

An Analysis of Habitat Utilization and Feeding Ecology
of Plethodon richmondi and Plethodon cinereus in northern West Virginia.

A Thesis
Presented to
the Faculty of the Graduate School
Marshall University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Peter A. Kramer
April 1996

THIS THESIS WAS ACCEPTED ON July 5 1996
Month Day Year

as meeting the research requirements for the Master's Degree.

Advisor: Thomas R. Paulsen
Department of Biological Sciences

Leonard Deutsch
Dean of the Graduate School

Table of Contents

	Page
Chapter I. Summary of Literature	1
Introduction	1
Density-independent Factors	1
Density-dependent Factors	7
Conclusion	18
Chapter II. Species and Study Site Description	19
Species Description	19
Site Description	23
Chapter III. Population Structure	33
Introduction	33
Materials and Methods	34
Results	35
Discussion	48
Conclusion	56
Chapter IV. Microhabitat Analysis	57
Introduction	57
Materials and Methods	57
Results	58
Discussion	72
Conclusion	82
Chapter V. Feeding Habits	83
Introduction	83

Table of Contents

	Page
Materials and Methods	84
Results	86
Discussion	90
Conclusion	95
Literature Cited	96

List of Tables

Table	Page
1. Number of <u>P. richmondi</u> and <u>P. cinereus</u> at each study site	36
2. Number of <u>P. richmondi</u> and <u>P. cinereus</u> by site and by sex	37
3. Summary of the chi-square contingency test for independence comparing male and female <u>P. richmondi</u>	40
4. Summary of the chi-square contingency test for independence comparing gravid and non-gravid <u>P. richmondi</u>	41
5. Summary of the chi-square contingency test for independence comparing gravid and non-gravid female <u>P. richmondi</u> during the spring and fall seasons	44
6. Summary of the chi-square contingency test for independence comparing male and female <u>P. cinereus</u>	45
7. Summary of the chi-square contingency test for independence comparing gravid and non-gravid <u>P. cinereus</u>	49
8. Summary of the chi-square contingency test for independence comparing gravid and non-gravid female <u>P. cinereus</u> during the spring and fall seasons	50
9. Description of environmental parameters measured for all <u>P. richmondi</u> and <u>P. cinereus</u> from NB, LR and ST	59
10. Mean values of environmental parameters measured for all <u>P. richmondi</u> and <u>P. cinereus</u> from NB, LR and ST. Values given are means \pm 1 SD. Values with different letters for a given parameter are significantly different at $P < 0.05$. See Table 9 for parameter abbreviations	62
11. F values for all environmental parameters measured for all <u>P. richmondi</u> and <u>P. cinereus</u> from NB, LR and ST	63
12. Factor loadings (eigenvectors) for environmental parameters from principal components analysis	73
13. Comparisons of invertebrate communities at each site using Spearman rank correlation coefficients. Rankings are based on the number of items found in each taxonomic category (n = the number of taxonomic categories compared between the sites)	87

List of Tables

Table	Page
14. Summary of prey items found in all <u>P. richmondi</u> collected	88
15. Summary of prey items found in all <u>P. cinereus</u> collected	89
16. Summary of diversity, average number and average volume of prey in subsamples	91
17. Percentage of overlap in diet (D) for subsample comparisons (n = number of individuals in each subset respectively)	92
18. Diet comparisons of subsamples by Spearman rank correlation coefficients. Rankings are based on the number of items consumed in each taxonomic category (n = the number of prey categories compared between the subsamples)	93

List of Figures

Figure	Page
1. Geographic distribution of <u>P. cinereus</u> (adapted from Conant and Collins, 1991).	20
2. Geographic distribution of <u>P. richmondi</u> (adapted from Conant and Collins, 1991)	21
3. Geographic distribution of <u>P. cinereus</u> and <u>P. richmondi</u> in West Virginia (adapted from Green and Pauley, 1987).	22
4. Dorsal view of <u>P. cinereus</u>	24
5. Ventral view of <u>P. cinereus</u> (adapted from Conant and Collins, 1991)	25
6. Dorsal view of <u>P. richmondi</u>	26
7. Ventral view of <u>P. richmond</u> (adapted from Conant and Collins, 1991)	27
8. North Bend study site in early spring	28
9. Long Run study site in early spring	30
10. Salem-Teikyo study site in early spring	31
11. Overall length-frequency histogram for <u>P. richmondi</u>	38
12. Monthly length-frequency histogram for <u>P. richmondi</u>	42
13. Overall length-frequency histogram for <u>P. cinereus</u>	46
14. Monthly length-frequency histogram for <u>P. cinereus</u>	47
15. Comparative overall length-frequency histogram for <u>P. richmondi</u> and <u>P. cinereus</u>	51
16. Comparative overall headwidth-frequency histogram for <u>P. richmondi</u> and <u>P. cinereus</u>	52
17. Scatter plot comparing snout-vent length and head widths of <u>P. richmondi</u> and <u>P. cinereus</u> . Estimated regression lines are shown; the minimum and maximum SVL and HW are indicated for each species	53

List of Figures

Figure	Page
18. Population range diagram of mean rock circumference (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in cm	64
19. Population range diagram of mean rock diameter length (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in cm	65
20. Population range diagram of mean rock diameter (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in cm	66
21. Population range diagram of mean impression diameter length (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in cm	67
22. Population range diagram of mean percent contact of rock to the ground (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line)	68
23. Population range diagram of mean soil pH (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line)	69
24. Population range diagram of mean soil temperature (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in $^{\circ}\text{C}$	70
25. Population range diagram of mean percent soil moisture (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line).	71
26. Scatter plot of all <u>P. richmondi</u> (squares) and <u>P. cinereus</u> (circles) based on principal components one and two. Closed symbols are averages for each species	74
27. Scatter plot of all <u>P. richmondi</u> (squares) and <u>P. cinereus</u> (circles) based on principal components two and three. Closed symbols are averages for each species	75
28. Scatter plot of all <u>P. richmondi</u> (squares) and <u>P. cinereus</u> (circles) based on principal components one and three. Closed symbols are averages for each species	76
29. Cross sectional diagram of typical rock utilized by <u>P. cinereus</u>	78

List of Figures

Figure	Page
30. Cross sectional diagram of typical rock utilized by <u>P. cinereus</u>	79

Acknowledgments

I would like to thank Dr. Thomas K. Pauley for his contributions to my thesis. He gave of himself freely and was always available to provide helpful insight concerning my research; without his help, none of this would have been possible. I would also like to thank the other members of my committee, Dr. Dan K. Evans and Dr. Donald Tarter for their helpful reviews of my thesis as well as the rest of my professors at Marshall University for helping to make my time here a great learning experience.

I would like to thank Christopher Wallis for his help with setting up my study sites and collecting specimens and James Barron for his help with programming SAS. I would also like to thank Timothy R. Brophy for his many hours spent in the field, his help with interpreting data, and especially for his friendship and encouragement. In addition, I want to thank Dr. Norman G. Reichenbach who introduced me to herpetology, for his help with statistical analysis as well as for being a great friend.

Finally I would like to thank my family, especially my mother for her constant support both emotionally and financially as well as my father who helped with the computer programming and statistical analysis necessary for this project.

Abstract

Studies were conducted on the comparative microhabitat requirements and feeding habits of the ravine salamander, Plethodon richmondi and the redback salamander, P. cinereus in northern West Virginia. Plethodon richmondi had a mean SVL of 49.7 ± 7.1 mm and were significantly larger than P. cinereus which had a mean SVL of 37.2 ± 8.0 mm. Both species had biennial egg laying patterns and deposited eggs in late spring or early summer. Juvenile P. richmondi were not surface active except for the early spring and neonates did not become surface active until the ensuing spring; conversely, P. cinereus juveniles exhibited more activity throughout the entire active season and neonates became surface active during the fall of the year they hatched. Neither species were surface active during the warmest and driest months of summer and early fall (June - October). Of the 22 environmental parameters measured, eight were significantly different between the two species. Plethodon richmondi utilized rocks with a significantly larger circumference, diameter length, mean diameter and impression diameter length; in addition, P. richmondi used rocks that exhibited more contact between the bottom of the rock and the surface of the ground. Plethodon richmondi also utilized soil with a lower pH and temperature as well as soil with a higher soil moisture content. Plethodon cinereus displayed more variability in measured environmental parameters and had a larger variance for 17 of the 22 environmental parameters. Principal components analysis revealed that P. cinereus utilized a broader range of habitats than P. richmondi. There was a significant correlation in the diets of P. richmondi and P. cinereus ($r_s = 0.813$); in addition, all diets compared were significantly correlated and resource overlap calculations were high for all comparisons except between P.

richmondi at North Bend and Long Run (0.45). Plethodon richmondi had a significantly smaller volume of food on days when rainfall for the previous three days was < 0.42 inches than for dates when rainfall for the previous three days was > 0.42 inches but there was not a significant difference for P. cinereus. The sum of the environmental and feeding data show that P. richmondi had a more narrow set of environmental requirements and may be affected more by extreme values which may explain at least partly the differences in macrodistributional patterns.

Chapter I

Summary of Literature

Introduction

There are many factors that affect the micro and macrodistributions and densities of terrestrial salamanders. Some of the most important are: soil moisture, soil temperature, soil pH and soil consistency (particle size). Directly related to these soil parameters are ambient parameters such as air temperature, insolation and relative humidity as well as topographical features such as slope (percent of incline) and aspect (the direction the slope is facing). In addition, competition for food, refugia and nesting space as well as predation can also contribute to the distribution and densities of salamander populations. Each of these can be placed into one of two groups: density-dependent and density-independent factors. Stilling (1992), defined density-dependent factors as those that have an increasing influence on a population as the density of the population increases. In relation to salamander communities, competition for food, refugia and nesting space, as well as predation are considered density-dependent factors. Density-independent factors are defined as those factors which affect a population in the same manner, regardless of the population size; soil moisture, soil temperature, soil pH and soil consistency, and other related physical factors such as air temperature, insolation, relative humidity, slope and aspect are all included under this definition (Stilling, 1992).

Density-independent Factors

A great deal of research has been conducted to determine the environmental limitations of terrestrial salamanders. The most important factors are considered to be soil moisture, soil temperature and soil pH. These factors are directly related to others such as air temperature, insolation, slope

and aspect in that all of these can be reflected in the soil moisture content and soil temperature. The soil pH is considered to be an important factor due to the fact that many terrestrial salamanders (Family Plethodontidae) are lungless and rely mainly on respiration through cutaneous gas exchange directly with the ambient environment.

In general, terrestrial salamanders utilize slightly acidic substrates; although in nature, basic substrates are relatively rare. Vernberg (1955) found that both Plethodon cinereus and P. glutinosus utilized acidic soils in the laboratory. Both species spent significantly more time in a substrate having a pH of 6.3 (82 percent) to substrate with a lower pH of 5.8 (18 percent). In a second test with substrate pH choices of 6.2 and 7.2, there was not a clear preference by either species (50 and 57.5 percent in a substrate pH of 7.2 for P. cinereus and P. glutinosus respectively). Field data collected by Vernberg conflicted with his laboratory findings in that P. glutinosus were found more often in soil with a pH between 5.4 and 5.6 (9 animals) than in soil with a pH ranging from 6.0 to 6.2 (4 animals). For P. cinereus however, the laboratory data corroborated the field data (12 animals found in soil with a pH ranging from 5.4 to 5.6 as opposed to 22 animals found in soil with a pH ranging from 6.0 to 6.2). Another finding of Vernberg was that P. cinereus had a broader range of pH tolerance than did P. glutinosus.

In another study, Mushinsky (1975) found that of 8 species of semi-terrestrial salamanders, 6 preferred a basic substrate in the laboratory (pH substrate choice of 5.5 and 7.7); however, his field data were similar to that of Vernberg's in that of the field pH collected, all were found in acidic substrates.

Wyman and Hawksley-Lescault (1987) found that given a choice of three substrate pH ranges (6.0 to 6.5, 4.0 to 4.5 and 3.0 to 3.5), 50 percent of the

time P. cinereus preferred a substrate pH of 6.0 to 6.5 as opposed to 31 and 19 percent for the other two substrate pH treatments respectively. The lethal substrate pH for P. cinereus was determined to be between 3.0 and 4.0.

Growth was reduced to 60 percent in salamanders living on substrates of pH 3.0 and 45 percent for those living on substrates of pH 4.0; in addition, oxygen consumption was reduced by 32 percent for salamanders maintained on substrates with pH 4.0. Field data from the same study revealed that of 284 1 m² quadrats searched with a pH \leq 3.7, only 25 (8.8 percent) contained a salamander and 386 (50.8 percent) of 760 1 m² quadrats with a pH \geq 3.8 contained a salamander.

Frisbie and Wyman (1991) conducted a study to determine the affects that low pH environments had on P. cinereus. Their laboratory results showed that several body characteristics of P. cinereus were significantly affected by low pH environments. As pH decreased from 5.0 to 3.5, sodium efflux rates increased significantly; also, as pH was decreased, the total amount of body water also decreased and wet mass lost increased. These results show that terrestrial salamanders may avoid soil with low pH because it may hinder their ability to maintain an osmoregulatory equilibrium. The field data collected by Frisbie and Wyman did not support the laboratory results. Salamanders collected in low pH environments (pH \leq 3.7), showed no difference in sodium levels, body water or wet mass when compared to salamanders found in higher pH environments (pH $>$ 3.7). The authors offer several explanations as to why there was no correlation between the laboratory and field results. The apparent contradiction was probably due to a combined effect of the artificial substrate used in the laboratory not modeling the true complexity of a forest soil environment and the fact that pH can vary

considerably over small areas of the forest soil.

Because of the relative permeability of the skin, another problem arises due to the rapid loss of water through the skin, even in relatively moist situations. Several researchers have addressed the question of water loss in terrestrial salamanders. Heatwole and Lim (1961) determined in a study of P. cinereus that the maximum amount of water loss (before death) expressed as a percentage of hydrated weight was 28.96 percent.

Heatwole (1962) found that soil moisture was directly related to forest floor micro-topography. Throughout spring and early summer, all micro topographic areas (mounds, flats and depressions) measured, were moist. As the summer progressed and rainfall decreased, there was a distinct pattern of drying. Mounds were the first to dry, then areas that were flat and finally, during the driest periods, the depressions became dry as well.

Microtopographical characteristics of the forest floor seemed to determine the microdistribution of P. cinereus. Only two salamanders were found on mounds indicating that even during moist periods, these areas were unsuitable for salamander habitation. In level areas, salamander densities were comparable to areas in depressions; however, during late summer, when soil moisture content was at its lowest, salamanders also disappeared from these areas. Only in depressed areas of the forest were salamanders consistently found throughout the summer. There was no detectable increase in salamander density in the depressed areas indicating that salamanders from level areas did not migrate to depressed areas during dryer periods, rather, they burrowed underneath the ground. These data were corroborated by another aspect of Heatwole's research. During the wettest periods, all salamanders were found in the L layer (leaf litter) or between the L and F

layer (humus). As the summer progressed salamanders burrowed deeper into the H layer and finally, during the driest periods, salamanders were not found and presumably burrowed down into much deeper soil in the H layer (deeper soil).

Jaeger (1980) obtained seemingly contradictory results to those of Heatwole. Over 22 sampling periods from 16 April to 12 August 1974, there was no significant difference in surface abundance (salamanders above ground) of P. cinereus ($\bar{x} = 2.2/\text{m}^2$). There was a significant positive correlation between salamanders found in the leaf litter and rainfall and a significant negative correlation between salamanders found under cover objects (logs and rocks) and rainfall. In addition, there was no correlation detected between surface density and soil temperature, leaf litter depth or soil depth. Jaeger hypothesized that salamanders maximize the amount of time spent on or near the surface (where prey is abundant) as opposed to within the soil (where prey is thought to be less abundant).

In a field study on Desmognathus fuscus, a partially terrestrial salamander, Keen (1984) found that D. fuscus showed significantly less activity in low soil moisture conditions than in high soil moisture conditions. In addition, he found that in the low soil moisture condition, salamanders tended to use larger rocks and to aggregate under the same rock to a greater extent than salamanders in a high soil moisture condition. In a laboratory experiment, Vernberg (1955) found that both Plethodon cinereus and P. glutinosus preferred a more moist soil substrate, but that P. glutinosus had a higher affinity for soil with a higher moisture content.

Studies have shown that different species of salamanders have different moisture requirements and that these differences may affect their

respective distributions. Pauley (1978a) found that P. cinereus and P. wehrlei have different soil moisture requirements and their distributions are affected by these moisture requirements. In the laboratory, Pauley found that P. wehrlei had a higher tolerance for water loss than P. cinereus and that P. cinereus lost water at a greater rate than did P. wehrlei. Field data collected by Pauley suggest that these moisture requirements affect the microdistributional patterns of the two species. In areas where P. cinereus were found, the soil had a significantly higher water holding capacity than the soil in areas where P. wehrlei were found. This may be interpreted as niche partitioning between the two species in response to variations in soil moisture content.

Vernberg (1955) conducted a comparative laboratory study on the physiological indexes of activity for P. cinereus and P. glutinosus. He found that P. glutinosus preferred a moist substrate (18 salamanders found in the substrate with a moisture content of 29.3 percent), as opposed to a dryer one (4 salamanders found in the substrate with a moisture content of 11.7 percent). Plethodon cinereus however, did not show a preference for either substrate.

Salamander activity can also be affected by the amount of moisture in the air. Jaeger (1978) found in a study on P. cinereus that activity on wet nights was significantly higher than during dry nights. The average number of salamanders active on wet nights on leaf litter and on plants was 12.3 and 17.8 per 300 m³ respectively in contrast to 2.1 and 0.3 per 300 m³ respectively for dry nights. Jaeger also showed that even on wet evenings, salamanders found climbing on plants lost between 5 and 35 percent of their total wet weight. This dependency upon moisture can have consequences on competition for vital resources such as food which will be discussed later in

the paper.

Other density-independent factors are closely related to soil moisture; related most directly is soil temperature but perhaps the controlling factor for both soil moisture content and soil temperature is insolation. The amount of sunlight to which the forest floor is exposed has been shown to affect not only moisture and temperature, but also salamander distribution.

In the laboratory, Pauley (1978b) found that salamanders showed no preference for any given light intensity. In the field, it was determined that habitat where P. wehrlei existed had a higher average insolation value and a higher average soil temperature than habitats where P. cinereus existed. The higher average soil temperature and lower soil moisture content (Pauley, 1978a) are probably directly affected by the higher insolation values obtained from areas where P. wehrlei were found.

Density-dependent Factors

Density-dependent factors are considered to be important regulatory agents in both monospecific and polyspecific salamander communities. One of the most important density-dependent factors is considered to be competition for food (Jaeger, 1972; Fraser, 1976). There is a great deal of information concerning food habits of salamanders. In general, salamanders are considered to be euryphagic (Whitaker and Rubin, 1971; Powders and Tietjen, 1974; Burton, 1976; Fraser, 1976; Lynch, 1985). Differences in prey size occur between species (Fraser, 1976; Burton, 1976; Lynch, 1985), which may relieve some of the competitive pressures associated with animals that have similar taxonomic diets. In addition to resource partitioning through utilization of different sized prey, another partitioning tactic may be non-synchronous foraging by sympatric salamanders (Holomuzki, 1980).

Pauley (1978c) found no correlation between microdistribution and the feeding habit of two plethodontids, P. cinereus and P. wehrlei. Ninety five percent of all salamander stomachs analyzed contained food, indicating that food was not in short supply. In addition, Pauley determined that while both species ingested similar types of prey (Formicidae, Acaria and Coleoptera), as well as similarly sized prey, competition may be reduced due to non-coincidental feeding strategies. Another factor which may reduce interspecific competition for food is the dissimilarity in size between the two species (adult P. wehrlei being much larger); however, there may still exist some competitive interactions between juvenile P. wehrlei and adult P. cinereus.

Whitaker and Rubin (1971) studied the food habits of two plethodontid subspecies, P. jordani metcalfi and P. jordani shermani in North Carolina. In general, there were no significant differences in food habit between the two subspecies. Hymenoptera (ants) were the predominant food item for both species in percent volume (13.8 percent and 22.5 percent respectively) and percent frequency (39.2 percent and 59.1 percent respectively). Araneida (spiders) were the next most important food item in both subspecies by percent volume and percent frequency. There were also no significant seasonal shifts in food habit. The similarities in diet were probably due to the close taxonomic relationship of the two salamanders.

Lynch (1985) studied the feeding ecology of Aneides flavipunctatus and three other sympatric plethodontid species, A. lugubris, Batrachoseps attenatus and Ensatina eschscholtzii. He determined that while salamanders may be euryphagic, they may not be as indiscriminant in their feeding habits as was once thought. All four species showed substantial dietary overlap, but

varied in the average and largest prey ingested. This indicated that while the four species may have similar diets taxonomically, they may reduce interspecific competition by utilizing different size classes of prey.

A majority of Lynch's study focused on the feeding ecology of A. flavipunctatus. For A. flavipunctatus, Lynch counted total food items per stomach, the volume of each item and the total volume of each stomach. Data were analyzed both from an ontogenic and a seasonal perspective. Four size classes were established for A. flavipunctatus as well (I = 20-34 mm; II = 35-49 mm; III = 50-64 mm; IV = 65-79 mm).

Two hundred and eighty A. flavipunctatus stomachs were examined with only 20 empty stomachs. Twenty five taxonomic orders of invertebrates were identified with 6 arthropod orders representing 78 percent of the total prey volume (Diplopoda, Coleoptera, Hymenoptera, Isoptera, Diptera and Collembola).

In the fall, millipedes were the most important prey item volumetrically for all size classes followed by Collembola for juveniles (size classes I and II) and Coleoptera for adults (size classes III and IV). In the spring, there was a reduction in the importance of Diplopoda and Collembola and an increase in the importance of Hymenoptera and Coleoptera.

For A. flavipunctatus, Lynch determined that as body size increased, the average prey volume also significantly increased on a log normal scale until class III and then tended to level off between classes III and IV which showed no significant differences. The total prey volume for an individual was as high as 900 mm³ but typically averaged between 10 and 20 mm³ for juveniles and 75 to 200 mm³ for adults. (mean log volume for each size class over all seasons: I, $\bar{x} = 1.14$; II, $\bar{x} = 1.69$; III, $\bar{x} = 2.04$; IV, $\bar{x} = 1.97$ mm³). This

finding indicates that there may be an absolute food intake rate when A. flavipunctatus reaches approximately 50 mm SVL. Lynch also determined that, on the average, an individual A. flavipunctatus ingested between 7 and 14 prey (one individual contained 500 prey items); however, 64 percent of the total food volume was contributed by a single prey item per individual. Regression analysis revealed that as salamander size increased, the total number of prey items significantly decreased for the three largest seasonal samples ($r^2 = -0.40, -0.52, -0.85$; $p < 0.05$). These findings indicate that while larger A. flavipunctatus have a greater average prey volume per stomach, they ingest fewer yet larger prey than smaller A. flavipunctatus.

