

DIVERGENCE OF TROPHIC MORPHOLOGY AND RESOURCE USE AMONG POPULATIONS OF *PLETHODON CINEREUS* AND *P. HOFFMANI* IN PENNSYLVANIA

A Possible Case of Character Displacement

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1. INTRODUCTION

Species of the genus *Plethodon* are widely distributed in the forests of eastern and western North America. They are terrestrial salamanders that have no aquatic larval stage, and live in moist woodland habitats. Many species of *Plethodon* are believed to be territorial (Hairston, 1951, 1981; Jaeger, 1971, 1972, 1981; Mathis et al., 1995; Nishikawa, 1985), and intraspecific competition is thought to be for food resources and for direct access to foraging sites (Jaeger, 1972). Several species of *Plethodon* often co-inhabit a particular location, with as many as five sympatric species in some southern Appalachian localities (Highton, 1995). Therefore, the likelihood of ecological interactions among congeners is high, and competitive exclusion has been suggested as a possible mechanism that affects species distributions (Hairston, 1951; Highton, 1995; Jaeger, 1971).

One of the most wide-ranging species of the genus, *P. cinereus*, is found from southeastern Canada to North Carolina. It is an effective competitor (Hairston, 1987; Jaeger, 1970, 1971) and in many cases has restricted the ranges of other less aggressive

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species, some nearly to the point of extinction (see Griffis and Jaeger, 1998; Jaeger, 1970, 1980). However, one species, the valley and ridge salamander, *P. hoffmani*, occupies a region completely surrounded by the distribution of *P. cinereus*. The range of *P. hoffmani* extends from north-central Pennsylvania south along the Virginia-West Virginia border; with the exception of a small area in the northern part of this range, *P. cinereus* is completely absent from this region (Highton, 1972). There are narrow bands of sympatry scattered along the contiguously allopatric ranges of these two species (Fraser, 1976a,b; Highton, 1972), but hybrids have never been found.

One explanation for the distribution patterns of these two species is that *P. hoffmani* has excluded *P. cinereus* from its range through competition (Highton, 1995), although this hypothesis has not been rigorously tested. The two species eat similarly-sized prey items in sympatry, but there was a significant difference in the frequency in which these prey were consumed (Fraser, 1976b). Unfortunately, Fraser did not compare his results to those from allopatric populations. To better understand the interactions of these species, I compared trophic morphology and food resource use in allopatric and sympatric populations of *P. hoffmani* and *P. cinereus* from an east-west geographic transect in southeastern Pennsylvania (Fulton Co.). For each species, I addressed the following questions: (1) Are there significant intraspecific morphological differences along the geographic transect? (2) Are there significant intraspecific differences in resource use along the geographic transect? and (3) Is trophic morphology associated with resource use in these populations?

2. MATERIALS AND METHODS

Three localities in Fulton County, Pennsylvania (identified by Highton, 1961, 1961, and 1958, respectively) were used in this study: McConnellsburg Quadrangle (39°58'29"N, 77°58'02"W: allopatric *P. cinereus*), Burn Cabins Quadrangle (40°02'00"N, 77°59'05"W: sympatric *P. cinereus* & *P. hoffmani*), and Meadow Grounds Quadrangle (39°56'20"N, 78°05'25"W: allopatric *P. hoffmani*). I collected 81 individuals of *P. cinereus* (50 allopatric, 31 sympatric) and 75 individuals of *P. hoffmani* (37 allopatric, 38 sympatric) on May 11, 1998, and May 14, 1998. These dates followed days of substantial rainfall, thus increasing the probability that the salamanders had recently foraged (Jaeger, 1972, pers. comm.). Immediately after capture, I anesthetized the individuals in MS-222, preserved them in 10% formalin, and stored them in 65% ethanol. From each specimen I recorded snout to anterior-vent length (SVL) and six trophic characters to the nearest 0.01 mm using digital calipers. These characters were chosen as a general description of head shape, and have been used in studies investigating the relationship of morphology and resource use (e.g., head width: Fraser, 1976a; jaw length: Emerson, 1985). The six trophic characters were: head width, head length, head depth, eye to nostril distance (for a description of these characters see Carr, 1996), jaw length, and gape width (Fig. 1). This set of characters was used to describe the general characteristics of trophic morphology, as well as to characterize head shape.

