 183 | 169 -197 | 0.0028 | 0.0022-0.0034 |

Table A-29 (Continued)

| Individual | Species | Sex | Age (Years) | Parameter | Predicted Asymptote | | Predicted r | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Value (mm) | 95% Confidence Interval (mm) | Value | 95% Confidence Interval |
| 22/9 | *N. rhombifera* | ♀ | 2 | W (g) | 118.7 | 116.8-120.5 | 0.0034 | 0.0024-0.0043 |
| | | | | L (mm) | 675 | 635 -716 | 0.0039 | 0.0031-0.0048 |
| | | | | SVL (mm) | 551 | 506 -596 | 0.0034 | 0.0024-0.0043 |
| | | | | TL (mm) | 133 | 128 -137 | 0.0061 | 0.0052-0.0070 |
| 22/10 | *N. rhombifera* | ♀ | 2 | W (g) | 115.3 | 111.2-119.3 | 0.0041 | 0.0021-0.0043 |
| | | | | L (mm) | 673 | 613 -733 | 0.0034 | 0.0023-0.0044 |
| | | | | SVL (mm) | 538 | 483 -593 | 0.0032 | 0.0021-0.0043 |
| | | | | TL (mm) | 137 | 126 -147 | 0.0041 | 0.0029-0.0053 |
| 22/27 | *N. rhombifera* | ♀ | 2 | W (g) | 159.6 | 155.8-163.3 | 0.0033 | 0.0027-0.0039 |
| | | | | L (mm) | 767 | 730 -803 | 0.0036 | 0.0030-0.0042 |
| | | | | SVL (mm) | 606 | 573 -639 | 0.0033 | 0.0027-0.0039 |
| | | | | TL (mm) | 165 | 155 -175 | 0.0047 | 0.0036-0.0057 |
| 22/32 | *N. rhombifera* | ♀ | 2 | W (g) | 152.3 | 148.3-156.3 | 0.0043 | 0.0039-0.0047 |
| | | | | L (mm) | 771 | 750 -791 | 0.0045 | 0.0041-0.0050 |
| | | | | SVL (mm) | 604 | 586 -621 | 0.0043 | 0.0039-0.0047 |
| | | | | TL (mm) | 168 | 160 -176 | 0.0052 | 0.0045-0.0060 |

# VITA

Leroy M. Scudder was born on December 31, 1951 in Trenton, New Jersey. He is the fourth of six sons born to Philmore M. and Cordelia J. Scudder. He was raised and attended public schools in Bristol, Pennsylvania, a small town northeast of Philadelphia, where he developed his interest in snakes. After leaving high school, he decided that Roy was a much better name to be called on a regular basis and was known by that appellation while working toward a Bachelor of Arts degree at Princeton University and a Master of Arts degree at Boston University.

In 1977, Roy entered The University of Tennessee, Knoxville, where he not only continued his graduate studies, but also maintained his interest in playing competitive volleyball, and developed an interest in calligraphy and dance. Roy received the degree of Doctor of Philosophy in Zoology in 1983. Upon leaving The University of Tennessee, Roy took with him a profound interest in growth as it relates to reproductive strategies, many fond memories, and a love for dance that rivaled his love of snakes.