As was mentioned previously, another way salamanders may reduce competitive interactions in relation to feeding is through staggering feeding cycles both intraspecifically and interspecifically. In a study conducted on the P. hubrichti (Kramer et al., 1993), it was estimated that on any given night suitable for salamander surface activity (i.e. moist leaf litter and high relative humidity), only about 5 to 10 percent of the population was surface active. This relatively low percentage of the population foraging on the surface may be one tactic used to lower the amount of competition within a species.

Holomuzki (1980), determined that for Desmognathus fuscus, D. ochrophaeus and Eurycea bislineata, there was no statistical difference in foraging times among the three species. All three species exhibited heightened surface activity one hour before sunset, peaked at sunset, began to decrease one hour after sunset and declined markedly 2 hours past sunset and beyond. In relation to this, the greatest mean stomach volume was at one hour after sunset for both D. fuscus and D. ochrophaeus. Stomach volumes for E. bislineata showed a high degree of variability with no distinct peak.

The feeding patterns observed for D. fuscus and D. ochrophaeus follow diel activity patterns of invertebrates. Using sticky traps both on the ground and up to 0.75 m above the ground, it was determined that invertebrate activity patterns were highly correlated with the activity patterns of all three species (Spearman rank analysis, $r^2 = 1.0$, $n = 4$, $p < 0.05$).

Dietary overlap was calculated using the similarity index:

$$D = [1.0 - 0.5 \sum |p_{x,i} - p_{y,i}|] \times 100$$

where D is the percentage of overlap, $p_{x,i}$ and $p_{y,i}$ are the proportions of the number of items species x and y utilized in resource category i. Comparisons were made between D. fuscus and D. ochrophaeus, D. fuscus and E. bislineata, D. ochrophaeus and E. bislineata and juvenile and adult D. ochrophaeus. Dietary overlap was high for all comparisons. The greatest overlap was between juvenile and adult D. ochrophaeus (81.9 percent) and lowest between D. fuscus and E. bislineata (70.6 percent); overlap between D. fuscus and D. ochrophaeus and between D. ochrophaeus and E. bislineata were similar (80.7 percent and 79.8 percent, respectively). These data suggest that for these salamanders, intra and interspecific interactions were of little importance in relation to feeding cycles which were more closely related to peak activity times of forest invertebrates.

Competition for food was studied by Fraser (1976) between two largely allopatric plethodontids, P. cinereus and P. hoffmani in a narrow zone of sympatry. Fraser used a cumulative diversity index to determine the number of salamanders needed to adequately determine prey utilization volumetrically and taxonomically between the two species. A total of 25 salamanders was calculated to be the total number needed after which diversity does not increase appreciably.

There was a significant correlation between salamander head width and the size of the largest prey ingested (P. hoffmani, $r = 0.20$, $p < 0.01$; P. cinereus, $r = 0.14$, $0.05 < p > 0.01$). Nine major taxa of prey were utilized by P. cinereus and P. hoffmani volumetrically and numerically; in addition, there was a significant difference in prey utilization between the spring and fall samples. In the spring and fall, Hymenoptera was the greatest contributor numerically; however volumetrically, Hymenoptera, Coleoptera and Pulmonata were the greatest contributors in the fall and Araneida, Diptera, Oligochaeta and Coleoptera were the greatest contributors in the spring.

Fraser determined that although taxonomically the diets of the two species were very similar, they differed greatly in the relative numbers taken by each species per taxon; this is especially true in relation to P. hoffmani utilization of Hymenoptera. This may be another way of reducing the amount of interspecific competition or it may only reflect a difference in the prey each species is exposed to in their natural microhabitat. It was also determined that the largest P. cinereus and P. hoffmani selected similarly sized prey even though the largest P. hoffmani have greater mean SVL and maximum head widths than P. cinereus.

A series of experiments were conducted by Fraser to determine the effects that environmental moisture has on foraging activities as well as to determine the amount of subterranean foraging that salamanders exhibit. In the first experiment, four treatments were used, each consisting of a container 30 cm x 50 cm x 60 cm fitted with a lid. The four treatments were: a wet substrate of soil that had been heated to kill all soil invertebrates, a wet substrate with non-heated soil, a wet substrate with 20 Drosophila hydei added per day and substrate air dried for 24 h prior to the experiment with 20

D. hydei added per day.

Salamanders kept in the preheated wet humus/unfortified treatment showed no significant difference in weight change from salamanders kept in the unheated wet humus/unfortified treatment (-0.11 g and -0.08 g respectively). Salamanders kept in the dried soil/fortified treatment did show a significant difference in weight change from salamanders kept in the wet soil/fortified treatment (+0.04 g and +0.21 g respectively). Also, there were no qualitative differences in Drosophila activity between the wet and dry treatments. In addition, the non dried wet/unfortified soil was analyzed to determine invertebrate fauna. A total of 5,259 invertebrates was found having a total volume of 1333.9 mm³. Even with a potentially large food source available, salamanders from this enclosure lost weight. The results of this experiment suggest that feeding activity may be reduced for salamanders in low soil moisture conditions as well as for salamanders in relatively moist conditions with no invertebrates available above the surface of the soil.

Field observations by Fraser on the emaciated state of salamanders that surfaced after an extended dry period (July and August) or after the coldest winter months suggest that salamanders forage little beneath the soil surface. This observation was the basis for a second experiment to determine the level of subterranean foraging activity.

Fraser constructed sixteen rectangular wooden boxes (1 x 1 x 30 cm) were constructed and hundreds of small holes (5 mm wide) were drilled over the entire surface. Salamanders with empty stomachs (by pumping the stomachs) were placed inside the boxes and the ends were enclosed. The boxes were placed at different depths of the forest floor: the leaf litter layer,

the humus layer, the A-horizon and the B-horizon and left for 5 days. Salamanders that were located in the leaf litter had a significantly higher number of prey per stomach than the other 3 treatments ($\bar{x} = 5.25 \pm 4.75$; $\bar{x} = 1.25 \pm 1.26$; $\bar{x} = 1.0 \pm 2.38$; $\bar{x} = 0.50 \pm 0.57$). These data suggest that the amount of foraging is inversely proportionate to the distance a salamander is beneath the soil surface.

The sum of these data suggest that food may be an important factor in relation to interactions between P. cinereus and P. hoffmani; however, these events are probably limited to times when the availability of food is low. Fraser's data also suggest that invertebrate activity does not appreciably change under drier conditions but that the reduction in available food items stems from the salamanders inability to function in a low moisture environment. One way P. cinereus and P. hoffmani may reduce competitive interactions for food is through resource partitioning in relation to the number of prey taken per taxon. Fraser's results suggest that P. hoffmani utilize Hymenoptera to a much greater extent than do P. cinereus; this may only be a reflection of individual "prey universes" to which each species is exposed.

Jaeger (1972) studied two salamanders, P. cinereus and P. shenandoah (formerly P. richmondi shenandoah) in Virginia. Plethodon cinereus is found in great numbers throughout the area; however, P. shenandoah is restricted almost entirely to three talus slopes along a single mountainside.

Salamanders were collected in and around the talus slopes. SVL and head width were recorded for all individuals. A total of 284 P. shenandoah and 485 P. cinereus was collected throughout the entire study. For any given SVL, P. shenandoah had a greater head width; in addition, they averaged 15

percent longer than P. cinereus. The locations of 321 P. shenandoah and 672 P. cinereus were recorded. This data revealed that P. shenandoah was mainly restricted to the talus slope area with some being found up to 80 m from the talus slope. Jaeger determined that body size was related to the distance that P. shenandoah was found from the talus slope in that 62.5 percent of the salamanders found > 3 m from the talus slope had an SVL between 41 and 45 mm while those found within the talus slope comprised only 34.4 percent of the total population. Further, 29.2 percent of the P. shenandoah found > 3 m from the talus were > 45 mm SVL; thus, a total of 91.7 percent of all P. shenandoah had an SVL of > 41 mm.

Jaeger proposed two hypotheses for the observed distributional pattern of only large P. shenandoah found > 3 m from the talus: (1) it was due to some interspecific interaction between large P. shenandoah and P. cinereus, or (2) large P. shenandoah tend to wander to a greater extent than smaller conspecifics. A laboratory experiment was conducted to determine if the latter hypothesis was correct. Ten aquaria with damp crushed quartz substrate were placed in an environmental chamber with an ambient temperature of 17°C and a day night cycle that matched late summer conditions. Sixteen burrows were made in each container using test tubes inserted in the substrate at 45° angles. Five P. shenandoah with SVL \geq 40 mm were placed in a separate container and 5 P. shenandoah with SVL \leq 30 mm were each placed in the remaining 5 containers. Observations were made at 30 minute intervals during different periods of day and night on the location of each salamander for 24 days so that each treatment had a total of 200 observations. Results of the experiment show that there were no significant differences between adult and juvenile P. shenandoah in total number of moves or total

distance moved using a two-tailed Mann-Whitney U-test ($U = 5$, $p = 0.150$ and $U = 7$, $p = 0.310$ respectively).

The feeding strategies of the two species were studied using 190 P. cinereus and 36 P. shenandoah (Jaeger, 1972). Stomach contents were identified using a dissecting microscope fitted with an ocular micrometer. Both species were euryphagic with 16 invertebrate taxa being represented throughout the sample. Two taxa were predominant in both species (Acarina and insect larvae, 39 and 28 percent respectively for P. cinereus and 22 and 34 percent respectively for P. shenandoah). Homopterans were utilized by P. cinereus more often (12 percent) than by P. shenandoah (1 percent); this difference was probably due to the scarcity of Homopterans (mostly aphids) in the lightly vegetated talus slopes.

Jaeger compared P. cinereus and P. shenandoah by separating specimens of P. shenandoah found in the talus slope from those found > 3 m from the talus slope as well as from all of P. cinereus. Plethodon shenandoah found > 3 m from the talus took significantly longer prey than conspecifics from the talus or P. cinereus. A similar pattern existed when comparing P. shenandoah from the talus slope and P. cinereus. There was no significant difference in the prey size of the largest P. cinereus and P. shenandoah in either length or width of prey. Jaeger concluded that no feeding strategy exists which might facilitate coexistence within the soil.

A key question in studying competitive interactions between two species is: does a resource utilized by both species (in this case food), ever become limited in supply. As was shown previously (Fraser, 1976), limitation of food may not be due to any scarcity of prey; rather, for an animal so dependent upon moisture, foraging activity may be limited during extended

periods of dryness.

A field experiment was conducted to determine when and if food ever becomes a limited resource (Jaeger, 1972). Plethodon cinereus were collected under three different soil conditions: dry (7 days since last rain), moist (3 days since last rain) and wet (< 1 day after rain). The results of the experiment showed that the number of prey found in the stomachs of P. cinereus were inversely proportional to the number of days since the last rain. The average number of prey items per stomach was 1.9 for dry soil days, 4.6 for moist soil days and 20.1 for wet soil days.

Jaeger pointed out that two conditions may have skewed the data: (1) on the dry soil days, P. cinereus may have ingested larger prey, therefore requiring fewer prey, or (2) the salamanders captured during the wet periods were larger than those captured during the dry periods. An analysis of prey size revealed that on the dry soil days, prey lengths averaged 1.7 mm, on moist days 2.0 mm and on wet soil days 1.6 mm; there was no significant difference in prey size taken between any of the three soil conditions. The average SVL for salamanders captured on wet days was larger than either the moist or dry soil days (34.4 mm, 31.6 mm and 28.9 mm, respectively); however, due to the large standard deviations there was no statistical significance in the sizes. These data suggest that soil moisture may create an environment where food becomes a limited resource and is probably due to the inability of a salamander to forage during dry periods rather than any decrease in prey density.

Jaeger conducted an experiment to determine if P. cinereus was able to capture prey more efficiently than P. shenandoah. Twenty-three cm of soil and 2 cm of leaf litter were placed in four, 41 x 21 x 25 cm aquaria; ten burrows

were bored into the soil of each aquaria, 5 with a diameter of 1.5 cm and 5 with a diameter of 0.5 cm. Ten P. cinereus were placed in one of the aquaria, 10 P. shenandoah were placed in another aquaria; into the remaining two aquaria, 5 animals of each species were placed so that there were 10 animals per aquaria. Aquaria were maintained in an environmental chamber at 17° C. After 5 days, 150 termites (15 per animal) were placed in each aquaria. After 10 hours, the salamanders were removed and sacrificed to analyze stomach content. The results of the experiment showed that both species were able to capture prey equally well (82 percent capture rate per salamander for P. cinereus and 88 percent capture rate per salamander for P. shenandoah). The experimental design may have been improved if moisture conditions had been varied over all treatments. A difference may have been detected if P. cinereus were able to tolerate drier conditions and capture more prey under these conditions (Jaeger, 1980).

Conclusion

There are undoubtedly many factors that contribute to the micro and macrodistributional patterns of terrestrial salamanders, many of which have not been addressed in this paper (e.g. nesting behavior and territoriality). Two of the most important factors are environmental parameters such as soil pH, soil temperature and soil moisture (collectively density-independent factors) as well as the density-dependent factors of prey abundance and accessibility. These two aspects work in conjunction to regulate the microdistribution of salamander communities and ultimately may result in overall changes in macrodistributional patterns.

Chapter II

Species and Study Site Description

Two species of terrestrial salamanders were studied, the redback salamander, Plethodon cinereus and the ravine salamander, P. richmondi. Plethodon cinereus is one of the most abundant terrestrial vertebrates in eastern North America (Burton and Likens, 1975), with a range extending from southern Quebec south to North Carolina and westward to Missouri and Minnesota (Conant, 1986) (Fig. 1). Plethodon richmondi has a smaller distribution ranging from Ohio and western Pennsylvania in the north to Tennessee and western North Carolina in the south (Conant, 1986) (Fig 2). The distributions of the two species overlap broadly in Ohio and Pennsylvania; however, in the south (West Virginia, Tennessee and Virginia), their distributions are largely allopatric with a relatively narrow zone of sympatry. This pattern is most apparent in West Virginia where P. cinereus inhabits the eastern two-thirds of the state and P. richmondi inhabits the western third of the state (Fig. 3). A narrow sympatric zone exists extending in the north from the northern panhandle through the central part of the state slightly east of Charleston, and extending southward into Summers and Raleigh Counties. It appears from the current distribution, that P. cinereus (generally thought to be competitively superior over other small woodland salamanders) may be extending its range westward replacing P. richmondi in areas where it once was common (Pauley, pers comm).

Species description

Plethodon cinereus is a small terrestrial salamander ranging in size from 57 to 92 mm in total length with a record length of 127 mm and a costal groove count ranging from 18 to 19 (Conant, 1986). The dorsum usually has a distinctive reddish stripe which may run from the crown of the head to

Figure 1. Geographic distribution of P. cinereus (adapted from Conant and Collins, 1991).



Figure 2. Geographic distribution of P. richmondi (adapted from Conant and Collins, 1991).

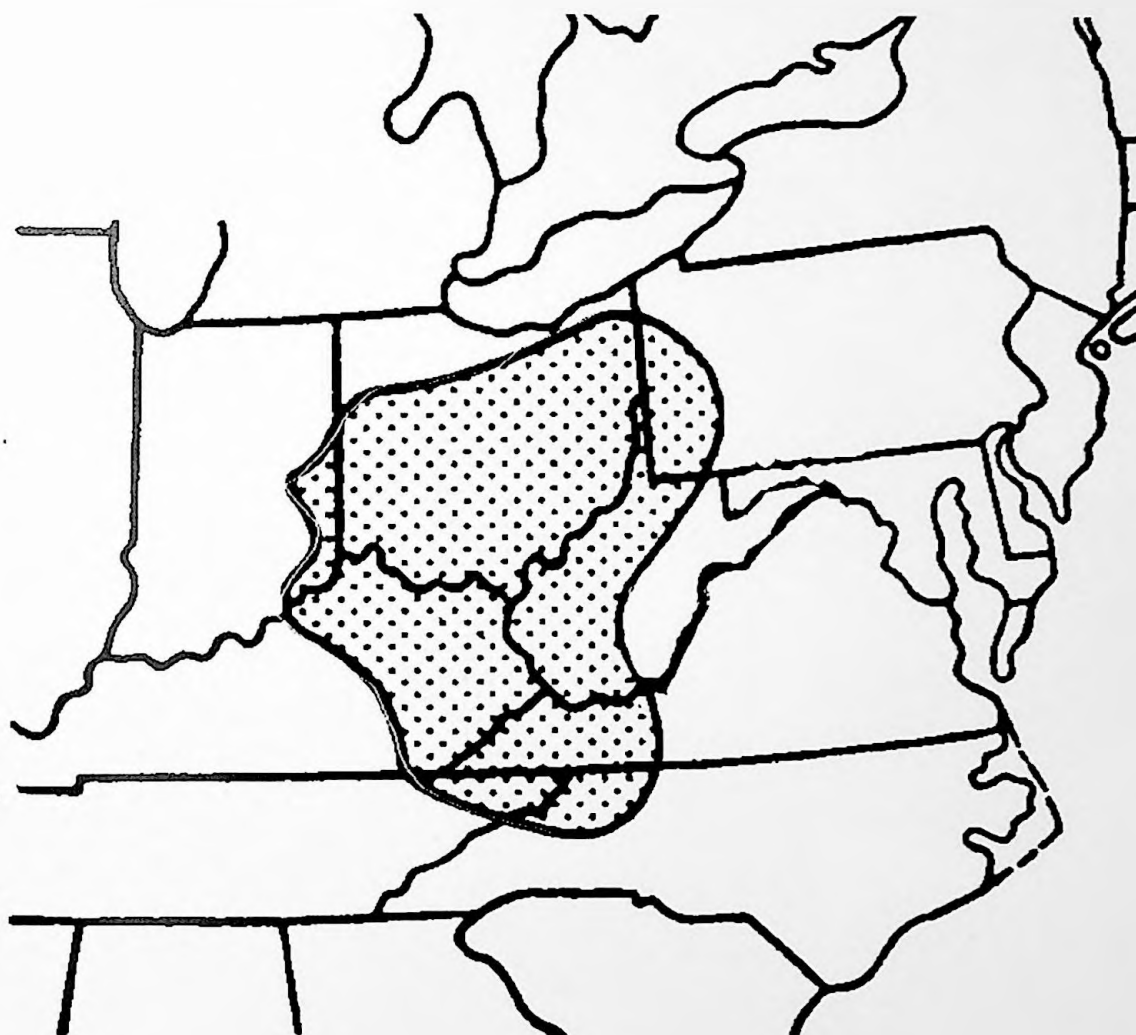
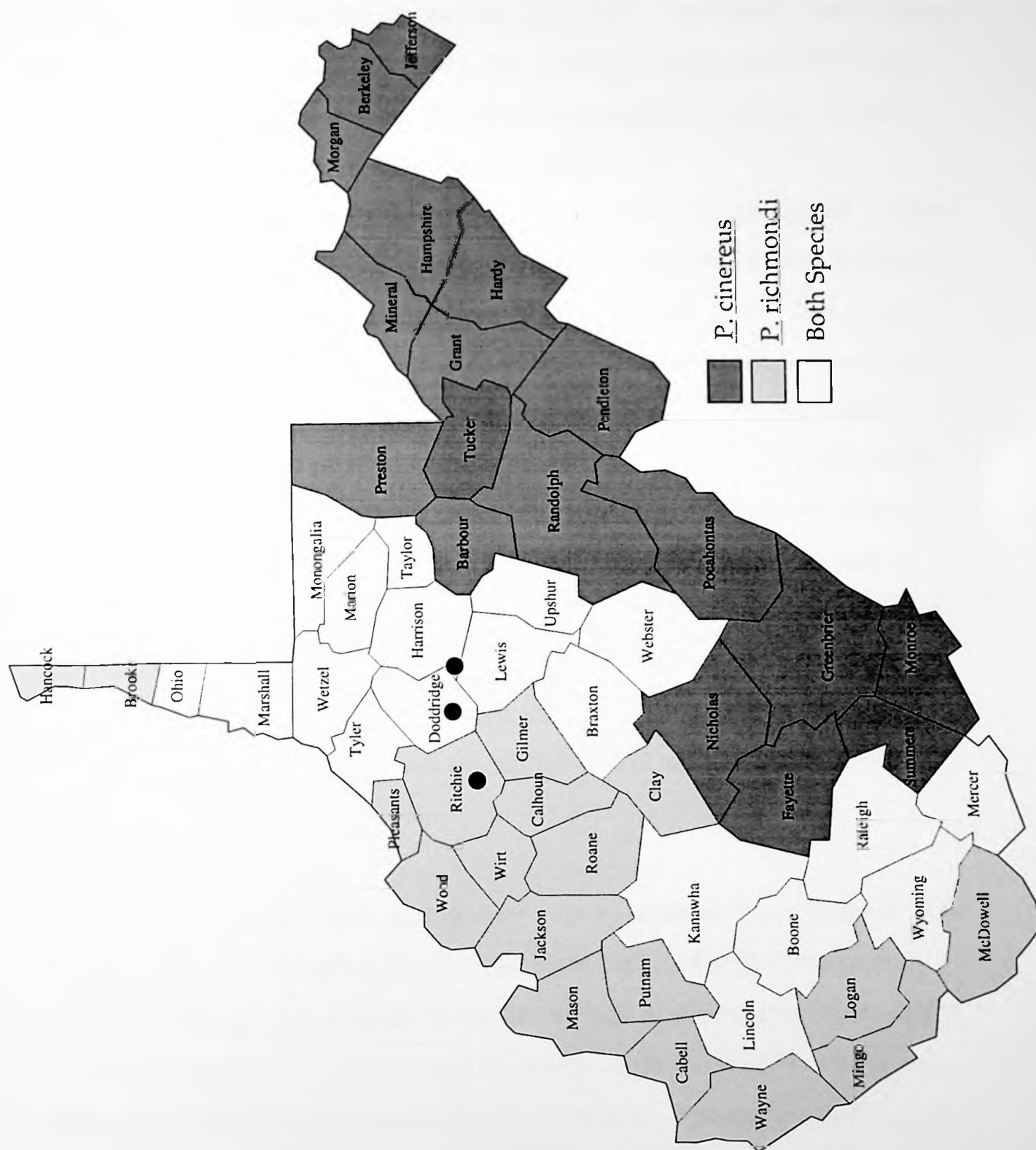


Figure 3. Geographic distribution of P. cinereus and P. richmondi in West Virginia (adapted from Green and Pauley, 1987).



almost the end of the tail (Fig. 4); however, there is a "lead back" phase where the dorsum may be completely dark. The venter is mottled and has a "salt and pepper" appearance (Fig. 5). Plethodon cinereus is commonly found in moist cool woodlands along hillsides and valleys.