To compare trophic morphology of allopatric and sympatric populations I performed analysis of variance (ANOVA) and multiple comparison tests (*T*, *GT2*; see Sokal and Rohlf, 1995) on each of the log-transformed variables. However, because morphological distance measurements are often highly correlated with size, variation in trophic characters may simply reflect variation in body size, making interpretation of these patterns difficult. To eliminate this difficulty, I adjusted the log-transformed

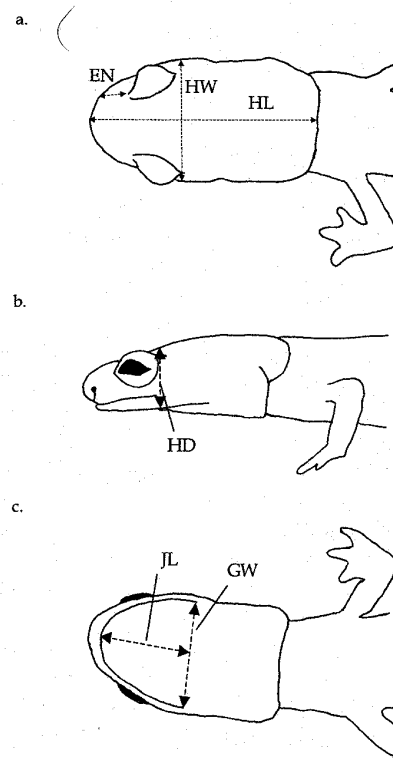


Figure 1. Locations of trophic measurements used in this study on a) dorsal, b) lateral, and c) ventral views of *P. hoffmani* (abbreviations are EN: eye-nostril distance, GW: gape width, HD: head depth, HL: head length, HW: head width, and JL: jaw length).

trophic characters for size and obtained a set of 'size-independent' shape variables. As many methods of size-adjustment exist (see Bookstein, 1989; Jungers et al., 1995), the results from four different methods were compared. The shape variables I used were (1) the set of ratios of trophic characters on SVL, (2) the set of residuals from regressions of trophic characters on SVL, (3) the set of principal component (PC) scores (except PC1, which is often used as a measure of size) from a PC analysis of all six trophic measurements and SVL, and (4) the set of Burnaby's (1966) size-independent shape variables using an isometric size vector (see Rohlf and Bookstein, 1987).

For each set of shape variables, I compared head shape variation among populations using multivariate analysis of variance (MANOVA). Canonical variates analysis (CVA) was used to visualize patterns of variability in canonical variates space based on the morphometric data, as well as to estimate the dissimilarity between allopatric and sympatric populations with generalized Mahalanobis distance (D^2). Finally, I determined whether the divergence between sympatric populations was greater than differences between allopatric populations by performing randomization tests (Adams and Anthony, 1996; Manly, 1991). For each iteration, specimens were randomly assigned to a sympatric or allopatric population (within species), the D^2 between population means were re-calculated, and a difference score ($D^2_{\text{sympatry}} - D^2_{\text{allopatry}}$) was obtained. The proportion of randomly generated data sets (of 1000) with a difference score equal to or greater than the observed data was taken to be the significance level.

Stomach contents were used to assess resource use. I classified all prey items eaten to the level of class or order, and recorded the number of prey consumed in each of 16 prey categories (e.g., see Burton, 1976; Fraser, 1976b; Jaeger, 1972; Maglia, 1996). I measured the length and width of each prey item, estimated its volume using the equation for a cylinder, and determined the total volume of prey in each category consumed by each salamander. I also calculated the total number of prey, and total volume of prey eaten by each salamander. Prey number, prey volume, and cube-root (prey volume) were then treated as estimates of resource use.

Because prey number was quantified categorically, I was unable to compare populations in the same manner as in the morphological analyses (i.e., MANOVA, CVA). I therefore compared profiles of resource use based on prey number using a *G*-test of independence, and estimated the dissimilarity between allopatric populations and sympatric populations using chi-squared distance. I then performed a randomization test (based on chi-squared distance) to determine if the divergence between sympatric populations was greater than between allopatric populations. Sympatric divergence in prey volume and cube-root(preay volume) were evaluated with a similar randomization procedure, using Euclidean distances between populations. I also compared the mean number of prey eaten, and the mean volume of prey eaten, using ANOVA. Finally, the total number of prey eaten in each category was used to obtain profiles of resource use for each population. These were sorted by prey size and then visually inspected.