Plethodon richmondi is a medium sized terrestrial salamander ranging in size from 80 to 110 mm in total length with a maximum length of 143 mm and a costal groove count ranging from 19 to 22 (Conant, 1986). The dorsum is uniformly dark and may have small white or brassy flecks and may look very similar to the lead back phase of P. cinereus (Fig. 6). The venter may have a slight "salt and pepper" mottling like P. cinereus but is usually much darker in appearance (Fig. 7). Another distinguishing characteristic is the length of the tail; P. richmondi has a long cylindrical tail usually as long or longer than the length of the body. Plethodon richmondi has similar habitat requirements to P. cinereus, living mainly along hillsides and valleys (Green and Pauley, 1987). During the warmest and driest summer months these salamanders retreat deep beneath the surface of the soil (Duellman, 1954; Pfingsten, 1989).

Site description

This study was conducted at three sites in northern West Virginia. The first site (NB) was located at North Bend State Park in Ritchie County on a northwest-facing slope adjacent to the North Fork of the Hughes River at 220 m elevation and had an area of approximately 15,000 m² (Fig. 8). Of the two study species, only P. richmondi inhabited this area. The understory was thin and consisted mainly of marginal shield fern (Dryopteris marginalis) and spicebush (Lindera benzoin). The overstory consisted mostly of silver maple (Acer sacharinum), yellow buckeye (Aesculus octandra), black cherry (Prunus

Figure 4. Dorsal view of P. cinereus (Photo by R. Jewell, 1991).



Figure 5. Ventral view of P. cinereus (adapted from Conant and Collins, 1991).



Figure 6. Dorsal view of P. richmondi (Photo by R. Jewell, 1991).

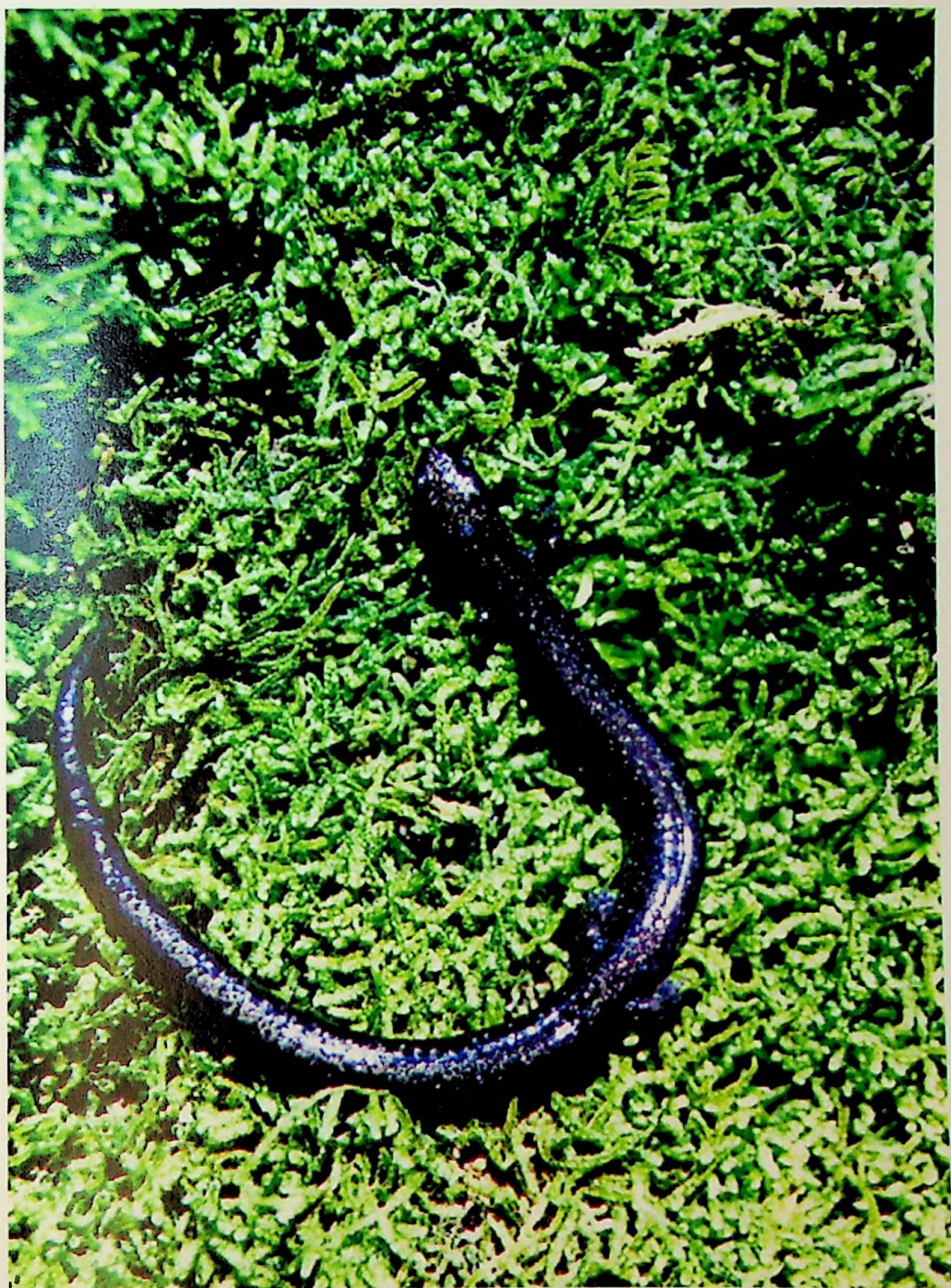


Figure 7. Ventral view of P. richmondi (adapted from Conant and Collins, 1991).



Figure 8. North Bend study site in early spring.



serotina) and white ash (Fraxinus americana). Other reptile and amphibian species found at NB were the eastern box turtle (Terrapene c. carolina), the northern ringneck snake (Diadophis punctatus edwardsii), the four-toed salamander (Hemidactylium scutatum), the southern two-lined salamander (Eurycea cirrigera) and Wehrle's salamander (Plethodon wehrlei).

The second site (LR) was located in Doddridge County at the intersection of U.S. Route 50 and Long Run road on a north-facing slope at 270 m elevation (Fig. 9). This site was selected as the intermediate site based on historical records that P. richmondi and P. cinereus were both present in about equal proportions (Pauley, pers. comm.). Unfortunately, the population numbers have shifted since those records were collected and is now weighted heavily in favor of P. cinereus. The understory was thick and consisted mainly of wild berry (Rubus sp.) christmas fern (Polystichum acrostichoides) and marginal shield fern (D. marginalis). The overstory consisted mainly of silver maple (A. saccharinum), black cherry (P. serotina) and mixed oak (Quercus spp.). Other reptile and amphibian species present at LR were the eastern box turtle (T. c. carolina), black rat snake (Elaphe o. obsoleta), mountain chorus frog (Pseudacris brachyphona) and the southern two-lined salamander (E. cirrigera).

The third study site (ST) was on the campus of Salem-Teikyo University in Harrison County (Fig. 10). This site was on a north-facing slope at 350 m elevation and had an area of approximately 6,000 m². This site was chosen as the 100 percent P. cinereus site, however 2 P. richmondi were found during the study. The understory was thin and dominated by marginal shield fern (D. marginalis) and spicebush (L. benzoin). The overstory consisted mainly of silver maple (A. saccharinum) and mixed oak (Quercus sp.).

Figure 9. Long Run study site in early spring.



Figure 10. Salem-Teikyo study site in early spring.



Other reptile and amphibian species found at this site were the American toad (Bufo americanus) and Wehrle's salamander (Plethodon wehrlei).

Chapter III

Population Structure

Introduction

Plethodon cinereus, as with most woodland salamanders, is primarily active during the spring and fall seasons at lower elevations. Most researchers have reported a biennial egg laying pattern (Sayler, 1966; Test and Bingham, 1948); however Nagel (1979), reported an annual egg laying pattern for a population in Tennessee. Nests have been found mainly in rotting logs and under rocks (Green and Pauley, 1987; Test, 1955). Female P. cinereus are usually larger than male P. cinereus; Pfingsten (1989) reported a mean snout-vent length (SVL) of 40.50 mm for males and 41.20 mm for females; similarly, Sayler (1966) reported a mean SVL for males of 39.98 mm and 40.28 mm for females from a spring collection. Two size classes are commonly reported with young of the year (YOY) becoming surface active in the fall of the year they are hatched (Pfingsten, 1989; Sayler, 1966)

Plethodon richmondi is primarily active during the early spring and late fall (Duellman, 1954). A biennial egg laying pattern has been reported for P. richmondi (Jewell and Pauley, 1995; Nagel, 1979) with egg deposition occurring in late April or May (Duellman, 1954; Jewell and Pauley, 1995). Most studies report that more females are surface active than males (Nagel, 1979; Pfingsten, 1989). Female P. richmondi are usually larger than male P. richmondi. Nagel (1979), reported an average SVL for male P. richmondi of 48.06 mm and 50.65 mm for female P. richmondi; similarly, Pfingsten (1989) reported an average SVL for male P. richmondi of 47.34 mm and 49.51 for female P. richmondi. Two size classes have been reported with YOY remaining subsurface through the first winter then becoming surface active during the spring of the next year (Pfingsten, 1989).

There has been little data collected on the life histories or population dynamics of either of these species in West Virginia. This study was conducted to collect some baseline information concerning population structure, sexual dimorphism, growth rates and basic natural history of these two species in northern West Virginia.

Materials and Methods

The study was conducted from March through November, 1994. Salamanders were collected from the three study sites (described in chapter 2) by turning all logs and rocks encountered. Thirteen site visits were made (6 in the spring, 4 in the summer and 3 in the fall); all spring trips were successful, however, none of the summer trips and only two of the fall trips yielded any animals.

Salamanders were sacrificed in 50 percent ethanol within 2 h of capture, then injected with 40 percent formalin. Specimens were subsequently placed in 40 percent formalin for 2 weeks and then water for 1 week before being stored in 70 percent ethanol. In the lab, SVL was measured using dial calipers to the nearest tenth of a mm from the tip of the snout to the anterior angle of the vent; head width (HW) was measured using a dissecting microscope fitted with an ocular micrometer to the nearest tenth of a mm at the widest part of the head behind the eyes. Specimens were classified as either male or female based on the presence of testes or ovaries; specimens that had no detectable reproductive organs were classified as juvenile. Female reproductive stage was also noted as being "gravid" (fully developed eggs), "non-gravid" (no eggs) or "immature" (small, undeveloped eggs).

Population size structure was determined by constructing monthly and

cumulative SVL frequency histograms and cumulative HW frequency histograms for each species. Mean SVL's and HW's were calculated and compared using t-tests to determine monthly differences as well as to determine if sexual dimorphism was displayed by either species. A chi-square test was used to ascertain if there were any differences in male to female ratios within each site as well as to assess differences in gravid to non-gravid ratios within each species.

Morphological characteristics were compared interspecifically. Mean SVL and HW data were compared using t-tests. SVL and HW values were regressed for each species; regression lines were fit using the least squares method and regression equations were computed for each line. Multiple regression analysis was performed on the best fit lines to determine if there was a significant difference between the slopes of the lines.

Results

A total of 164 animals was collected from the three study sites, of which, 62 were P. richmondi and 102 were P. cinereus (Table 1,2). All animals collected from NB were P. richmondi (n = 54). At LR, 43 P. cinereus and 6 P. richmondi were collected, and at ST 59 P. cinereus and 2 P. richmondi were collected. Neither species was surface active during the warmest and driest months of summer and early fall (June - October).

Plethodon richmondi

Size class distribution data showed that P. richmondi ranged in SVL from 18.7 mm to 59.9 mm for the entire study period with a majority of the animals ranging from 42.0 to 59.9 mm SVL (Fig. 11). The overall frequency distribution was unimodal for the entire study period; however, two size

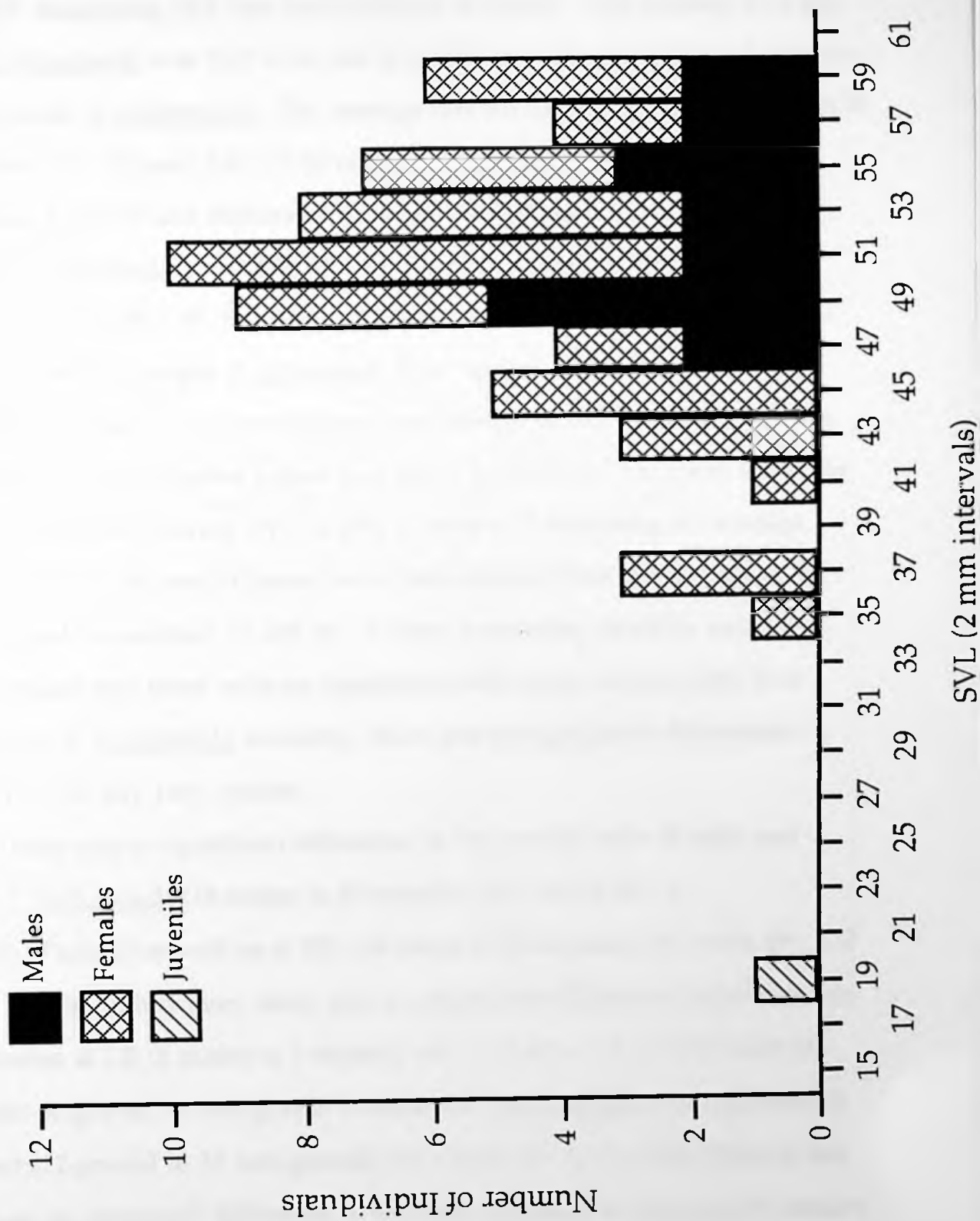
Table 1. Number of P. richmondi and P. cinereus at each study site.

Species	NB	LR	ST
<u>P. richmondi</u>	54	6	2
<u>P. cinereus</u>	0	43	59
Total	54	49	61

Table 2. Number of P. richmondi and P. cinereus by site and by sex.

Species	Site	Male	Female	Juvenile
<u>P. richmondi</u>	NB	16	38	0
	LR	1	4	1
	ST	1	1	1
<u>P. cinereus</u>	LR	18	18	7
	ST	8	37	14

Figure 11. Overall length-frequency histogram for P. richmondi.



classes could be detected from analysis of the monthly frequency histograms. One YOY measuring 18.7 mm was collected in March. The average SVL for male P. richmondi was 52.5 ± 3.6 mm ($\bar{x} \pm 1SD$) ($n = 18$) and 49.3 ± 6.5 mm ($n = 43$) for female P. richmondi. The average HW for male P. richmondi was 5.98 ± 0.32 mm ($n = 18$) and 5.60 ± 0.53 mm ($n = 43$) for female P. richmondi. There was a significant difference between the average SVL's of male and female P. richmondi ($t = -2.456$, $df = 54$, $P < 0.05$) as well as for the average HW's ($t = -2.793$, $df = 59$, $P < 0.05$). Monthly size class frequency histograms revealed that only larger P. richmondi were surface active over the entire active season (Fig . 12). Two cohorts were present in the April samples; the average SVL of the smaller cohort was 38.5 ± 3.8 ($n = 6$). The same cohort in November had an average SVL of 48.6 ± 1.8 ($n = 7$) indicating an average growth rate of 0.04 mm/d (based on a time interval from the beginning of April to mid-November of 228 d). A t-test comparing monthly mean SVL data revealed that there were no significant differences between any two months for P. richmondi; similarly, there was no significant differences in mean HW for any two months.

There was a significant difference in the overall ratio of male and female P. richmondi (18 males to 43 females) ($X^2 = 10.25$, $df = 1$, $P < 0.05$) (Table 3) as well as at NB (16 males to 38 females) ($X^2 = 8.96$, $df = 1$, $P < 0.05$) (Table 3); however, there was no significant difference between males and females at LR (4 males to 1 female) ($X^2 = 1.8$, $df = 1$, $P > 0.05$) (Table 3). The ratio of gravid to non-gravid females for P. richmondi was significantly different (12 gravid to 31 non-gravid) ($X^2 = 8.39$, $df = 1$, $P < 0.05$) (Table 4) but there was no statistical difference in the ratio of gravid to non-gravid females between spring and fall (Spring: 7 gravid, 28 non-gravid; Fall: 0 gravid, 3

Table 3. Summary of the chi-square contingency test for independence comparing male and female *P. richmondi*.

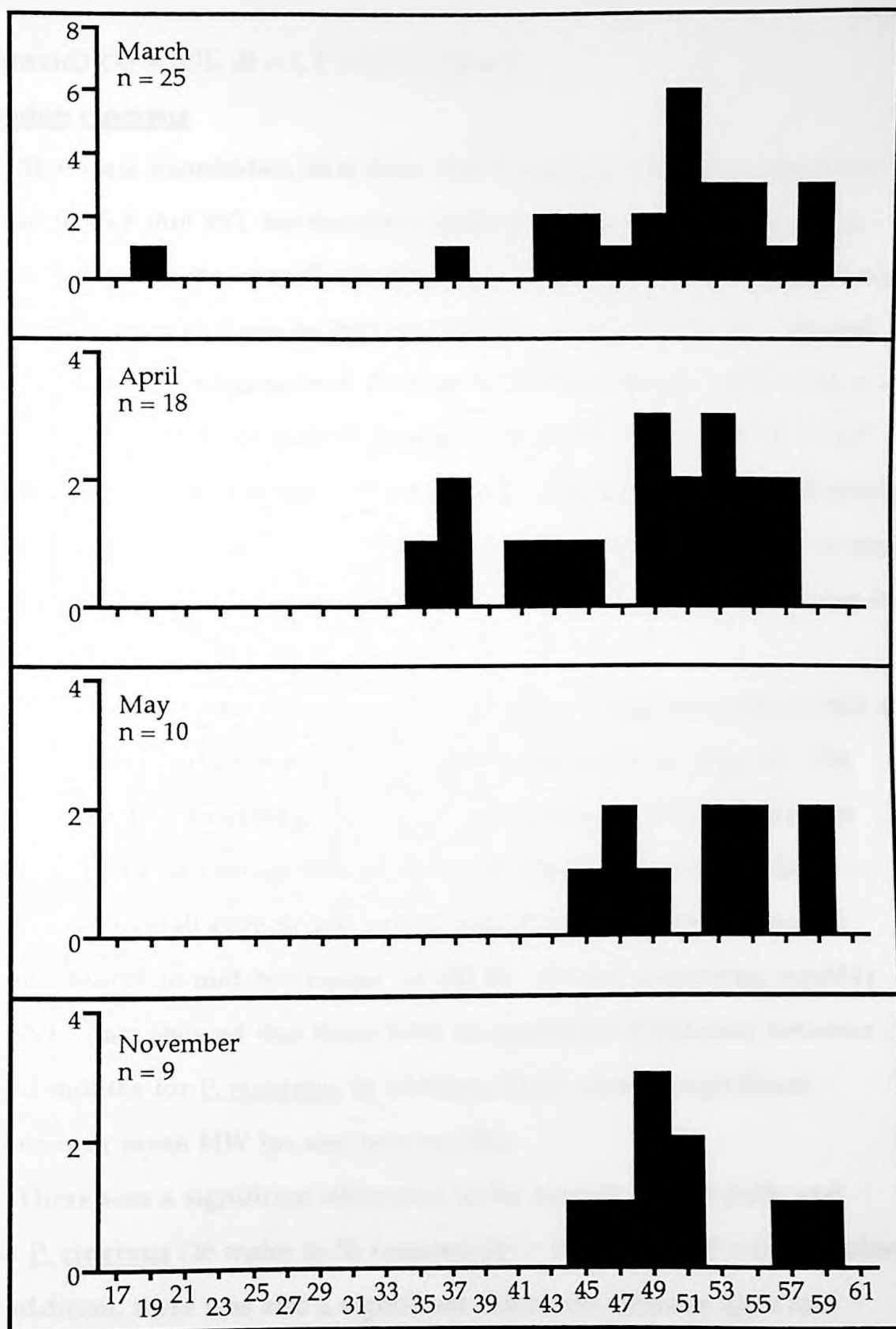
Subset	Observed	Expected	Contribution to the total χ^2
Total			
<u>P. richmondi</u> male	18	30.5	5.123
<u>P. richmondi</u> female	43	30.5	5.123
		$\Sigma \chi^2 =$	10.25
NB			
<u>P. richmondi</u> male	16	27	4.48
<u>P. richmondi</u> female	38	27	4.48
		$\Sigma \chi^2 =$	8.96
LR			
<u>P. richmondi</u> male	4	2.5	0.9
<u>P. richmondi</u> female	1	2.5	0.9
		$\Sigma \chi^2 =$	1.8

Table 4. Summary of the chi-square contingency test for independence comparing gravid and non-gravid P. richmondi.

Subset	Observed	Expected	Contribution to the total χ^2
Total			
<u>P. richmondi</u> gravid	12	21.5	4.197
<u>P. richmondi</u> non-gravid	31	21.5	4.197
		$\Sigma \chi^2 =$	8.39

Figure 12. Monthly length-frequency histogram for P. richmondi.

Number of Individuals



SVL (2 mm intervals)

non-gravid) ($X^2 = 0.75$, $df = 1$, $P > 0.05$) (Table 5).

Plethodon cinereus

Size class distribution data show that P. cinereus ranged in size from 15.8 mm to 49.8 mm SVL for the entire study period (Fig. 13). There was a bimodal pattern in the overall size frequency histogram with the smaller size class ranging from 15.8 mm to 28.2 mm SVL ($\bar{x} = 23.3 \pm 2.8$ mm, $n = 20$) and the larger size class ranging from 32.4 mm to 49.8 mm SVL ($\bar{x} = 40.6 \pm 4.4$, $n = 82$). The average SVL for male P. cinereus was 41.7 ± 3.9 mm and 40.1 ± 4.6 mm for females. The average HW for male P. cinereus was 5.38 ± 0.38 mm ($n = 26$) and 5.13 ± 0.50 mm ($n = 55$). There was no significant difference in mean SVL ($t = -1.58$, $df = 79$, $P > 0.05$), however, there was a significant difference in mean HW ($t = -2.320$, $df = 79$, $P < 0.05$).

Monthly size class frequency histograms for P. cinereus indicate that all size classes were surface active over the entire active season (Fig. 14). The YOY size class had an average SVL of 23.7 ± 2.4 mm ($n = 11$) in March; the same cohort had an average SVL of 35.6 ± 2.8 mm ($n = 4$) in November indicating an overall growth rate of 0.06 mm/d (based on a time interval from mid-March to mid-November of 243 d). A t-test comparing monthly mean SVL data showed that there were no significant differences between any two months for P. cinereus; in addition, there were no significant differences in mean HW for any two months.

There was a significant difference in the overall ratio of male and female P. cinereus (26 males to 55 females) ($X^2 = 10.38$, $df = 1$, $P < 0.05$) (Table 6); in addition, there was also a significant difference between male and female P. cinereus at ST (8 males to 37 females) ($X^2 = 18.69$, $df = 1$, $P < 0.05$) (Table 6). There was no significant difference between male and female

Table 5. Summary of the chi-square test for independence comparing gravid and non-gravid female P. richmondi during the spring and fall seasons.

Gravid	Observed	Expected	Contribution to the total χ^2
Gravid			
Spring	7	7	0.00
Fall	0	0.6	0.6
Non-gravid			
Spring	28	28	0.00
Fall	3	2.4	0.15
		$\Sigma \chi^2 =$	0.75

Table 6. Summary of the chi-square contingency test for independence comparing male and female P. cinereus.

Subset	Observed	Expected	Contribution to the total χ^2
Total			
<u>P. cinereus</u> male	26	40.5	5.191
<u>P. cinereus</u> female	55	40.5	5.191
		$\Sigma \chi^2 =$	10.38
LR			
<u>P. cinereus</u> male	18	18	0.00
<u>P. cinereus</u> female	18	18	0.00
		$\Sigma \chi^2 =$	0.00
ST			
<u>P. cinereus</u> male	8	22.5	9.344
<u>P. cinereus</u> female	37	22.5	9.344
		$\Sigma \chi^2 =$	18.68

Figure 13. Overall length-frequency histogram for P. cinereus.

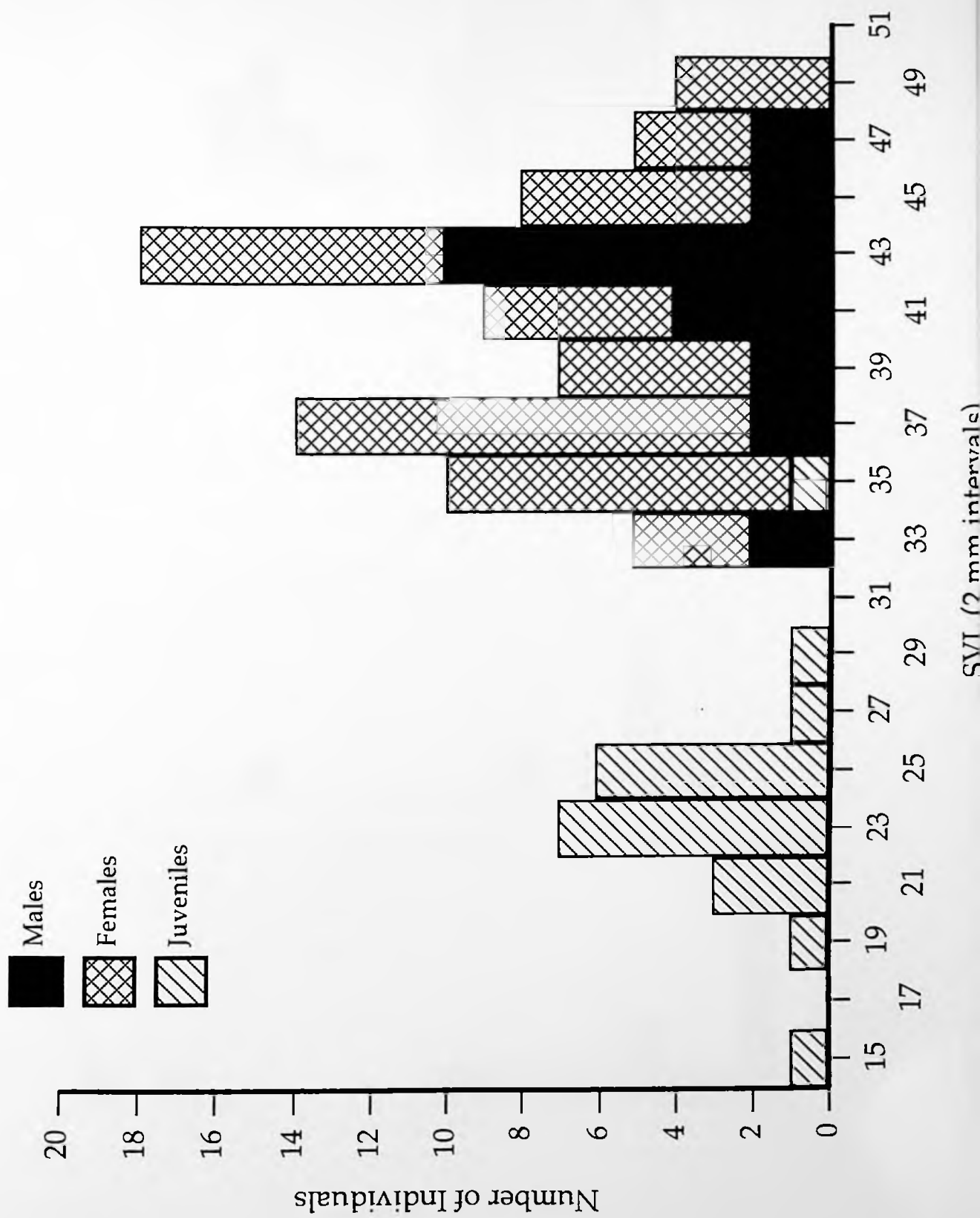
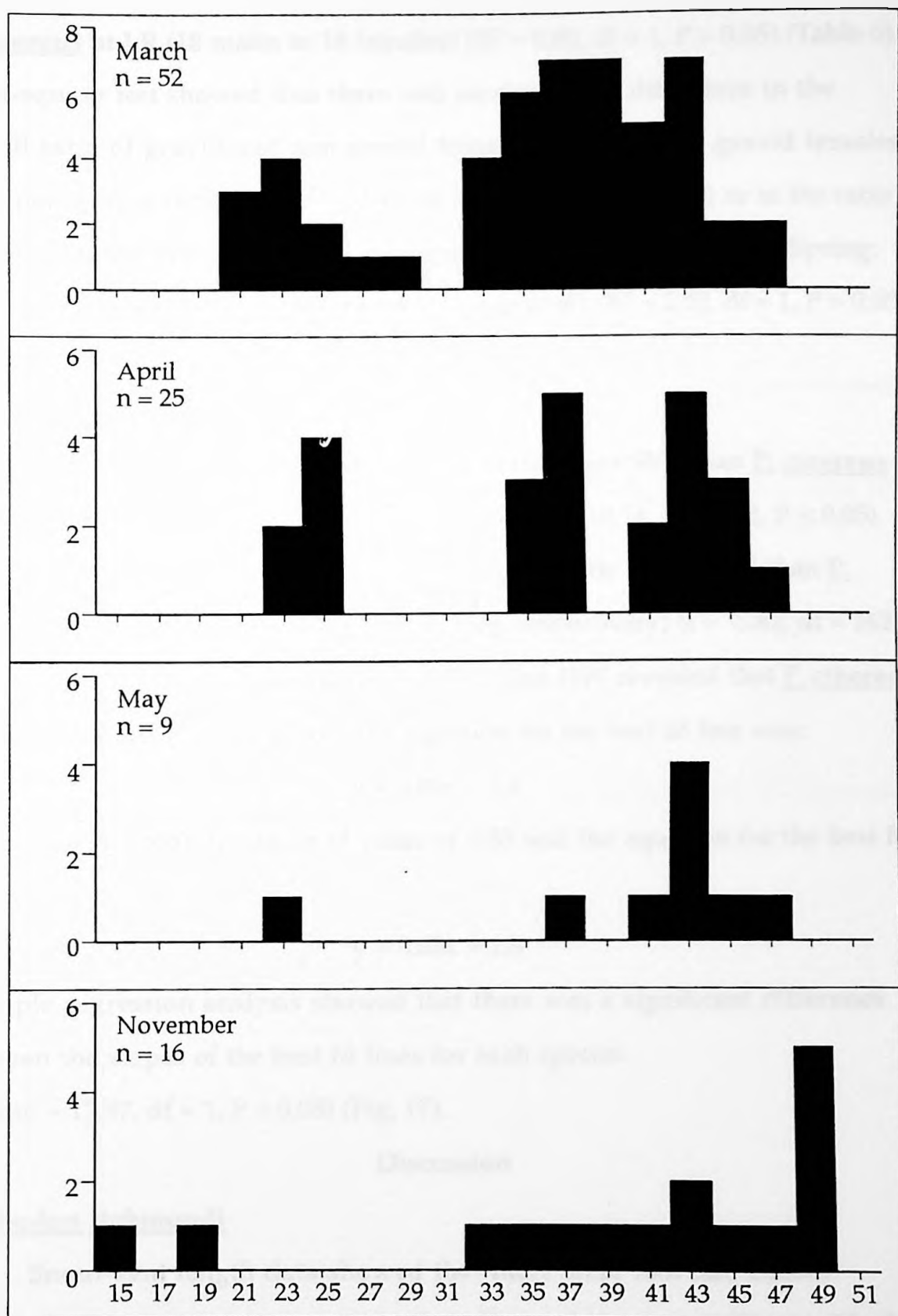


Figure 14. Monthly length-frequency histogram for P. cinereus.

Number of individuals



SVL (2 mm intervals)

P. cinereus at LR (18 males to 18 females) ($X^2 = 0.00$, $df = 1$, $P > 0.05$) (Table 6).

A chi-square test showed that there was no significant difference in the overall ratio of gravid and non-gravid female P. cinereus (30 gravid females to 25 non-gravid females) ($X^2 = 0.45$, $df = 1$, $P > 0.05$) (Table 7) or in the ratio of gravid and non-gravid female P. cinereus between spring and fall (Spring: 16 gravid, 22 non-gravid; Fall: 7 gravid, 3 non-gravid) ($X^2 = 2.02$, $df = 1$, $P > 0.05$) (Table 8).

Morphological comparison

Plethodon richmondi had a significantly larger SVL than P. cinereus (49.7 ± 7.1 mm and 37.2 ± 8.0 mm respectively) ($t = -10.14$, $df = 162$, $P < 0.05$) (Fig. 15); in addition, P. richmondi had a significantly larger HW than P. cinereus (5.68 ± 0.60 mm and 4.87 ± 0.80 mm, respectively) ($t = -6.82$, $df = 162$, $P < 0.05$) (Fig. 16). Regression analysis of SVL and HW revealed that P. cinereus had an r^2 value of 0.92 (Fig. 17); the equation for the best fit line was:

$$y = 0.09x + 1.3 \quad (1)$$

Plethodon richmondi had an r^2 value of 0.85 and the equation for the best fit line was:

$$y = 0.08x = 1.8 \quad (2)$$

Multiple regression analysis showed that there was a significant difference between the slopes of the best fit lines for each species (F-ratio = 13.97, $df = 1$, $P < 0.05$) (Fig. 17).

Discussion

Plethodon richmondi

Snout-vent length data showed that there were two size classes represented over the entire study period. These data are consistent with the data collected by others (Duellman, 1954; Nagel, 1979; Pfingsten, 1989). Only

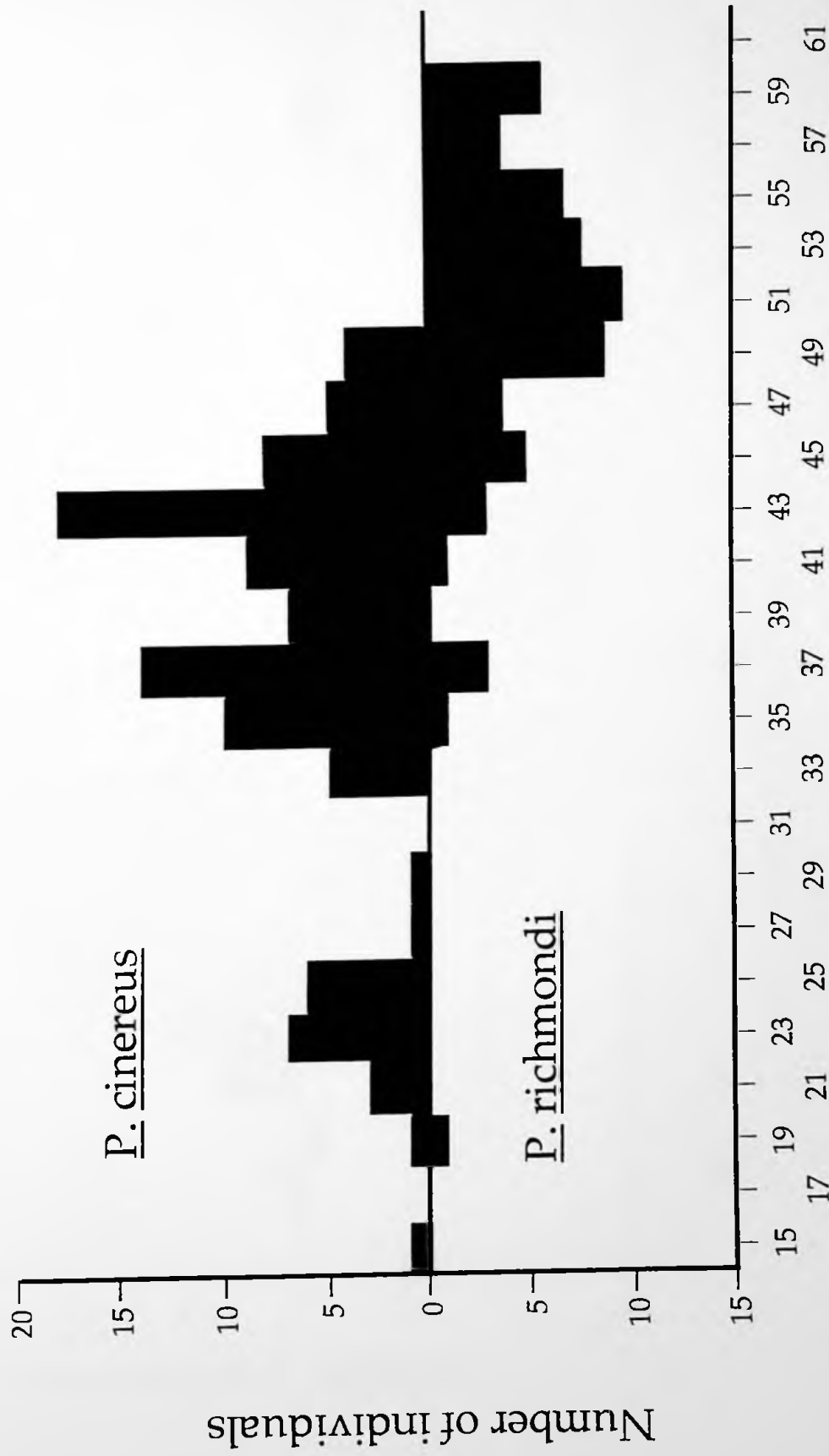
Table 7. Summary of the chi-square contingency test for independence comparing gravid and non-gravid P. cinereus.

Subset	Observed	Expected	Contribution to the total χ^2
Total			
<u>P. cinereus</u> gravid	30	27.5	0.227
<u>P. cinereus</u> non-gravid	25	27.5	0.227
		$\Sigma \chi^2 =$	0.45

Table 8. Summary of the chi-square test for independence comparing gravid and non-gravid female P. cinereus during the spring and fall seasons.

Gravid	Observed	Expected	Contribution to the total χ^2
Gravid			
Spring	16	18	0.22
Fall	7	5	0.8
Non-gravid			
Spring	22	38	0.2
Fall	3	10	0.8
		$\Sigma \chi^2 =$	2.02

Figure 15. Comparative overall length-frequency histogram for P. richmondi and P. cinereus.



SVL (2 mm intervals)

Figure 16. Comparative overall headwidth-frequency histogram for P. richmondi and P. cinereus.

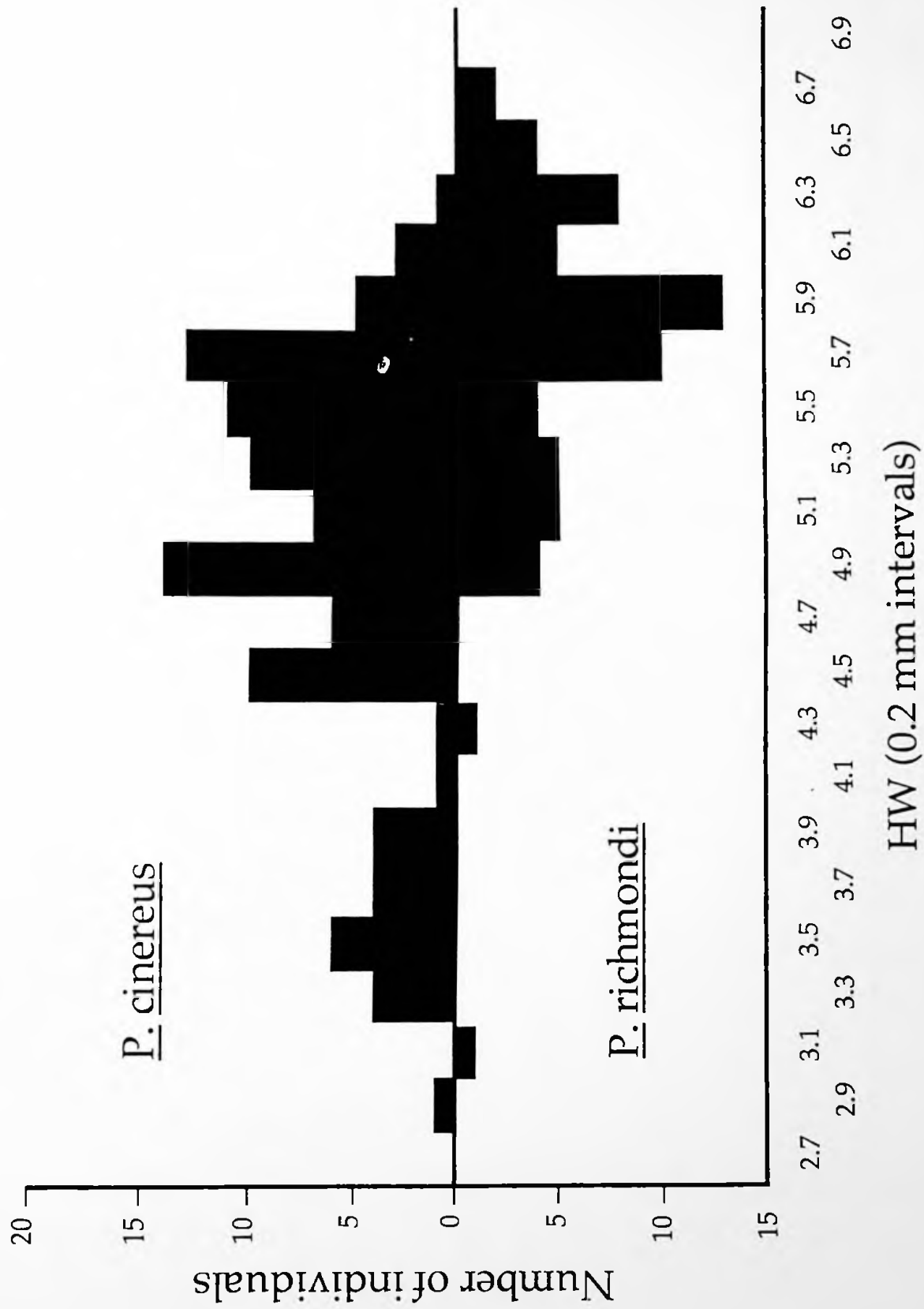
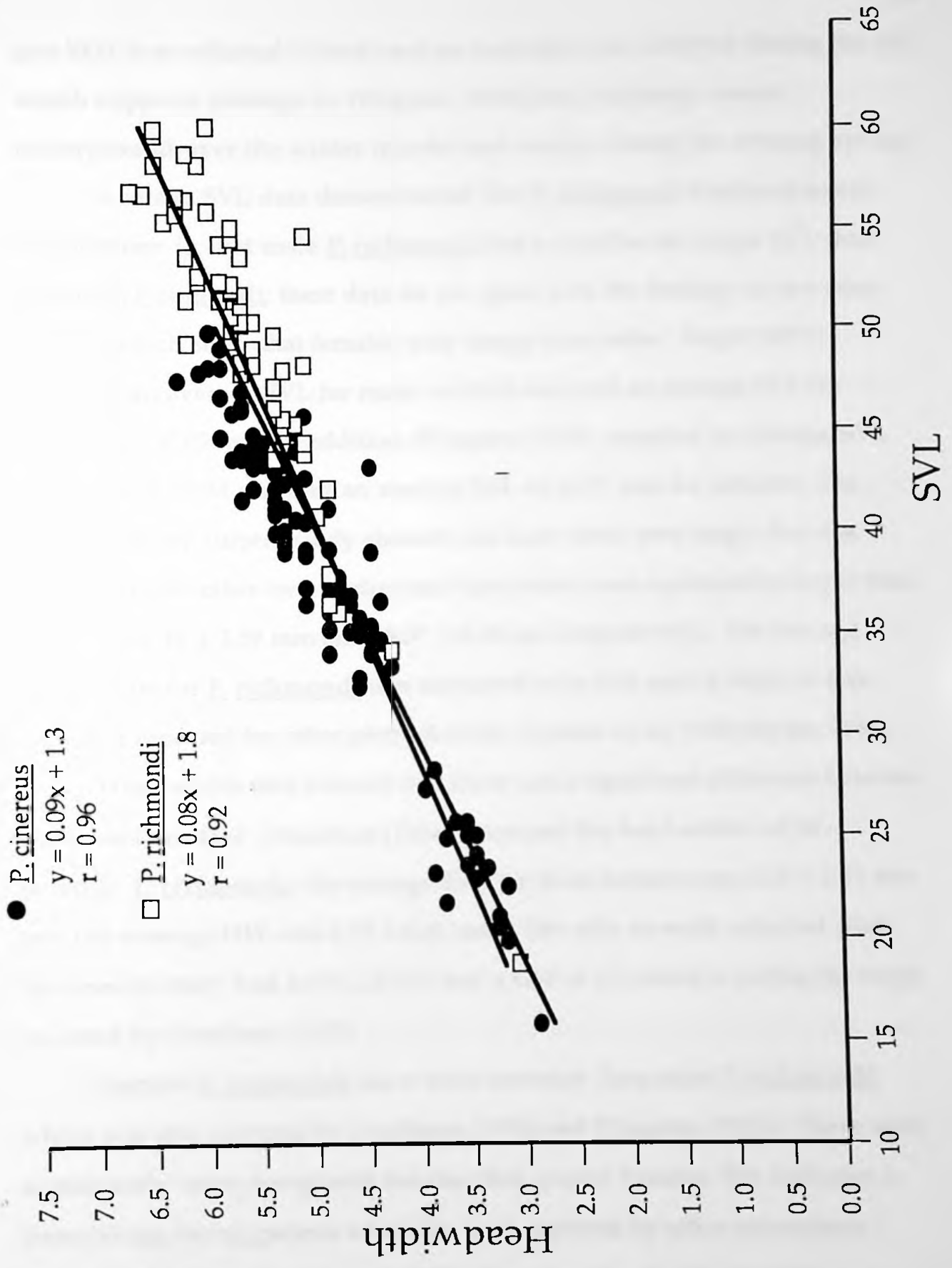


Figure 17. Scatter plot comparing snout-vent length and head widths of P. richmondi and P. cinereus. Estimated regression lines are shown; the minimum and maximum SVL and HW are indicated for each species.



one YOY was collected (March) and no neonates were collected during the fall which supports findings by Pfingsten (1989) that hatchlings remain underground over the winter months and emerge during the ensuing spring.