To address whether there was a relationship between trophic morphology and resource use, I performed canonical correlation and partial least squares analyses, using the set of log-transformed trophic characters and the three separate estimates of resource use. These techniques find the linear association between two sets of variables, and can be considered measures of multivariate correlation. To determine if these associations were significant, I performed randomization tests, where the set of prey items eaten was randomly shuffled among specimens, and the multivariate correlation recalculated. The proportion of randomly generated data sets (of 1000) with a greater association between trophic morphology and resource use than the observed data was taken to be the significance level.

Finally, I qualitatively compared the resource bases of each population using insect traps and pooled stomach contents. First, for each collection locality, all prey items eaten were combined, and the number of prey categories (of 16) represented was used as a qualitative estimate of the resource base of that population. Additionally, three pit traps and three sticky traps were placed at each collection locality, and were retrieved two weeks later. The number of prey categories represented by insect trap collections was used as a qualitative estimate of that population's resource base.

3. RESULTS

3.1. Morphological Variation

I found significant differences among populations for SVL, as well as for each of the six trophic characters (Fig. 2). *F*-ratios and significance levels from ANOVA were: $F = 20.46, P < 0.0001$ (SVL); $F = 16.99, P < 0.0001$ (Head Length); $F = 21.41, P < 0.0001$ (Head Width); $F = 22.21, P < 0.0001$ (Head Depth); $F = 33.82, P < 0.0001$ (Gape Width); $F = 28.10, P < 0.0001$ (Jaw Length); $F = 7.90, P < 0.0001$ (Eye-Nostril Distance). For all characters except eye-nostril distance, multiple comparison tests detected a significant