Average SVL data demonstrated that P. richmondi displayed sexual dimorphism in that male P. richmondi had a significantly larger SVL than female P. richmondi; these data do not agree with the findings of two other studies which show that females were larger than males. Nagel (1979) reported an average SVL for males of 48.06 mm and an average SVL for females of 50.65 mm; in addition, Pfingsten (1989), reported an average SVL for males of 47.34 mm and an average SVL of 49.51 mm for females. The findings of the current study showed that both sexes were larger than the animals in the other two studies and that males were significantly larger than females (52.49 ± 3.59 mm and 49.31 ± 6.45 mm respectively). The average growth rate for P. richmondi was estimated to be 0.04 mm/d which is less than that reported for other plethodontids (Kramer et al., 1993; Saylor, 1966).

Head width data showed that there was a significant difference between males and females. Duellman (1954) measured the head widths of 30 juvenile P. richmondi; the average SVL for these animals was 17.8 ± 1.31 mm and the average HW was 2.90 ± 0.21 mm. The only juvenile collected from the present study had a SVL of 18.7 and a HW of 3.1 which is within the range reported by Duellman (1955).

Female P. richmondi were more common than male P. richmondi, which was also reported by Duellman (1954) and Pfingsten (1989). There were significantly more non-gravid females than gravid females; this indicates a biennial egg laying pattern which has been reported by other researchers (Jewell and Pauley, 1995; Nagel, 1979). There was no significant difference

between the ratio of gravid to non-gravid females in the spring and fall; however, no gravid females were collected during the fall season. These data suggest that P. richmondi lay eggs sometime before the fall and is in line with the findings of Duellman (1954) and Jewell and Pauley (1995) who reported that eggs were probably layed in late spring or early summer.

Plethodon cinereus

The bimodal pattern of the SVL histograms indicate that there were at least two size classes present over the entire study period which is consistent with findings from other researchers (Fraser, 1976; Pfingsten, 1989; Sayler, 1966) . A distinct group of YOY individuals was collected in March and April, one individual from this cohort was capture in May indicating an overall decrease in the surface activity of this cohort towards the warmer and drier periods of the study (in relation to the larger size class). Two individuals with SVL's of 15.8 and 19.8 were collected in November indicating that neonates became surface active the same year they were born which has also been reported by Pfingsten (1989). Sexual dimorphism was displayed in HW but it was not exhibited when comparing SVL; these data are similar to those of Sayler (1966) who reported an average SVL for male P. cinereus of 39.98 mm and 40.28 mm for females and Pfingsten (1989) who reported an average SVL for males of 40.50 mm and 41.20 mm for females. As with P. richmondi, these data are opposite from what was found in the present study in that male P. cinereus had a larger average SVL then female P. cinereus. The average growth rate for P. cinereus was 0.06 mm/d which is in line with the growth rate reported by Sayler (1966) of 0.08 mm/d.

Female P. cinereus were more common then male P. cinereus at ST; however, at LR there were an equal number of males and females. There was

not a significant difference in the proportion of gravid to non-gravid females in the spring and fall; however, most of the gravid females were found in the spring indicating that eggs were laid during the late spring and early summer which is in concurrence with other researchers data (Sayler, 1966; Pfingsten, 1989). The egg laying pattern of P. cinereus appears to be biennial due to the equal number of gravid and non-gravid females in the spring which is consistent with the findings of other researchers (Sayler, 1966, Test and Bingham, 1948).

Plethodon richmondi was the larger of the two species and had a significantly larger SVL and HW than P. cinereus. Regression analysis revealed that HW for both species was significantly correlated to SVL; in addition, the larger size class of P. cinereus had a larger HW for any given SVL.

Conclusion

The population characteristics of P. richmondi and P. cinereus showed overall similar patterns to most other small woodland plethodontids. Adult P. richmondi exhibited sexual dimorphism with males being significantly larger than females. Both species had a biennial egg laying pattern and females outnumbered males approximately 2:1 for both species. Juvenile P. richmondi were not surface active during most of the year and neonates did not become surface active until the spring of the year after they were hatched; conversely, P. cinereus juveniles were active during most of the active season with neonates becoming surface active in the fall of the same year they were hatched.

Chapter IV

Microhabitat Analysis

Introduction

Salamanders of the family Plethodontidae are lungless and rely on the cutaneous exchange of gas through a semi-permeable skin to obtain oxygen; because of this, terrestrial plethodontids are limited in terms of the types of environments they can inhabit. Factors such as soil pH, soil temperature and soil moisture content as well as ambient parameters such as relative humidity, air temperature are thought to be important elements in defining the micro and macrodistributions of these salamanders.

Laboratory research has shown that P. cinereus utilizes slightly acidic soil (Wyman and Hawksley-Lescault, 1987; Vernberg, 1955). Frisbie and Wyman (1991) determined that the lethal pH for P. cinereus was between 3.0 and 4.0; in addition, it was reported that growth rate, body mass, and osmoregulatory response were all decreased as a result of a low pH environment.

Research relating to moisture requirements show that P. cinereus can loose up to 29 percent in wet mass before death (Heatwole and Lim, 1961). Jewell (1991) reported a critical thermal maxima (CTM) of 30.3 °C for P. cinereus and 32.3 °C for P. richmondi. Other research has demonstrated that the microdistribution of P. cinereus is directly related to the amount of moisture in the environment (Heatwole, 1962).

Materials and Methods

Environmental data were collected during 2 site visits in the fall of 1994 and 3 visits in the spring of 1995. Sites were searched during the day time by searching under all logs and rocks encountered. The order in which sites were visited was randomized to minimize the likelihood of weighting

temperature and moisture values in relation to the time of day. When a salamander was found, 22 environmental parameters were measured (Table 9). Soil samples were collected from beneath each rock where a salamander was located and sealed in a heavy duty zip lock freezer bag. Bags were stored on ice for transport to the lab at which time they were placed in a 0° C freezer until they could be analyzed for pH and moisture content. Soil temperature, soil moisture and soil pH measurements were collected from each site at random to determine if there were any inherent differences between the sites. Mean environmental measurements for each species as well as for the random samples were compared using t-tests; in addition, differences in variance for environmental parameters were tested using F tests. Mean SVL data for P. cinereus found beneath rocks and logs were compared using a t-test.

Environmental data were subjected to principal components analysis (PCA-SAS; Barr et al., 1982). Clustering of individuals on bivariate plots of their principal component scores was used to determine similarity or divergence between P. richmondi and P. cinereus in relation to habitat utilization. Due to limitations with PCA concerning missing data, only data from salamanders found under rocks were examined using PCA.

Results

Twenty three P. richmondi microhabitats (all rocks) and 28 P. cinereus microhabitats (6 logs, 22 rocks) were analyzed for this study. Random samples from the three study sites showed that the average soil temperature was 8.27 ± 0.90 for NB, 11.00 ± 1.73 for LR and 12.73 ± 1.62 for ST. There was a significant difference between NB and LR ($t = -6.33$, $df = 20$, $p < 0.05$) as well as NB and ST ($t = -7.97$, $df = 20$, $p < 0.05$) but there was not a significant difference between

Table 9. Description of environmental parameters measured for all P. richmondi and P. cinereus from NB, LR and ST.

Environmental Parameter	Description
Distance to edge (DTE)	Distance (cm) from location of salamanders head to the nearest edge of the rock impression.
Substrate type (SUB)	Substrate type found underneath rock. Leaf litter = 1, humus = 2, dirt = 3, rock = 4.
Rock circumference (RC)	Rock circumference (cm).
Thickest point of rock (TCKPT)	Thickness (cm) of rock measured at the thickest part of the rock.
Thinnest point of rock (THNPT)	Thickness (cm) of rock measured at the thinnest part of the rock.
Average thickness of rock (ATHK)	$(TCKPT + THNPT) / 2$
Difference in thickness (DTHK)	$(TCKPT - THNPT)$
Rock diameter width (RDW)	Diameter (cm) of the rock at the most narrow point.
Rock diameter length (RDL)	Diameter (cm) of the rock at the widest point.
Rock average diameter (AD)	$(RDW + RDL) / 2$
Rock surface area (RA)	Surface area (cm^2) of rock determined using the formula, $\text{area} = \pi r^2$ where $r = AD / 2$.
Rock volume (RV)	$RA \times ATHK$
Average depth of impression (ADI)	The average of the deepest and most shallow point of the impression.
Impression diameter width (IDW)	Diameter (cm) of the impression at the most narrow point.
Impression diameter length (IDL)	Diameter (cm) of the impression at the widest point.

Table 9 . Continued.

Impression surface area (IA)	Surface area (cm ²) of impression determined using the formula, area = πr^2 where r = average impression diameter/2.
Percent coverage of rock (PCR)	(IA / RA)
Refuge hole (REFH)	Recorded as present if a distinct hole was detectable under the rock where a salamander could retreat.
Soil pH (PH)	pH of the soil directly under the rock. A soil sample was collected and pH was measured in the lab.
Soil temperature (ST)	Temperature (°C) of the soil directly under the rock. Measured at 2 cm beneath the surface of the soil.
Soil moisture (SM)	Moisture content expressed as a ratio of total water weight (g)/total wet soil weight (g).
Tree present (TP)	Recorded as present if a tree was present within 2 m of the salamander's head.

LR and ST ($t = -1.02$, $df = 20$, $p > 0.05$). The average soil moisture content was 33.91 ± 5.49 for NB, 36.45 ± 5.37 for LR and 37.36 ± 6.74 for ST; there was not a significant difference between any of the sites for soil moisture content ($t = -1.10$, $df = 20$, $p > 0.05$; $t = -1.32$, $df = 20$, $p > 0.05$; $t = -0.35$, $df = 20$, $p > 0.05$, respectively). The average soil pH was 4.84 ± 0.55 for NB, 5.28 ± 0.69 for LR and 5.25 ± 0.62 for ST; none of the means were significantly different ($t = -1.67$, $df = 20$, $p > 0.05$; $t = -1.64$, $df = 20$, $p > 0.05$; $t = 0.13$, $df = 20$, $p > 0.05$, respectively).

Of the twenty two environmental parameters measured, eight were significantly different between P. richmondi and P. cinereus (Table 10). In relation to P. cinereus, P. richmondi utilized rocks with significantly larger circumferences (Fig. 18), rock diameter lengths (Fig. 19) and average rock diameters (Fig. 20) as well as rocks with significantly larger impression diameter lengths (Fig. 21); in addition, P. richmondi utilized rocks with a smaller rock area to impression area ratio than P. cinereus (Fig. 22). Plethodon richmondi also utilized soil that had a lower pH (Fig. 23) and temperature (Fig. 24) as well as a higher soil moisture content (Fig. 25).

Variances were larger in 17 of the 22 environmental parameters measured for P. cinereus than for P. richmondi and 4 of those (TCKPT, ATHK, DTHK and ADI) were significantly larger (Table 11). The mean SVL for P. cinereus found beneath rocks was 41.63 ± 8.17 mm and 32.9 ± 10.7 mm for P. cinereus found beneath logs; however there was no significant difference between the two means ($t = 1.94$, $df = 7$, $p > 0.05$).

The first principle component (PRIN 1) accounted for 38 percent of the variation, the second (PRIN 2) accounted for 19 percent of the variation and the third (PRIN 3), accounted for 10 percent of the variation (67 percent cumulatively). A bivariate plot of PRIN 1 and PRIN 2 scores revealed that

Table 10. Mean values of environmental parameters measured for all P. richmondi and P. cinereus from NB, LR and ST. Values given are means \pm 1 SD. Values with different letters for a given parameter are significantly different at $P < 0.05$. See Table 9 for parameter abbreviations.

Environmental Parameter	<u>P. richmondi</u> (n = 23)	<u>P. cinereus</u> (n = 22)
DTE	5.39 \pm 2.80a	6.09 \pm 3.53a
SUB	3.00 \pm 0.00a	2.72 \pm 0.70a
RC	108.87 \pm 25.93a	81.64 \pm 34.32b
TCKPT	11.61 \pm 4.57a	14.36 \pm 12.36a
THNPT	8.52 \pm 4.79a	8.82 \pm 6.65a
ATHK	10.06 \pm 4.55a	11.59 \pm 9.44a
DTHK	3.09 \pm 2.15a	5.55 \pm 6.13a
RDW	26.70 \pm 10.39a	21.41 \pm 12.00a
RDL	38.43 \pm 11.52a	28.27 \pm 13.23b
TA	909.09 \pm 554.00a	579.20 \pm 523.95a
AD	32.57 \pm 10.10a	24.84 \pm 11.25b
RV	10707.86 \pm 10746.10a	6752.37 \pm 7263.08a
ADI	3.47 \pm 2.67a	3.35 \pm 4.09a
IDW	25.22 \pm 9.04a	22.23 \pm 11.18a
IDL	35.43 \pm 11.42a	27.23 \pm 12.34b
IA	976.13 \pm 629.61a	688.91 \pm 587.00a
PCR	1.09 \pm 0.26a	1.25 \pm 0.27b
REFH	1.78 \pm 0.42a	1.77 \pm 0.43a
PH	4.83 \pm 0.59a	5.33 \pm 0.44b
ST	8.78 \pm 3.37a	12.41 \pm 1.47b
SM	32.84 \pm 7.53a	23.42 \pm 6.21b
TP	1.65 \pm 0.49a	1.5 \pm 0.51a

Table 11. F values for all environmental parameters measured for all P. richmondi and P. cinereus from NB, LR and ST.

Environmental Parameter	F value (F')	Prob > F'
DTE	1.58	0.29
SUB	-----	-----
RC	1.75	0.20
TCKPT	7.31	0.00
THNPT	1.93	0.13
ATHK	4.30	0.00
DTHK	8.12	0.00
RDW	1.33	0.51
RDL	1.32	0.52
TA	1.12	0.80
AD	1.24	0.62
RV	2.19	0.08
ADI	2.34	0.05
IDW	1.53	0.33
IDL	1.17	0.72
IA	1.15	0.75
PCR	1.11	0.81
REFH	1.03	0.94
PH	1.78	0.22
ST	5.27	0.00
SM	1.47	0.38
TP	1.10	0.82

Figure 18. Population range diagram of mean rock circumference (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in cm.

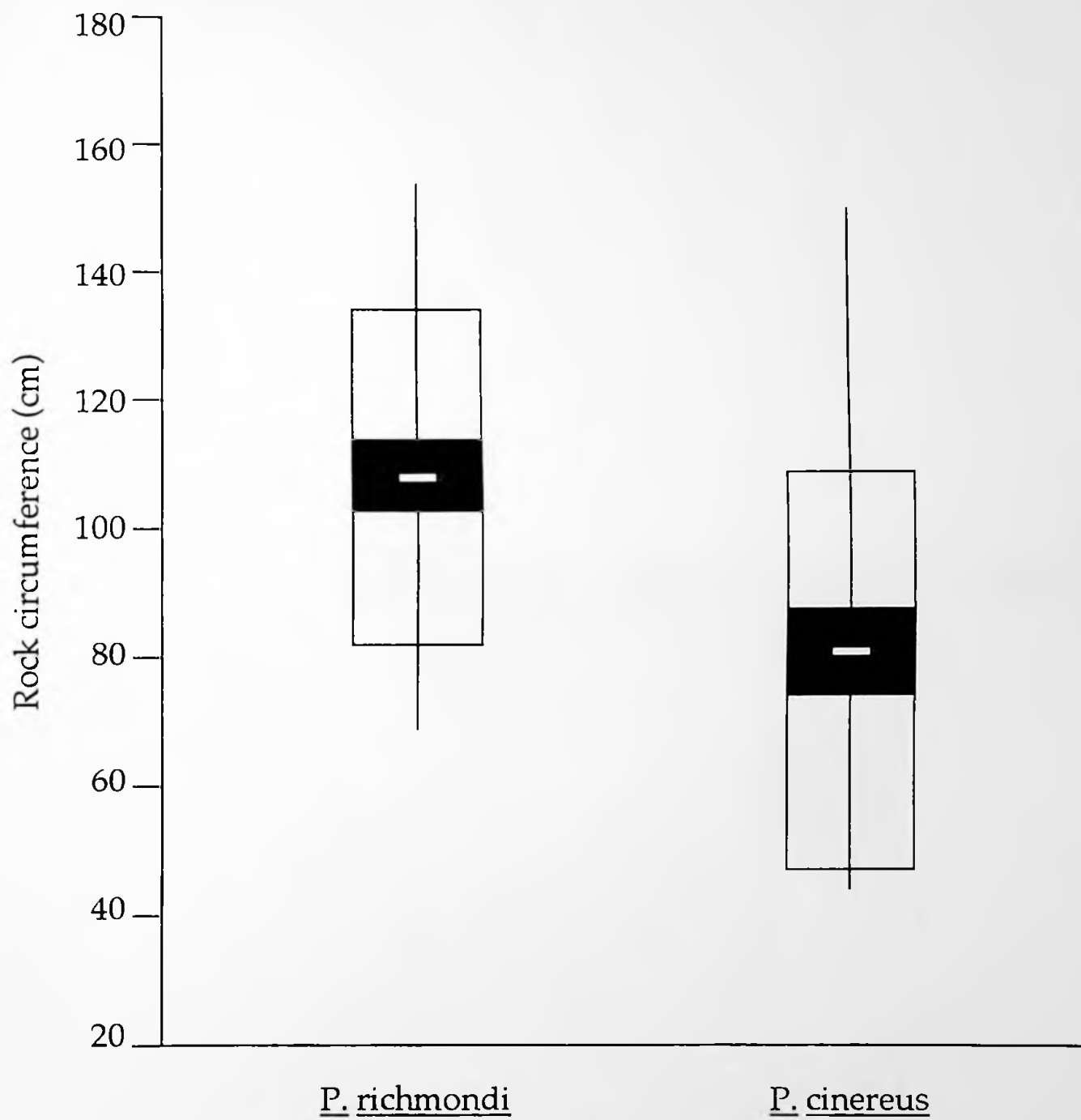


Figure 19. Population range diagram of mean rock diameter length (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in cm.