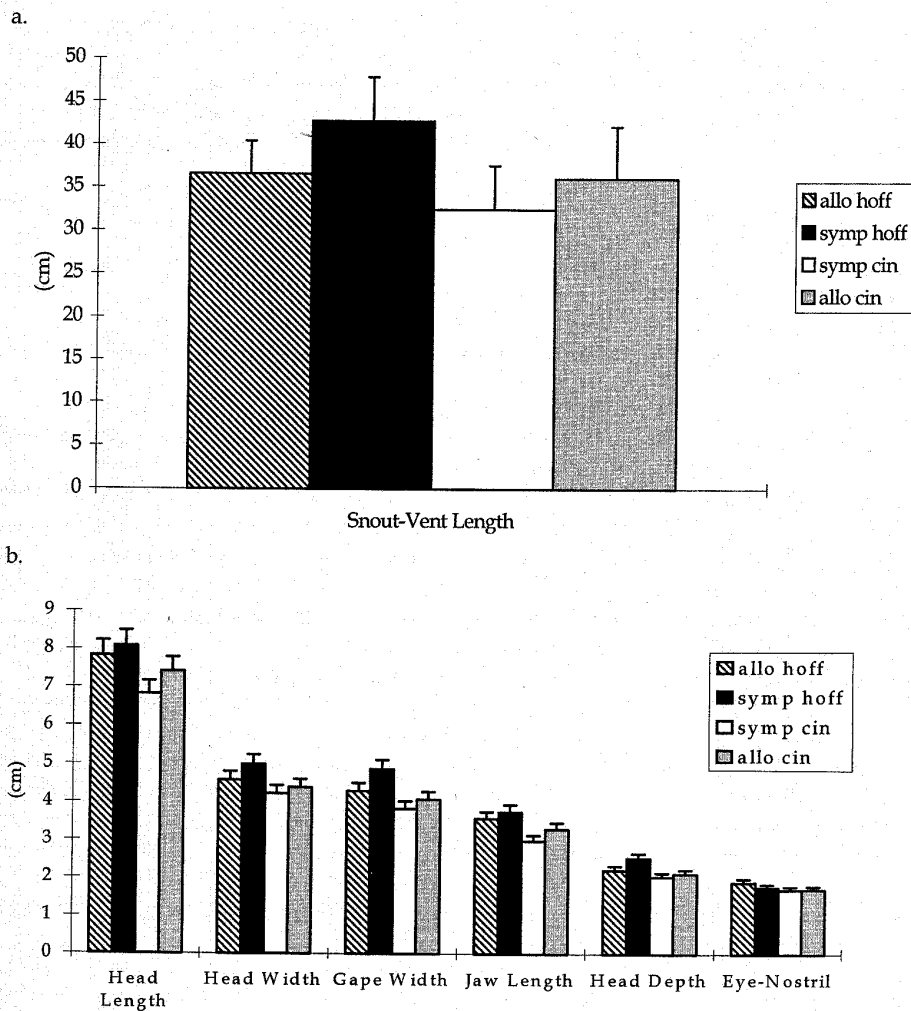


Figure 2. Population mean values and standard error bars for (a) snout-vent length and (b) six head characters. For each variable tested, ANOVA revealed statistically significant among-population differences (see text).

difference between sympatric populations, but no difference between allopatric populations. In sympatry, *P. hoffmani* always attained greater size than *P. cinereus*, regardless of which morphological character was examined. *P. hoffmani* was roughly 1.3 times larger than *P. cinereus* for SVL, and was 1.2–1.3 times larger than *P. cinereus* for all head characters except eye-nostril distance. Thus, univariate statistical analyses revealed a pattern of morphological divergence in sympatry consistent with the hypothesis of character displacement (Brown and Wilson, 1956; Grant, 1975), with sympatric *P. hoffmani* attaining larger values for body size and trophic characters relative to *P. cinereus*.

Table 1. Results from multivariate analyses of log-transformed trophic measurements and size-adjusted shape variables that compare allopatric and sympatric populations of *P. cinereus* and *P. hoffmani*. Column 1 specifies the variables used, columns 2 & 3 contain results from MANOVA, columns 4 & 5 contain Mahalanobis distances from CVA, and column 6 specifies the significance level from permutation tests. All analyses show significant morphological divergence in sympatry. See text for description of variables.

Variables	Wilk's Λ	<i>P</i> -value	D^2 -Allopatry	D^2 -Sympatry	<i>P</i> -value
Log (Trophic Meas.)	0.218	0.00001	1.069	4.063	0.001
Burnaby	0.224	0.00001	0.971	4.063	0.001
PCA 2-7	0.308	0.00001	1.677	2.270	0.001
Ratios	0.184	0.00001	1.373	4.071	0.001
Residuals	0.302	0.00001	1.739	2.267	0.001

Because both SVL and the trophic characters displayed similar patterns of variability, it was not clear whether sympatric divergence of trophic characters was due to character displacement or simply body size. Using MANOVA on size-adjusted variables, however, I also found significant differences among populations for head shape. Further, allopatric populations were morphologically more similar to one another than were sympatric populations. This pattern of sympatric divergence was present regardless of which method of size correction was used to generate the shape variables (Table 1). Randomization tests indicated that head shape divergence between sympatric populations was significantly larger than between allopatric populations. Thus, univariate and multivariate analyses of trophic morphology revealed a similar pattern of morphological variation among populations.

This pattern of sympatric divergence was most evident when visualizing the relationships among specimens in morphological shape space. Figure 3 shows the CVA ordination of specimens in morphological shape space, using ratio-adjusted shape variables. This figure clearly reveals the morphological separation of sympatric phenotypes,

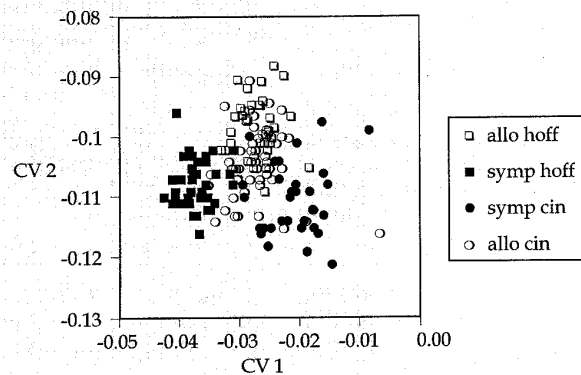


Figure 3. Plot of specimens in morphological shape space found from analysis of ratio-adjusted shape variables. The first canonical variate (CV) axis explains 72% of the variability, and the first two CV axes explain 97%. From this analysis, 75% of the specimens are correctly classified to their original group. Of the misclassified specimens, 18 specimens were classified incorrectly between allopatric populations, but none were classified incorrectly between sympatric populations. Similar results were found from CVA of other shape variables (Burnaby, PCA-Scores, Residuals).

and the similarity of allopatric phenotypes. Along the first CV axis, there is complete separation of sympatric phenotypes, while variation in head shape within populations is expressed primarily along the second CV axis. Head width and gape width loaded most heavily on the first CV axis, and thus the between-population differences can be interpreted as relative differences in head and gape width.

3.2. Variation in Resource Use

Populations differed significantly in both the total number of prey eaten per salamander ($F = 9.27, P < 0.0001$), and the total volume of prey eaten per salamander ($F = 20.89, P < 0.0001$). Using multiple comparison tests, I found a significant reduction in the mean number of prey eaten in sympatric locations relative to allopatric populations (≈ 15 vs. ≈ 20 prey, respectively). However, there was a statistically significant increase in prey volume for sympatric *P. hoffmani* relative to the other three populations, as well as a significant decrease in prey volume for sympatric *P. cinereus*. Thus, sympatric *P. hoffmani* ate fewer, but larger prey, and sympatric *P. cinereus* ate fewer, but smaller prey, suggesting a partitioning of resources in sympatry along a prey-size axis.

Comparisons of profiles of resource use for each population also revealed this pattern. For each population, the total number of prey eaten in each taxonomic category was ordered according to prey size (Fig. 4a, b). In allopatry, both *P. cinereus* and *P. hoffmani* consumed prey from all categories, and in relatively the same frequency. In sympatry, prey from all categories were consumed as well, but several smaller prey items were present only in the diet of *P. cinereus*, and several larger prey items were present only in the diet of *P. hoffmani*. Further, the relative consumption of prey differed between these two populations, such that *P. hoffmani* (the larger species in sympatry) consumed a relatively larger portion of large prey, and *P. cinereus* (the smaller species in sympatry) consumed a relatively larger portion of smaller prey. This difference lends further support to the hypothesis that these two species segregated prey on the basis of size, when sympatric.

To further investigate this potential sympatric divergence, I conducted multivariate analyses on resource use, and found that populations differed significantly in the number of prey eaten per category ($G = 666.8, P < 0.00001$). Randomization tests showed that sympatric populations were more divergent than allopatric populations for all three estimates of resource use (Table 2). Finally, data from insect traps and pooled stomach contents revealed that each taxonomic prey category was present at each collection location, although sample sizes prohibited a statistical comparison. Thus, even though the resource base was qualitatively similar at all localities, there was resource partitioning between sympatric populations.

Table 2. Results from comparisons of resource use among populations for allopatric and sympatric populations of *P. cinereus* and *P. hoffmani*. Column 2 identifies the distance measure used in each analysis, columns 3 and 4 contain allopatric and sympatric distance measures, and column 5 specifies the significance level from permutation tests. All analyses show significant resource use divergence in sympatry.

Prey Data	Distance Measure	$D_{\text{Allopatry}}$	D_{Sympatry}	P -value
Prey Number	Chi-Squared	0.197	1.395	0.001
Volume	Euclidean	2.435	32.117	0.001
Cube Root (Volume)	Euclidean	1.684	5.408	0.001