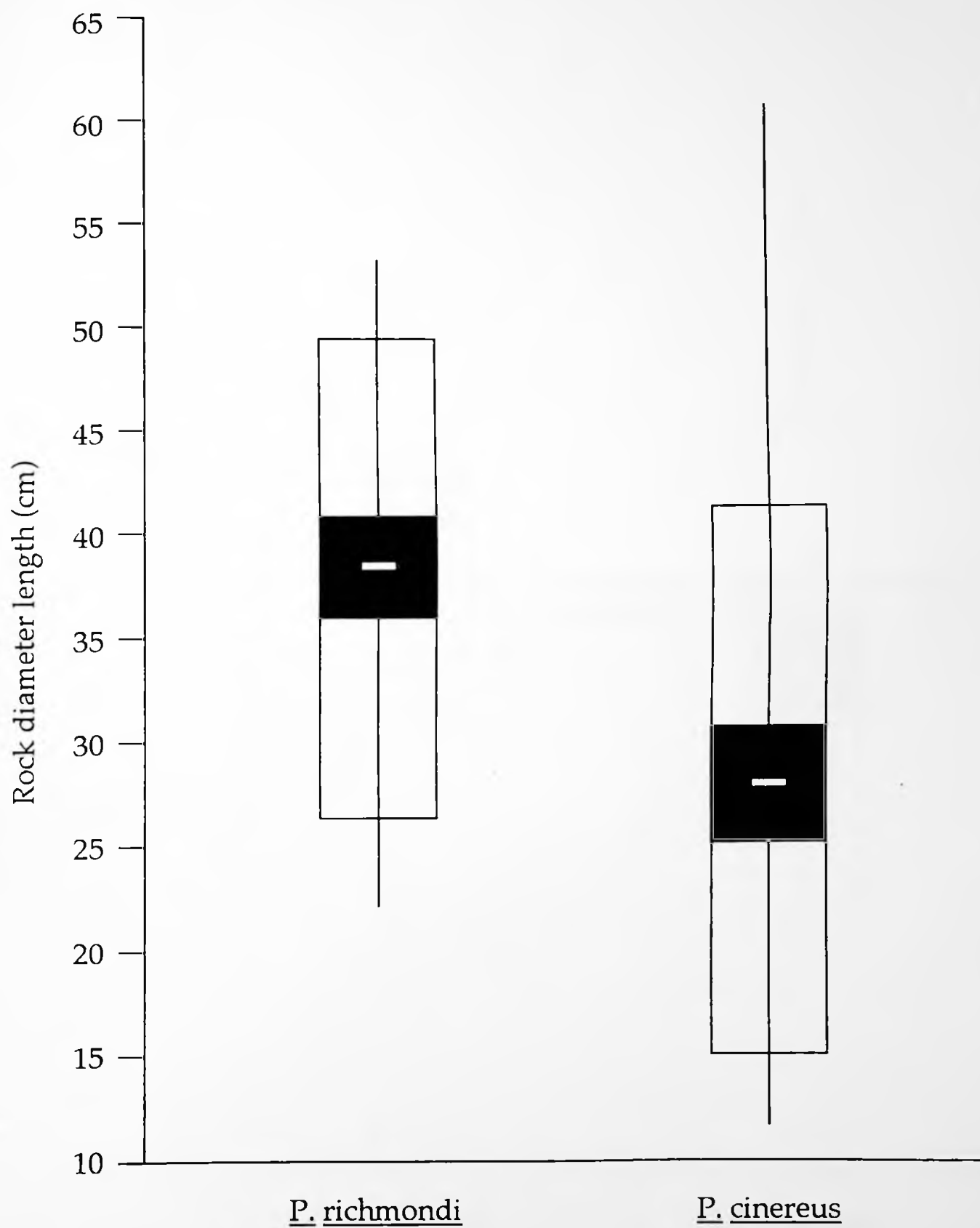


Figure 20. Population range diagram of mean rock diameter (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in cm.

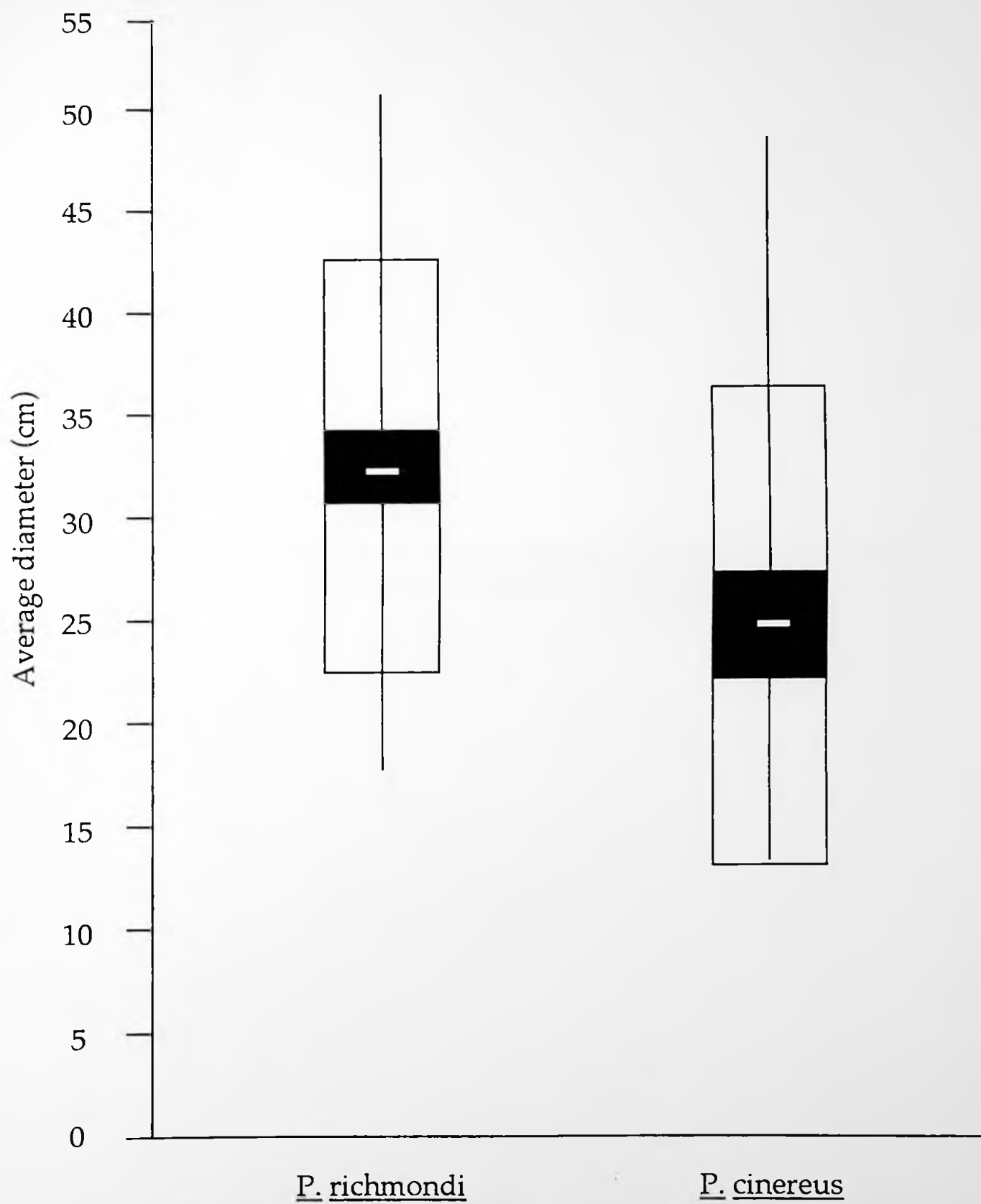


Figure 21. Population range diagram of mean impression diameter length (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in cm.

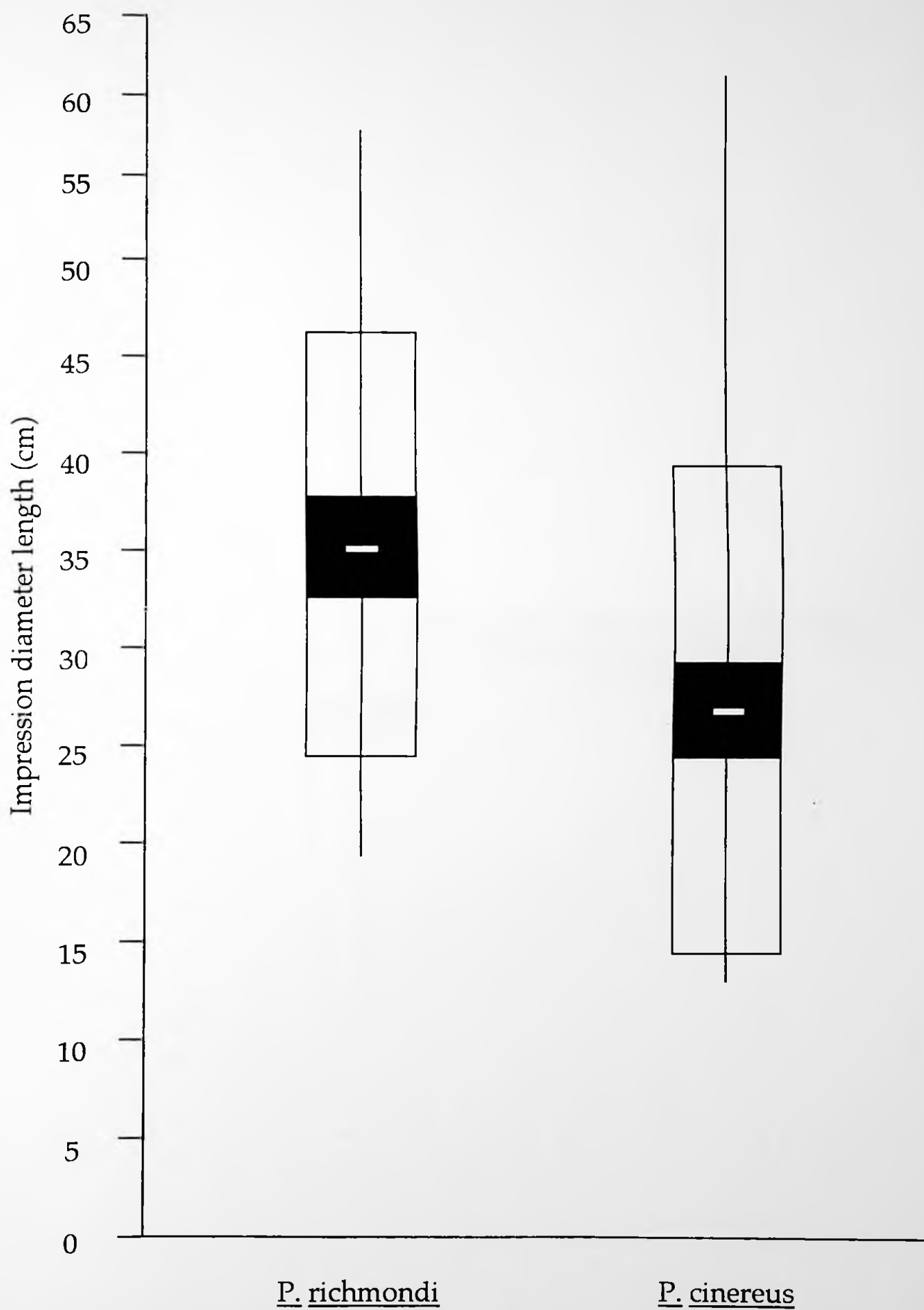


Figure 22. Population range diagram of mean percent contact of rock to the ground (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line).

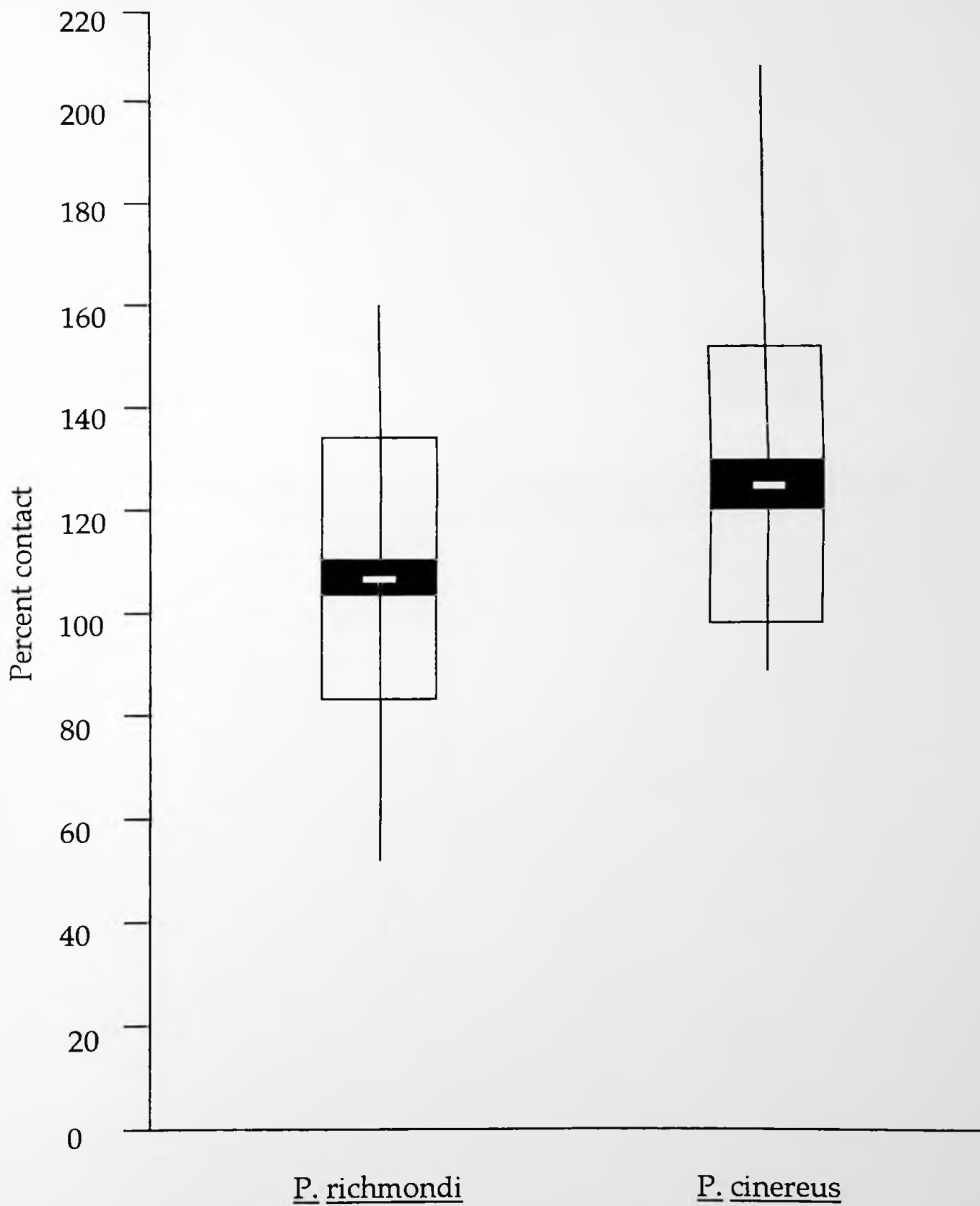


Figure 23. Population range diagram of mean soil pH (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line).

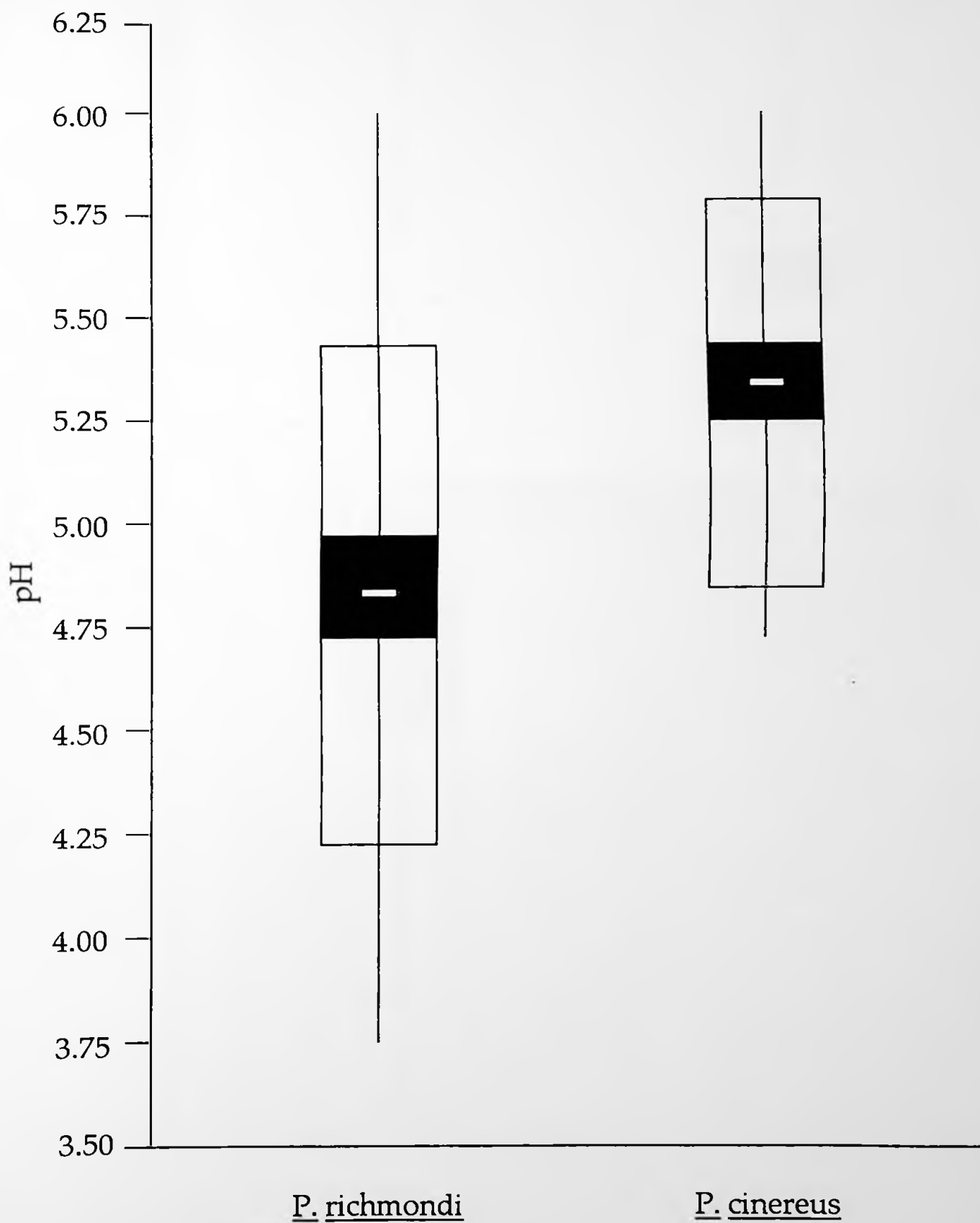


Figure 24. Population range diagram of mean soil temperature (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line) in $^{\circ}\text{C}$.

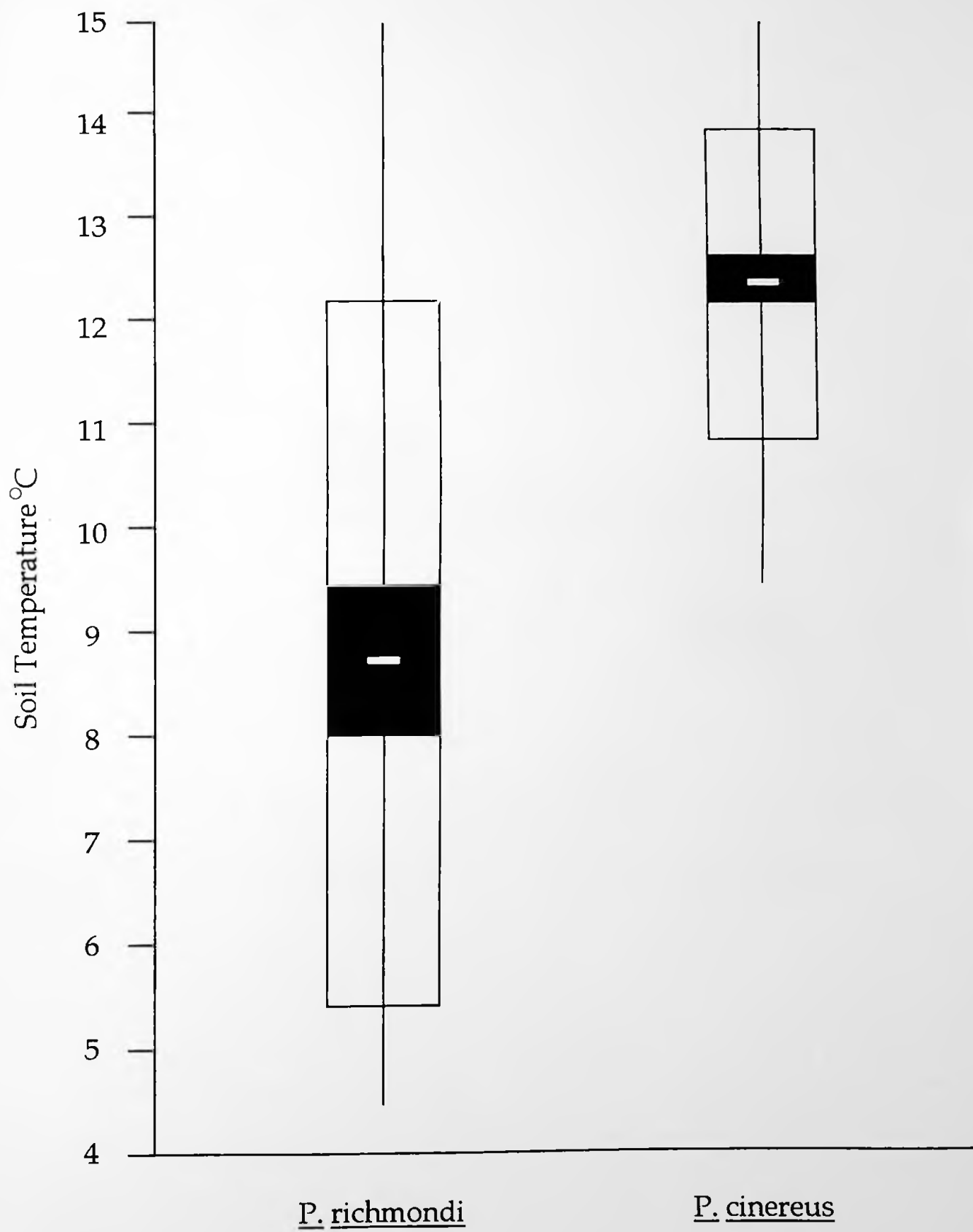
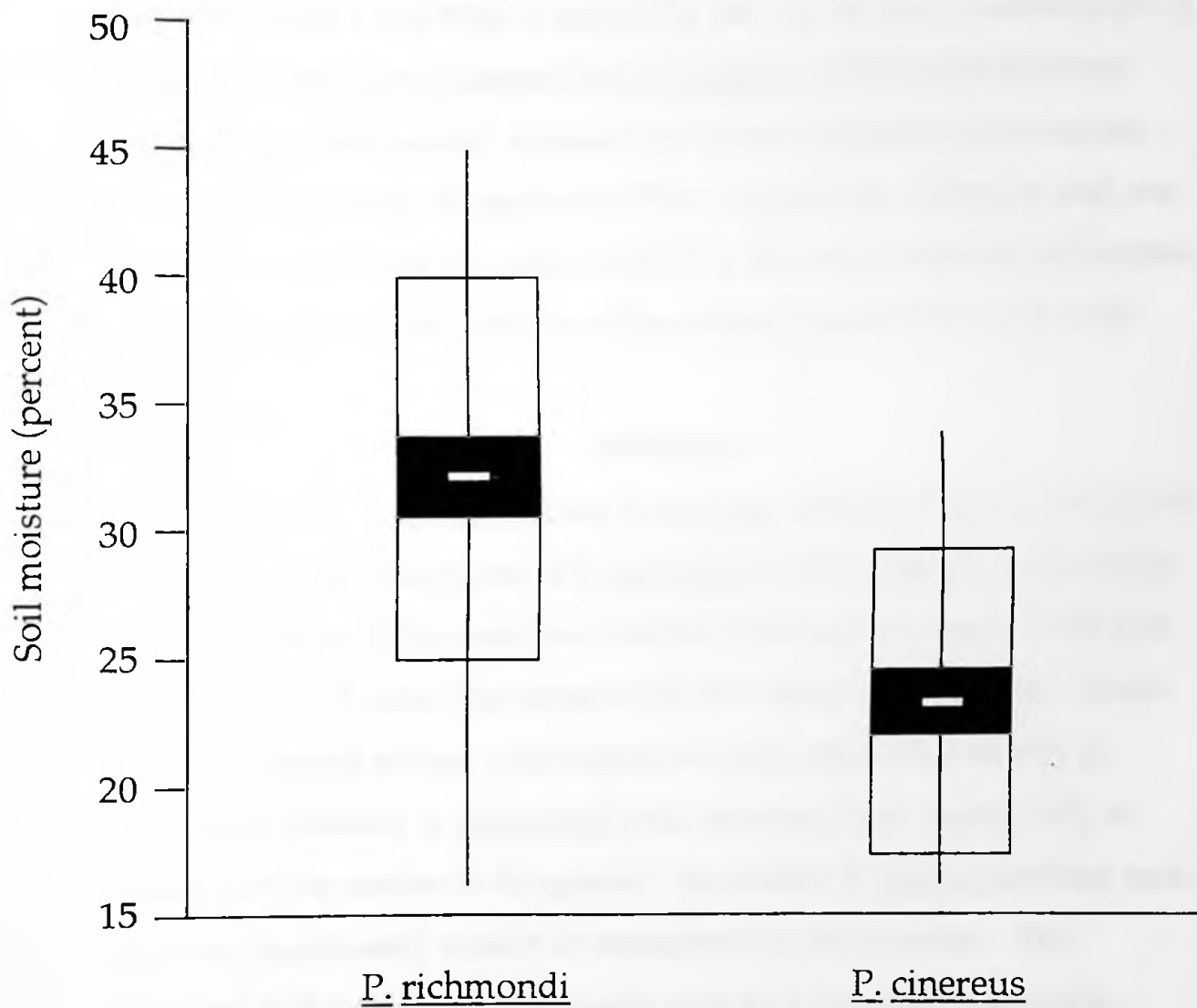


Figure 25. Population range diagram of mean percent soil moisture (light vertical bar), ± 1 SE (closed box), ± 1 SD (open box), range (dark line).



most of the separation between the two species was on PRIN 2 (Fig. 26).