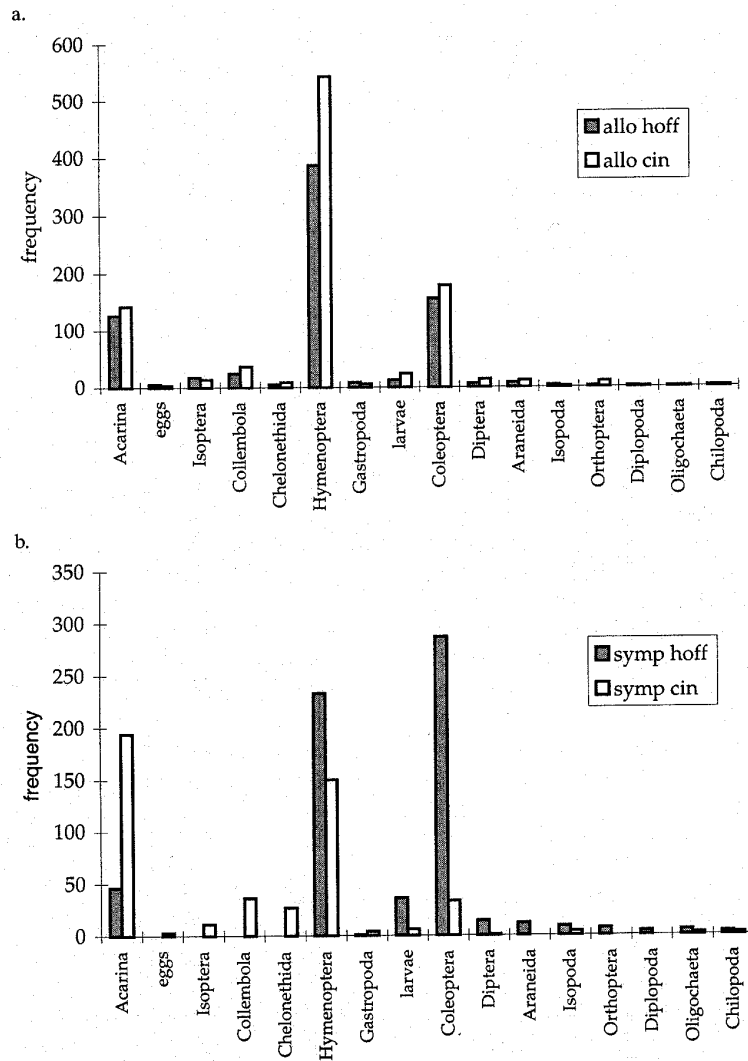


Figure 4. Prey utilization profiles for (a) allopatric populations and (b) sympatric populations of *P. cinereus* and *P. hoffmani* (prey categories are sorted by mean prey size).

3.3. Association of Morphology and Resource Use

Using canonical correlation and partial least squares analyses, I found a strong positive relationship between trophic morphology and resource use. This result was consistent for both canonical correlation and partial least squares analyses, regardless of which estimate of resource use was tested. Further, I found that this association was statistically greater than expected by chance, as revealed by randomization tests (Table 3). Therefore, the association between trophic morphology and resource use was strongly supported in this sample.

Table 3. Results from canonical correlation and partial least squares analyses of trophic morphology and resource use. Significance tests are based on 1000 permutations of the original data matrix (randomization test).

Prey Data	<i>r</i> Can Corr	<i>P</i> -value	<i>r</i> PLS	<i>P</i> -value
Prey Number	0.752	0.001	0.620	0.001
Volume	0.687	0.001	0.551	0.001
Cube Root (Volume)	0.729	0.001	0.569	0.001

For the morphological data, gape width was the most influential character, with high positive loadings on the morphology axis. The largest positive loadings on the resource use axis were for oligochaetes and Coleoptera, and Acarina and Isoptera had the largest negative loadings. Thus, the multivariate correlation between trophic morphology and resource use can be interpreted as an association between large-gaped salamanders and relatively larger prey, versus small-gaped salamanders and relatively smaller prey.

One weakness of this study is that, although I have identified significant morphological differences among populations, it is difficult to integrate a series of linear measurements to visualize and describe these shape differences. An analysis of morphology using landmark-based geometric morphometric methods (e.g., Adams and Funk, 1997; Calcecutt and Adams, 1998) would help fill this void.

4. DISCUSSION

Sympatric populations of *P. cinereus* and *P. hoffmani* diverged significantly in both trophic morphology and resource use. Allopatric populations of these species were morphologically similar in both body size and head shape, and were found to have similar profiles of resource use. Sympatric *P. hoffmani* attained a relatively larger body size, and had a larger skull, with wider and larger jaws, while sympatric *P. cinereus* were relatively smaller, with smaller skulls. Significant differences were found in both the number of prey eaten per salamander, as well as the volume of prey consumed per salamander, with sympatric populations eating fewer prey. Resource segregation was found only between sympatric populations. The smaller species in sympatry, *P. cinereus*, tended to eat smaller prey, while the larger sympatric species, *P. hoffmani*, ate larger prey. Finally, trophic morphology was significantly associated with resource use in these populations, where larger animals tended to specialize on larger prey, and smaller animals specialized on smaller prey.