When comparing PRIN 2 and PRIN 3 scores, most of the separation was again on PRIN 2 (Fig. 27). There was little separation between the two species when comparing PRIN 1 and PRIN 3 scores (Fig. 28). For all three bivariate plots, P. richmondi were more clustered than P. cinereus which tended to be less clustered and have several outliers. The most influential environmental parameters separating the species on PRIN 1 were those relating to rock and impression size (Table 12); while on PRIN 2, the most influential parameters were related to rock thickness as well as percent contact of the rock to the ground.

Discussion

In general, P. richmondi and P. cinereus utilized similar microhabitats. In relation to the comparison of P. richmondi and P. cinereus found under rocks, most of the differences were related to the size and shape of the rock and how the rock came into contact with the surface of the ground. Rocks that P. richmondi utilized were larger and flatter than those used by P. cinereus; in addition, P. richmondi used rocks that were usually fully in contact with the surface of the ground. In contrast, P. cinereus utilized rocks that were significantly smaller in circumference and diameter. The parameter PCR indicates that the rocks used by P. cinereus tended to be embedded in the soil in an irregular fashion. This parameter was calculated as a ratio of the area of the top of the rock to the area of the impression the bottom of the rock made. Plethodon cinereus had an average PCR of 1.25 ± 0.27 ; there are at least two situations that would cause the ratio to be greater than 1.00. First, the under side of the rock may be in full contact with the ground but the rock was irregularly shaped, with the bottom being less in area

Table 12. Factor loadings (eigenvectors) for environmental parameters from principal components analysis.

Environmetal Parameter	PRIN 1	PRIN 2	PRIN 3
DTE	----	----	0.29
SUB	----	----	0.37
RC	0.30	----	----
TCKPT	----	0.46	----
THNPT	----	0.40	----
ATHK	----	0.45	----
DTHK	----	0.43	----
RDW	0.31	----	----
RDL	0.31	----	----
TA	0.34	----	----
AD	0.34	----	----
RV	0.32	----	----
ADI	----	----	0.49
IDW	0.31	----	----
IDL	0.31	----	----
IA	0.33	----	----
PCR	----	0.26	----
REFH	----	----	0.39
PH	----	----	----
ST	----	----	-0.40
SM	----	----	----
TP	----	----	-0.33

Figure 26. Scatter plot of all P. richmondi (squares) and P. cinereus (circles) based on principal components one and two. Closed symbols are averages for each species.

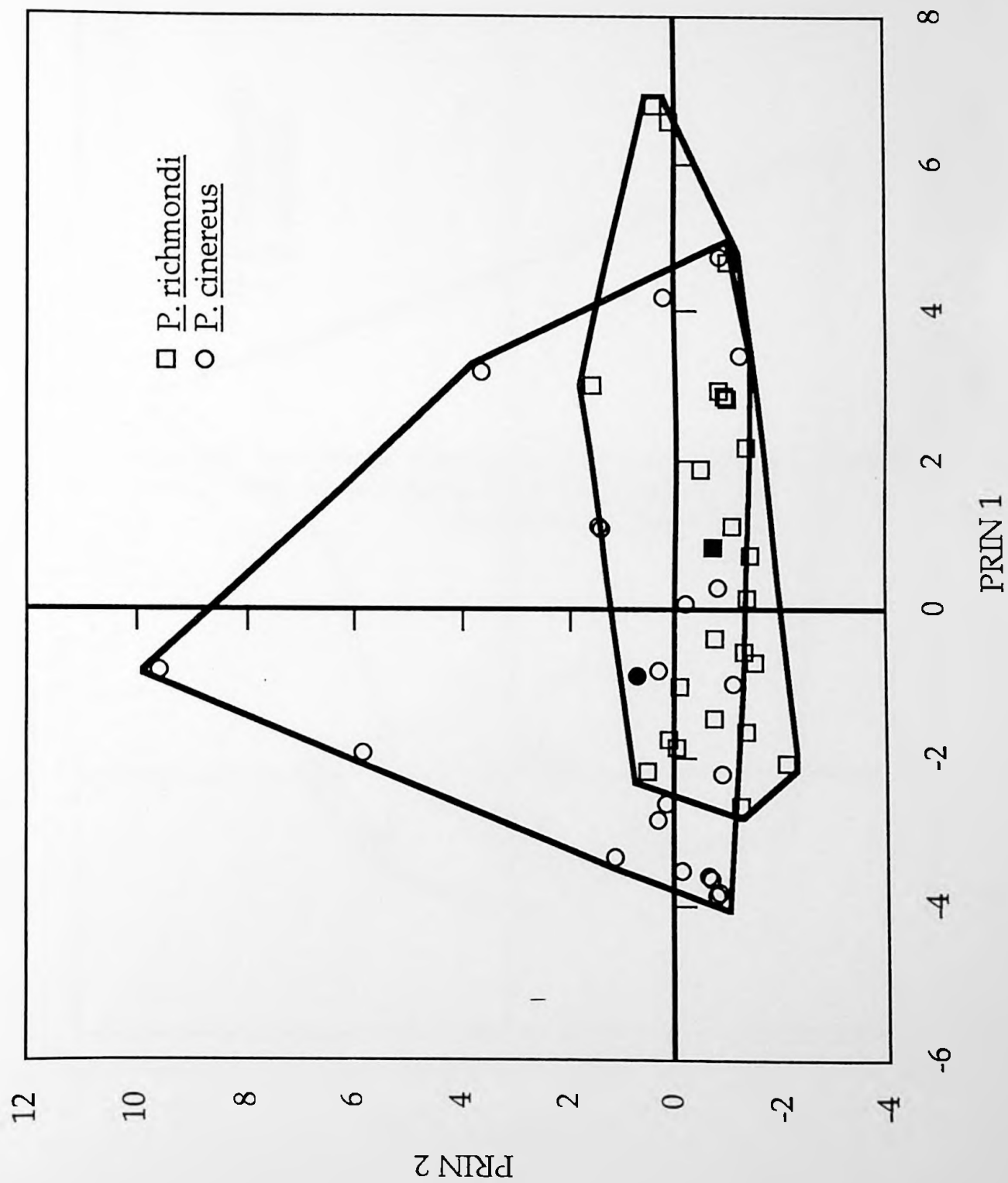


Figure 27. Scatter plot of all P. richmondi (squares) and P. cinereus (circles) based on principal components two and three. Closed symbols are averages for each species.

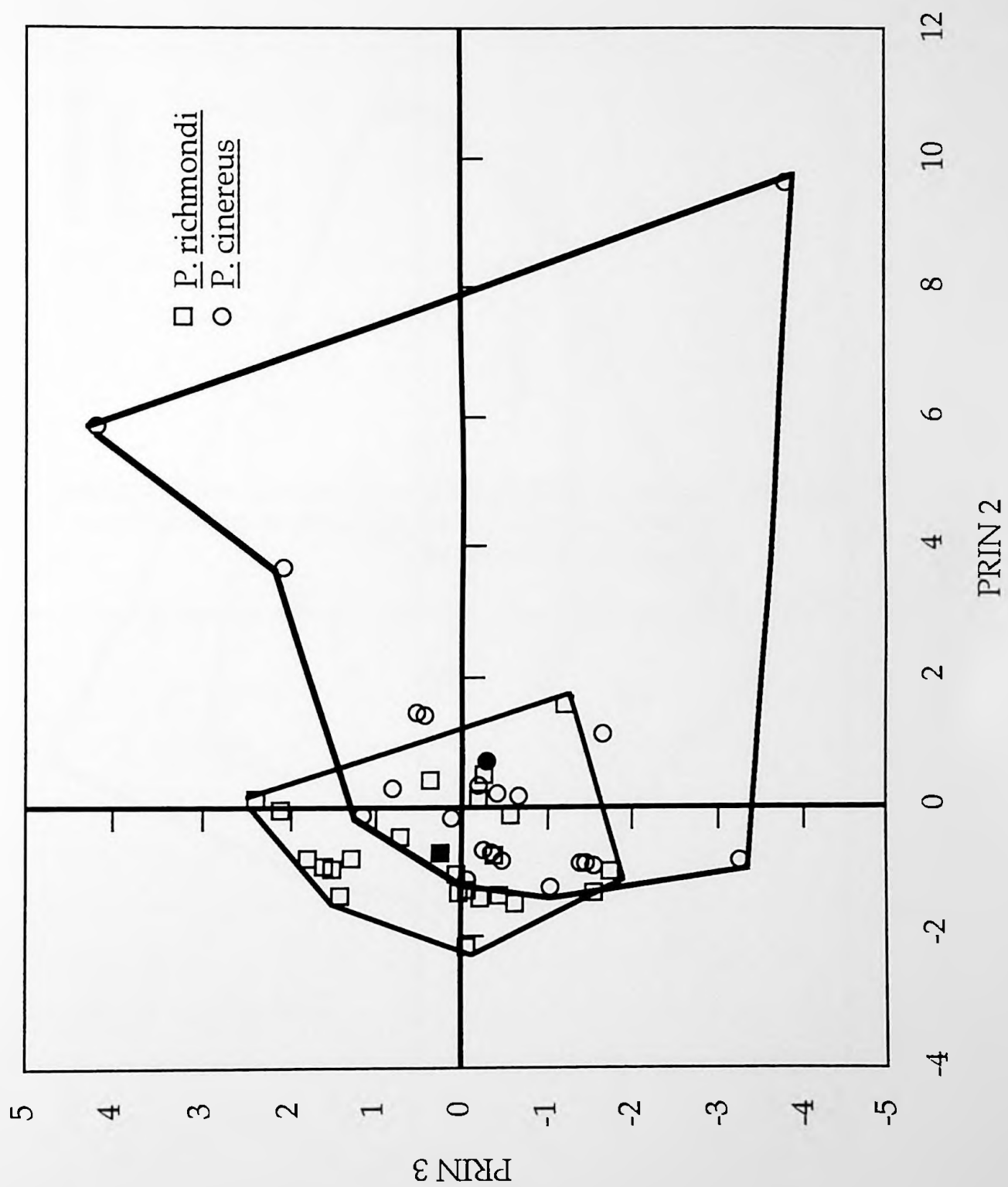
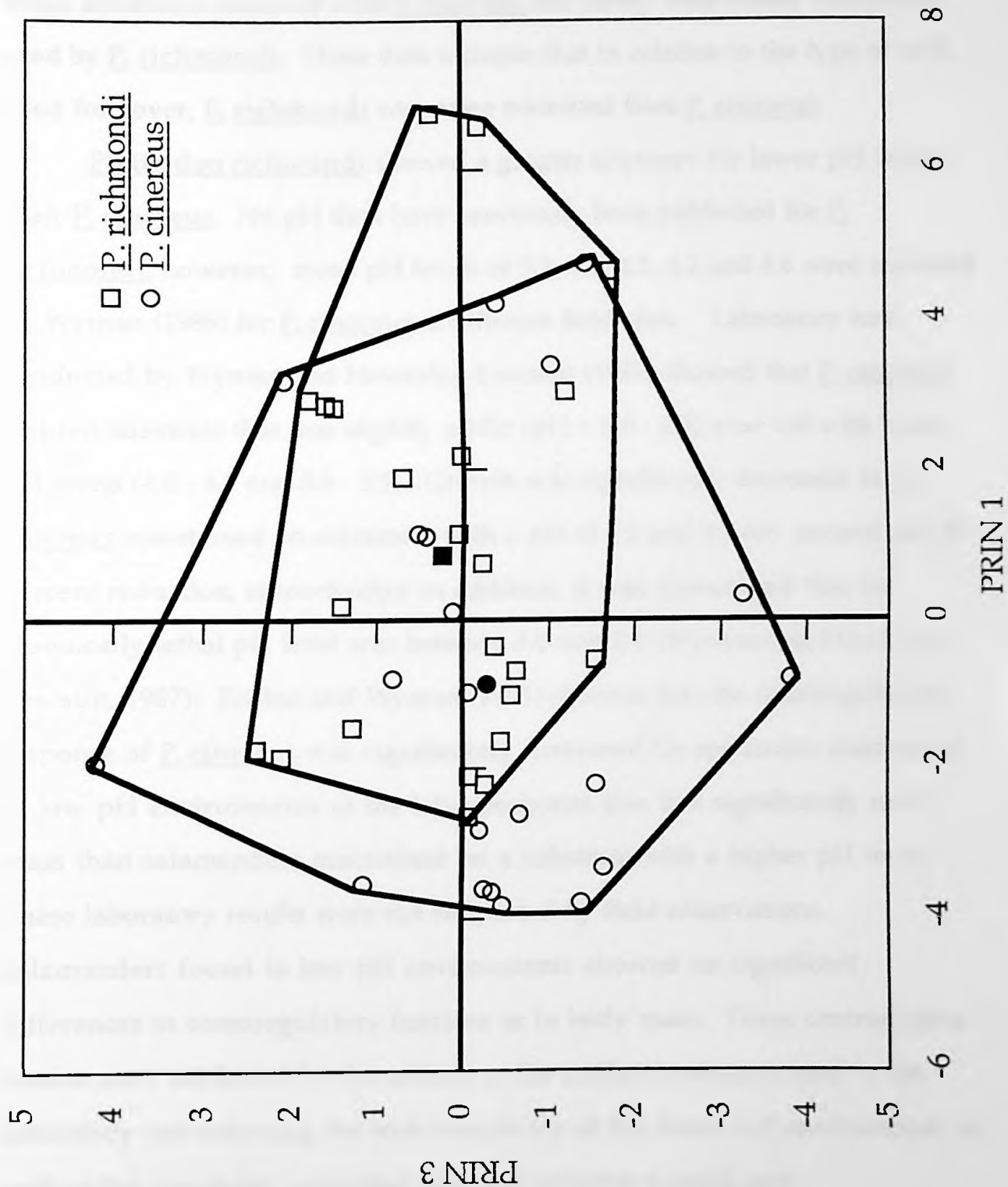


Figure 28. Scatter plot of all P. richmondi (squares) and P. cinereus (circles) based on principal components one and three. Closed symbols are averages for each species.



then the top of the rock (Fig. 29); second, while the rock may have been flat and regular in shape, it was embedded in the soil at an angle (Fig. 30). Both of these situations occurred with P. cinereus but rarely were found with rocks used by P. richmondi. These data indicate that in relation to the type of rock used for cover, P. richmondi was more restricted than P. cinereus.

Plethodon richmondi showed a greater tolerance for lower pH levels than P. cinereus. No pH data have previously been published for P. richmondi; however, mean pH levels of 5.2, 4.0, 4.1, 4.2 and 4.6 were reported by Wyman (1988) for P. cinereus at different field sites. Laboratory tests conducted by Wyman and Hawksley-Lescault (1987) showed that P. cinereus utilized substrate that was slightly acidic (pH = 6.0 - 6.5) over soil with lower pH levels (4.0 - 4.5 and 3.0 - 3.5). Growth was significantly decreased for P. cinereus maintained on substrates with a pH of 3.0 and 4.0 (60 percent and 40 percent reduction, respectively); in addition, it was determined that the chronically lethal pH level was between 3.0 and 4.0 (Wyman and Hawksley-Lescault, 1987). Frisbie and Wyman (1991) showed that the osmoregulatory response of P. cinereus was significantly decreased for specimens maintained in low pH environments in the lab; specimens also lost significantly more mass than salamanders maintained on a substrate with a higher pH level. These laboratory results were not supported by field observations. Salamanders found in low pH environments showed no significant differences in osmoregulatory function or in body mass. These contradictory results were attributed by the authors to the artificial substrate used in the laboratory not reflecting the true complexity of the forest soil environment as well as the variability associated with soil pH over a small area.

The mean pH value for P. cinereus microhabitats in the current study

Figure 29. Cross sectional diagram of typical rock utilized by P. cinereus.

Rock

Substrate

Figure 30. Cross sectional diagram of typical rock utilized by P. cinereus.

Rock

Substrate

were significantly higher than those for P. richmondi; this indicates that P. richmondi were more successful in exploiting habitats with lower pH levels than P. cinereus. Random samples from all three sites show that mean pH values were higher at LR and ST (where P. cinereus were found) than NB (where P. richmondi were found), however, there was not a significant difference between these three sites.

Soil where P. cinereus were found had a significantly higher temperature than soil where P. richmondi was found. These data correspond with those of Jewell (1991) who also found that P. cinereus utilized soil that had a significantly higher temperature than P. richmondi. In a study comparing P. cinereus and P. wehrlei, Pauley (1978b) determined that P. cinereus utilized soil that had a lower average soil temperature than P. wehrlei. Random soil temperature readings from each site show that there was a significant difference in mean soil temperature for the ST and NB as well as between LR and NB. While precautions were taken to randomize the order of site visitation, these differences may have been caused by some sort of sampling bias due to the time of day the readings were collected or it may reflect some difference in the temperature regime of the three sites.

Soil moisture data showed that P. richmondi utilized soil that had a higher soil moisture content than soil utilized by P. cinereus. Pauley (1978a) found that soil where P. cinereus were found had a higher moisture content than soil where P. wehrlei were found. Other researchers have shown that foraging success is directly related to the ability of a salamander to remain surface active under varying moisture regimes (Jaeger, 1972; Jaeger, 1980; Fraser, 1976). The ability of P. cinereus to utilize soil with significantly lower moisture content indicates that it may be able to exploit a wider variety of

habitats than P. richmondi.

Due to the variability in soil temperature in relation to the time of day, the temperature data was probably not an accurate measurement of the temperature regimes utilized by the two species. Soil moisture data however, were more than likely accurate because soil moisture is not as variable as soil temperature is in relation to the time of day data are collected.

A comparison of the variances of the environmental parameters showed that there were significant differences in 5 of the 22 parameters with P. cinereus having the larger variance in 4 of the 5. Overall, P. cinereus had a larger variance for 17 of the 22 parameters. This trend indicated that P. cinereus were more variable in relation to the type of microhabitat that it utilized.

One of the most interesting aspects of this study was the difference in the utilization of logs by the two species. Plethodon richmondi were never found beneath logs during the collection of the environmental data and only one time during the entire study period was a P. richmondi found beneath a log; this observation has been reported by others as well (Duellman, 1954, Pfingsten, 1989). Conversely, P. cinereus were found 6 times (21 percent) during this portion of the study and were commonly found under logs throughout the entire study period. The average SVL for P. cinereus found beneath rocks was almost 10 mm more than that of P. cinereus found beneath logs; while the means were not statistically different, there is still an indication that P. cinereus may partition habitat utilization based on ontogeny.

As expected, there was little definitive separation between the two species using PCA. With the exception of several outliers for P. cinereus, the

two species overlapped on all three bivariate plots. Most of the separation that did occur was on PRIN 2 and loaded toward characters relating to rock thickness and the way the rock came into contact with the soil surface. There was some separation on PRIN 1 which loaded toward characters relating to overall rock area. Perhaps the most important aspect of this analysis is that most P. richmondi and P. cinereus had similar microhabitat requirements; however, P. cinereus has the ability to exploit a greater range of environmental parameters than P. richmondi.

Conclusion

The environment that woodland salamanders inhabit (the forest floor) can be highly variable even over small areas; for this reason, determining interspecific differences in microhabitat utilization can be difficult. Data presented in this study however, show that P. richmondi and P. cinereus utilize the environment in different ways.

Perhaps the most interesting finding of this study is not the actual differences detected but the increased variability that P. cinereus exhibits over P. richmondi. Plethodon cinereus has the largest macrodistribution of all small plethodontid salamanders; one reason for this may be the ability of P. cinereus to exploit a broader range of environmental parameters than other species in this family.

Chapter V

Feeding Habits

Introduction

The feeding habits of terrestrial plethodontid salamanders have been documented by several researchers (Burton, 1976; Duellman, 1954; Fraser, 1976; Jaeger, 1972; Pauley, 1978c; Powders and Tietjen, 1974). Most plethodontid salamanders are generalists in terms of prey selection and probably feed on the invertebrates that are most common (Duellman, 1954; Pauley, 1978c; Whitaker and Rubin, 1971). Common prey items found are the orders Collembola, Hymenoptera, Coleoptera and Diplopoda.

It has been suggested that competition for food may play a role in the micro and macrodistributional patterns observed in this genus (Fraser, 1976; Jaeger, 1972). Jaeger (1972) determined that under low moisture conditions, food may become a limited resource for P. cinereus and P. shenandoah due to restrictions in the movements, therefore limiting foraging opportunities. Fraser (1976) showed that during times of low moisture, P. cinereus and P. hoffmani probably do not forage and therefore competition would not occur; conversely, during moist periods, staggered feeding schedules would prevent densities from becoming high enough for food to become limited. Other research supports Fraser's findings. Pauley (1978c) showed that there were no significant differences in the diets of P. cinereus and P. wehrlei and that 95 percent of all stomachs examined contained food indicating that prey was abundant.

There has been little data collected on the feeding habits of these two species in West Virginia. This study was conducted to determine the general feeding habits of P. richmondi and P. cinereus as well as to gain an understanding of how environmental conditions affect these species in

relation to foraging success.

Materials and Methods

The feeding ecologies of P. cinereus and P. richmondi were analyzed for the spring and fall of 1994. Salamanders were collected from the three study sites by turning all logs and rocks encountered. Every salamander found was taken for analysis in the feeding study. Thirteen site visits were made (6 in the spring, 4 in the summer and 3 in the fall); salamanders were collected on all of the spring trips, however, none of the summer trips and only two of the fall trips yielded any animals.

Salamanders were sacrificed within 2 h of capture in 50 percent ethanol and then injected with 40 percent formalin to fix the contents of the stomachs. Salamanders were subsequently placed in 40 percent formalin for 2 weeks and then water for 1 week before being stored in 70 percent ethanol. In the lab, SVL was measured using dial calipers to the nearest 0.1 mm from the tip of the snout to the anterior angle of the vent and head width was measured using a dissecting microscope fitted with an ocular micrometer to the nearest 0.1 mm at the widest part of the head behind the eyes. After morphometric data were collected, salamanders were dissected and the contents of the stomachs were removed and placed in microcentrifuge tubes containing 70 percent ethanol; only the contents of the stomach from the duodenum to the base of the esophagus were collected. Individual prey items were identified and sorted into 22 taxonomic categories according to the nomenclature of Borror et al. (1989). Length and greatest width were recorded for each item and the volume was estimated using the formula for a cylinder:

$$V = (\pi r^2)L$$

where r is $1/2$ the diameter of the prey item at the widest point and L is the

length of the prey item.

To determine the similarity of the invertebrate communities of the three sites, three 400cm² sticky traps constructed from 3 mm thick Plexiglass® squares that were covered with Tanglefoot® insect trap. The traps were placed on the forest floor sticky side up for three weeks and were then collected and stored in a freezer until they could be analyzed. In addition, five 10 cm square soil and leaf litter samples were collected at each site under and adjacent to an object where a salamander was collected; the samples were separated in Berlese funnels. The macroinvertebrates collected using the above technique were identified to order and analyzed using Spearman rank correlation coefficients.

Numeric and volumetric data were tallied and percent number and volume for each prey category were calculated for seasonal and site totals of each species as well as the percent of salamanders containing each prey category. Simpson's diversity was also calculated for each subsample.

The feeding patterns of both species were compared by season, site, sex and SVL. Dietary overlap was calculated using the similarity index:

$$D = [1.0 - 0.5 \sum |P_{x,i} - P_{y,i}|] \times 100$$

where D is the percentage of overlap and $P_{x,i}$ and $P_{y,i}$ are the proportions of the number of items species x and y utilized in resource category i (Rathcke, 1976; Schoener, 1970; Holomuzki, 1980). To determine statistical differences, diets were compared using Spearman rank correlation coefficients.

Daily rainfall amounts from West Union, West Virginia (central to all three sites) were obtained from the National Oceanic and Atmospheric Administration. Rainfall amounts were summed for three days prior to each site visit date and an average rainfall amount was calculated. Stomach

volumes for salamanders collected on days that rainfall amounts were above the average were pooled and compared to stomach volumes for salamanders collected on days that rainfall amounts were below the average using a t-test.

Results

There was not a significant difference at the 0.05 confidence level in the invertebrate communities at any of the three sites (Table 13). LR and ST were most similar ($r_s = 0.889$) while NB and ST were least similar ($r_s = 0.638$); NB and LR were also very similar in community structure ($r_s = 0.829$).

Sixty one P. richmondi (53 from NB, 6 from LR, 2 from ST) were collected during 1994. Of the 61 guts examined, 59 contained at least 1 prey item. The most important prey categories numerically were Hymenoptera, Collembola, Acari, Gastropoda and Coleoptera larvae (Table 14); volumetrically, the most important categories were Coleoptera larvae, Oligochaeta, Hymenoptera, Araneae and Coleoptera. Prey items found most often in P. richmondi stomachs were the orders Hymenoptera, Acari, Collembola, Coleoptera larvae and Coleoptera. One hundred-two P. cinereus (43 from LR and 59 from ST) were collected; 7 empty stomachs were recorded for P. cinereus. The most important prey categories numerically were Collembola, Hymenoptera, Acari, Isopoda and Coleoptera larvae (Table 15); volumetrically, the most important categories were Coleoptera larvae, Oligochaeta, Coleoptera, Isopoda and Lepidoptera larvae. Prey items found in the highest proportion of P. cinereus stomachs were Acari, Hymenoptera, Collembola, Coleoptera and Coleoptera larvae.

Simpson's diversity for all P. richmondi was 0.22 and 0.12 for all

Table 13. Comparisons of invertebrate communities at each site using Spearman rank correlation coefficients. Rankings are based on the number of items found in each taxonomic category (n = the number of taxonomic categories compared between the sites).

Comparison	n	r_s	Probability
NB/LR	6	0.829	< 0.05
NB/ST	7	0.638	< 0.05
LR/ST	7	0.899	< 0.05

Table 14. Summary of prey items data found in all *P. richmondi* during 1994 (n = 61).

Taxa	Frequency of Prey	Percent Frequency of Prey	Volume of Prey	Percent Volume of Prey	Percent of Stomachs containing Prey
Acari	93	9.79	43.01	1.38	59.02
Araneae	25	2.63	169.19	5.43	31.15
Chilopoda	6	0.63	71.65	2.3	8.2
Coleoptera	33	3.47	160.45	5.15	55.74
Collembola	298	31.37	86.53	2.78	40.98
Dermaptera	1	0.11	6.28	0.2	1.64
Diplopoda	3	0.32	31.97	1.03	4.92
Diplura	2	0.21	0.46	0.01	3.28
Diptera	1	0.11	0.05	0	1.64
Gastropoda	51	5.37	14.2	0.46	26.23
Hemiptera	0	0	0	0	0
Homoptera	1	0.11	25.12	0.81	1.64
Hymenoptera	309	32.53	519.8	16.69	62.3
Isopoda	26	2.74	145.79	4.68	8.2
Coleoptera larvae	47	4.95	943.41	30.29	47.54
Lepidoptera	3	0.32	24.79	0.8	4.92
Oligochaeta	36	3.79	806.35	25.89	26.23
Orthoptera	0	0	0	0	0
Protura	5	0.53	0.72	0.02	4.92
Pseudoscorpiones	8	0.84	6.65	0.21	0
Psocoptera	0	0	0	0	9.84
Thysanura	2	0.21	58.29	1.87	3.28

Table 15. Summary of prey items data found in all *P. cinereus* during 1994 (n = 102).

Taxa	Frequency of Prey	Percent Frequency of Prey	Volume of Prey	Percent Volume of Prey	Percent of Stomachs containing Prey
Acari	113	13.45	42.3	1.02	48.04
Araneae	30	3.57	133.1	3.22	22.55
Chilopoda	6	0.71	47.83	1.16	5.88
Coleoptera	76	9.05	515.71	12.49	42.16
Collembola	158	18.81	26.18	0.63	46.08
Dermaptera	0	0	0	0	0
Diplopoda	3	0.36	63.14	1.53	2.94
Diplura	0	0	0	0	0
Diptera	10	1.19	20.36	0.49	9.8
Gastropoda	36	4.29	27.22	0.66	25.49
Hemiptera	3	0.36	104.3	2.53	1.96
Homoptera	0	0	0	0	0
Hymenoptera	154	18.33	195.49	4.73	47.06
Isopoda	92	10.95	398.76	9.65	24.51
Coleoptera larvae	91	10.83	1015.6	24.59	40.20
Lepidoptera	7	0.83	320.41	7.76	5.88
Oligochaeta	46	5.48	903.04	21.86	27.45
Orthoptera	3	0.36	307.38	7.44	2.94
Protura	0	0	0	0	0
Pseudoscorpiones	7	.83	1.88	0.05	5.88
Psocoptera	5	0.6	7.9	0.19	2.94
Thysanura	0	0	0	0	0

P. cinereus (Table 16). Resource overlap between P. richmondi and P. cinereus was 71.0 percent (Table 17) and the diets were significantly correlated ($r_s = 0.813$, $P < 0.05$) (Table 18). There was a significant difference in the average number of invertebrates per stomach for P. richmondi (15.57 ± 15.83) and P. cinereus (8.24 ± 7.01) ($t = 2.26$, $df = 161$, $P < 0.05$) but not in the average stomach volume (51.06 ± 59.01 and 40.50 ± 56.60 , respectively) ($t = 0.12$, $df = 161$, $P > 0.05$).

Intraspecific comparisons between sex, study sites and seasons using Spearman rank correlation coefficients showed that there was a significant correlation between the diets of the subsamples (Table 18). Likewise, resource overlap calculations showed a high percentage of overlap between the sexes of the two species (Table 17).

The average rainfall amount for the three days prior to each collection date was 0.42 ± 0.45 inches. For P. richmondi, the mean gut volume of days when the cumulative rainfall amount was above 0.42 inches was 69.63 ± 69.23 mm³ which was significantly higher than the mean gut volume of 26.06 ± 26.56 mm³ for days when the cumulative rainfall amount was below 0.42 inches ($t = 3.40$, $df = 46$, $P < 0.05$). Gut volumes for P. cinereus were not significantly different for high and low rainfall dates (45.87 ± 53.45 mm³ and 35.52 ± 59.44 mm³, respectively) ($t = 0.926$, $df = 99$, $P > 0.05$).

Discussion

Data collected on the feeding ecologies of P. richmondi and P. cinereus showed that both species had similar feeding habits. Both species were euryphagic which has been reported by others (Burton, 1976; Fraser, 1976; Lynch, 1985; Powders and Tietjen, 1974; Whitaker and Rubin, 1971). Most of the subsamples were dominated by only a few taxa and none of the

Table 16. Summary of diversity, average number and average volume of prey in subsamples.

Subsample	Simpson's Diversity	Number ($\bar{x} \pm 1 \text{ SD}$)	Volume (mm^3) ($\bar{x} \pm 1 \text{ SD}$)
<u>P. cinereus</u> All	0.12	8.24 ± 7.01	40.50 ± 56.60
<u>P. cinereus</u> LR	0.14	10.16 ± 8.00	54.16 ± 63.55
<u>P. cinereus</u> ST	0.14	6.83 ± 5.86	30.54 ± 49.15
<u>P. cinereus</u> Spring	0.13	8.71 ± 7.32	34.39 ± 49.50
<u>P. cinereus</u> Fall	0.18	5.69 ± 4.30	73.31 ± 79.53
<u>P. cinereus</u> Adult	0.12	8.54 ± 7.34	48.40 ± 60.41
<u>P. cinereus</u> Juvenile	0.19	7.00 ± 5.40	8.11 ± 9.97
<u>P. cinereus</u> Male	0.14	10.69 ± 8.61	43.20 ± 53.60
<u>P. cinereus</u> Female	0.11	7.60 ± 6.56	51.67 ± 63.90
<u>P. richmondi</u> All	0.22	15.57 ± 15.83	51.06 ± 59.01
<u>P. richmondi</u> NB	0.25	15.96 ± 16.60	50.63 ± 59.87
<u>P. richmondi</u> LR	0.12	15.00 ± 10.49	61.90 ± 64.69
<u>P. richmondi</u> Spring	0.23	16.15 ± 16.81	52.71 ± 62.36
<u>P. richmondi</u> Fall	0.23	12.22 ± 8.03	41.52 ± 34.72
<u>P. richmondi</u> Male	0.17	13.39 ± 9.26	60.10 ± 48.86
<u>P. richmondi</u> Female	0.25	16.81 ± 17.99	48.27 ± 63.34

Table 17. Percentage overlap in diet (D) for subsample comparisons
(n = number of individuals in each subset respectively).

Comparison	n	Dietary Overlap
<u>P. cinereus</u> / <u>P. richmondi</u>	102/61	71.0 %
<u>P. cinereus</u> LR / <u>P. richmondi</u> LR	43/6	65.3%
<u>P. cinereus</u> spring / <u>P. cinereus</u> fall	86/16	55.8%
<u>P. cinereus</u> male / <u>P. cinereus</u> female	26/55	81.4%
<u>P. cinereus</u> ST / <u>P. cinereus</u> LR	59/43	74.7%
<u>P. cinereus</u> adult / <u>P. cinereus</u> Juvenile	82/20	69.7%
<u>P. rimondi</u> spring / <u>P. richmondi</u> fall	52/9	75.3%
<u>P. richmondi</u> male / <u>P. richmondi</u> female	18/42	79.6%
<u>P. richmondi</u> NB / <u>P. richmondi</u> LR	53/6	45.0%

Table 18. Diet comparisons of subsamples by Spearman rank correlation coefficients. Rankings are based on the number of items consumed in each taxonomic category (n = the number of prey categories compared between the subsamples).			
Comparison	n	r _s	Probability
<u>P. cinereus</u> / <u>P. richmondi</u>	22	0.813	< 0.05
<u>P. cinereus</u> LR / <u>P. richmondi</u> LR	18	0.758	< 0.05
<u>P. cinereus</u> spring / <u>P. Pcinereus</u> fall	17	0.752	< 0.05
<u>P. cinereus</u> male / <u>P.cinereus</u> female	17	0.865	< 0.05
<u>P. cinereus</u> ST / <u>P. cinereus</u> LR	17	0.813	< 0.05
<u>P. cinereus</u> adult / <u>P.cinereus</u> Juvenile	17	0.861	< 0.05
<u>P. richmondi</u> spring / <u>P. richmondi</u> fall	19	0.869	< 0.05
<u>P. richmondi</u> male / <u>P. richmondi</u> female	20	0.856	< 0.05
<u>P. richmondi</u> NB / <u>P. richmondi</u> LR	19	0.773	< 0.05

subsamples had a diversity value of more than 0.25. The diversity of P. richmondi at NB where there were no P. cinereus was 0.25; however, at LR, where both species were found, the diversity value dropped by more than 50 percent to 0.12. Diversity values for P. cinereus, although low, were identical at ST and LR. In addition, while still significantly correlated, the r_s value (0.773) and the percent resource overlap (45.0 percent) for P. richmondi at NB and LR was the lowest of all comparisons made. These data indicate that P. richmondi might be negatively affected by P. cinereus in relation to the diversity and type of prey available to P. richmondi.

The similarity of the diets of the two species as well as the high percentage of stomachs containing prey (94.5 percent) indicate that most of the time food was abundant and competition between the two species was theoretically low (Jaeger, 1972, Pauley, 1978c). It has been proposed that environmental conditions such as periods of low moisture or low temperature might create a situation where food becomes a limited resource either by reducing the population numbers of potential prey, or more likely by reducing the mobility of salamanders and therefore restricting foraging opportunities (Jaeger, 1972; Fraser, 1976; Keen, 1979). Data from this study showed that P. richmondi had a significantly lower prey volume for dates when the average rainfall amount for the previous three days was < 0.42 inches than for the dates when the rainfall amounts were > 0.42 inches. Conversely, there was no significant difference in the stomach volumes of P. cinereus between the two moisture regimes. These data suggest that P. cinereus was not as restricted by periods of low moisture and may have been able to exploit food resources more efficiently than P. richmondi.

Conclusion

Data presented here showed that P. richmondi and P. cinereus were similar in the type and diversity of prey taken. While P. cinereus seemed to be unaffected by the presence of P. richmondi, the opposite was not true based on the diversity values for P. richmondi at NB and LR; in addition, P. richmondi was negatively affected by low moisture conditions in relation to stomach volume while P. cinereus was not significantly influenced by low moisture conditions. The sum of the data suggests that P. cinereus exhibits a capability to adapt to a broader set of environmental parameters which may be one reason for its larger macrodistribution.

Literature Cited

- Barr, A.J., J.H. Goodnight, J.P. Sall and J.T. Helwig. 1982. SAS user's guide: statistics. SAS Institute Inc., Cary, NC. 584 pp.
- Borror, D.J., C.A. Triplehorn and N.F. Johnson. 1989. An introduction to the study of insects, 6th ed. Harcourt Brace Jovanovich College Publishers, Fort Worth. 875 pp.
- Burton, T. M. 1976. An analysis of the feeding ecology of the salamanders (Amphibia, Urodela) of the Hubbard Brook experimental forest, New Hampshire. J. Herpetol. 10:187-204.
- and G. E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook experimental forest, New Hampshire. Copeia 1975:541-546.
- Conant, R. 1991. A field guide to reptiles and amphibians: eastern and central North America. 3rd ed. Houghton Mifflin Co., Boston. 450 pp.
- Duellman, W. E. 1954. The salamander Plethodon richmondi in southwestern Ohio. Copeia 1954:40-45.
- Fraser, D. F. 1976. Empirical evaluation of the hypothesis of food competition in salamanders of the genus Plethodon. Ecology 57:459-471.
- Frisbie, M. P. and R. L. Wyman. 1991. The effects of soil pH on sodium balance in the Red-backed salamander, Plethodon cinereus, and three other terrestrial salamanders. Physiol. Zool. 64:1050-1068.
- Green, N. B., and T. K. Pauley. 1987. Amphibians and reptiles in West Virginia. University of Pittsburgh Press. Pittsburgh. 241 pp.
- Heatwole, H. 1962. Environmental factors influencing local distribution and activity of the salamander, Plethodon cinereus. Ecology 43:460-472.
- and K. Lim. 1961. Relation of substrate moisture to absorption and loss of water by the salamander, Plethodon cinereus. Ecology 42:814-819.
- Holomuzki, J. R. 1980. Synchronous foraging and dietary overlap of three species of plethodontid salamanders. Herpetologica 36:109-115.

- Jaeger, R. G. 1972. Food as a limited resource in competition between two species of terrestrial salamanders. *Ecology* 53:535-546.
- . 1978. Plant climbing by salamanders: periodic availability of plant-dwelling prey. *Copeia* 1978:686-691.
- . 1980. Microhabitats of a terrestrial forest salamander. *Copeia* 1980:265-268.
- Jewell, R.D. 1991. Life history, ecology, and morphology of the ravine salamander, Plethodon richmondi, in northern West Virginia. Unpubl. Thesis, Marshall University. 105 pp.
- . and T.K. Pauley. 1995. Notes on the reproductive biology of the salamander Plethodon richmondi (Netting and Mittleman) in West Virginia. *Herpetol. Nat. Hist.* 3:91-93.
- Keen, W. H. 1984. Influence of moisture on the activity of a plethodontid salamander. *Copeia* 1984:684-688.
- Kramer, P., N. Reichenbach, M. Hayslett and P. Sattler. 1993. Population dynamics and conservation of the Peaks of Otter salamander, Plethodon hubrichti. *J. Herpetol.* 27:431-435.
- Lynch, J. F. 1985. The feeding ecology of Aneides flavipunctatus and sympatric plethodontid salamanders in northwestern California. *J. Herpetol.* 19:328-352.
- Mushinsky, H. R. 1975. Selection of substrate pH by salamanders. *Amer. Mid. Nat.* 93:440-443.
- Nagel, J.W. 1979. Life history of the Ravine salamander (Plethodon richmondi) in northeastern Tennessee. *Herpetologica* 35:38-43.
- Pauley, T. K. 1978a. Moisture as a factor regulating habitat partitioning between two sympatric Plethodon (Amphibia, Urodela, Plethodontidae) species. *J. Herpetol.* 12:491-493.
- . 1978b. Temperature and insolation as factors regulating the partitioning of habitats of two sympatric Plethodon species. *Proc. West Virginia Acad. Sci.* 77-84.
- . 1978c. Food types and distribution as a Plethodon habitat partitioning factor. *Bull. Maryland Herpetol. Soc.* 14:79-83.

- Pfingsten, R. A. 1989. Plethodon richmondi Netting and Mittleman. In R. A. Pfingsten and F. L. Downs (eds.), Salamanders of Ohio, pp 253-261. College of Biological Sciences the Ohio State University, Columbus, Ohio.
- Powders N. V. and W. L. Tietjen. 1974. The comparative food habits of sympatric and allopatric salamanders, Plethodon glutinosus and Plethodon jordani in eastern Tennessee and adjacent areas. Herpetologica 30:167-175.
- Rathcke, B.J. 1976. Competition and coexistence within a guild of herbivorous insects. Ecology 57:76-87.
- Sayler, A. 1966. The reproductive ecology of the red-backed salamander, Plethodon cinereus, in northeastern Tennessee. Herpetologica 53:535-546.
- Schoener, T.W. 1970. Non-synchronous spatial overlap of lizards in patch habitats. Ecology 51:408-418.
- Stilling, P. D. 1992. Introductory Ecology. Prentice Hall, Englewood Cliffs, NJ. 597 pp.
- Test, F.H. 1955. Seasonal differences in populations of the red-backed salamander in southeastern Michigan. Papers Mich. Acad. 40:137-153.
- _____. and B.A. Bingham. 1948. Census of a population of the redbacked salamander Plethodon cinereus. Amer. Midl. Natur. 37: 362-372.
- Vernberg, F. J. 1955. Correlation of physiological and behavior indexes of activity in the study of Plethodon cinereus (Green) and Plethodon glutinosus (Green). Amer. Mid. Nat. 54:382-393.
- Whitaker, J. O., and D. C. Rubin. 1971. Food habits of Plethodon jordani metcalfi and Plethodon jordani shermani from North Carolina. Herpetologica 27:81-86.
- Wyman, R.L. 1988. Soil acidity and moisture and the distribution of amphibians in five forests of southcentral New York. Copeia 1988:394-399.

- ____. and D. S. Hawksley-Lescault. 1987. Soil acidity affects distribution, behavior, and physiology of the salamander Plethodon cinereus. Ecology 68:1819-1827.