The association between diet and morphology has been found in other amphibians. For example, Emerson (1985) found that frogs eating small, slow prey had relatively shorter jaws, while frogs eating large, slow prey had relatively longer jaws and wider heads. Fraser found a significant correlation between head width and the largest prey item eaten for *P. cinereus* and *P. punctatus* (Fraser, 1976a), and for *P. cinereus* and *P. hoffmani* (Fraser, 1976b). Maglia (1996) did not find this relationship for adult and sub-adult *P. cinereus*, but did find an association of head size and the largest prey item eaten in juveniles. Thus, an association between trophic morphology and diet appears to be relatively common in amphibians.

When two species with overlapping distributions diverge morphologically in sympatry, character displacement may be a mechanism that explains this pattern (Brown and Wilson, 1956; Grant, 1994). Character displacement has been hypothesized as an explanation for morphological divergence in a number of organisms, including Darwin's finches (Grant, 1986; Schluter et al., 1985), stickleback fish (Schluter and McPhail, 1992), and two species of western *Plethodon* (Brodie, 1970). The differences between sympatric and allopatric populations of *P. cinereus* and *P. hoffmani* also can be evaluated in terms of this hypothesis. Recently, Schluter and McPhail (1992) described six criteria that must be satisfied before character displacement may be invoked as a mechanism driving morphological divergence of trophic characters. In addition to sympatric divergence of morphology, one must demonstrate that: (1) chance can be ruled out as an explanation for the observed pattern, (2) sympatric divergence is the outcome of an evolutionary shift, and not some other factor, such as body size or a geographic cline, (3) morphological differences reflect differences in resource use, (4) there is evidence of competition for resources, (5) allopatric and sympatric sites should have a similar resource base, and (6) the morphological traits examined should have a genetic basis. The present study addresses aspects of five of these criteria.

First, using permutation tests I found that the sympatric divergence was greater than expected by chance (Table 1). Second, I demonstrated that the morphological divergence of trophic shape was not simply a reflection of body size, thus eliminating one possible alternative explanation for the observed patterns. Third, I established the association between morphology and resource use through multivariate correlation methods (Table 3). Evidence of competition for resources was demonstrated by finding a reduction in the average number of prey eaten in sympatry, as well as the apparent partitioning of resources (see Robinson and Wilson, 1994). Finally, my initial sampling results did not indicate any differences in the resource bases for each population.

In this study, I have presented evidence addressing five of Schluter and McPhail's (1992) six criteria for character displacement. No evidence is available concerning the genetic basis of morphology, but heritability estimates for trophic characters would help fill this void. The analysis of additional allopatric and sympatric populations would address the possibility of clinal variation in trophic characters, as well as provide further evidence on whether sympatric divergence is greater than expected by chance. Nevertheless, based on the evidence presented here, I hypothesize that the ecological interactions between *P. cinereus* and *P. hoffmani* in this geographic transect are best described in terms of character displacement. Further studies on additional transects, as well as behavioral experiments between allopatric and sympatric salamanders, will determine whether this finding is a general explanation of the ecological interactions of these two species.

5. SUMMARY

I examined morphological variation and resource use variation of *Plethodon cinereus* and *P. hoffmani* among allopatric and sympatric populations from an east-west transect in south-central Pennsylvania. Trophic morphology was quantified using six head measurements, and stomach contents were used to ascertain resource use. I found differences in body size, six cranial characters, and size-adjusted head shape,

with significantly larger differences between sympatric populations. There was a significant difference between populations in the number of prey eaten per salamander, as well as the volume of prey eaten per salamander. There was segregation of resource use in sympatry: *P. hoffmani* ate fewer, but larger, prey and *P. cinereus* ate fewer, but smaller, prey. Thus, sympatric populations segregated resources along a prey-size axis. Finally, trophic morphology and resource use were significantly associated with one another in these populations, with larger salamanders eating larger prey, and smaller salamanders eating smaller prey. These results are consistent with the hypothesis of character displacement, which may explain the ecological interactions between these two species.

ACKNOWLEDGMENTS

I thank M. A. Bell, F. J. Rohlf, D. E. Slice, and N. Valenzuela for suggestions and comments on versions of this manuscript. This work was sponsored in part by NSF grants IBN-9800636 (to FJR and DCA), and IBN-9728160 (to FJR), and by a Sigma Xi Grant-in-aid of Research (DCA). This work is contribution number 1041 from the program in Ecology and Evolution at the State University of New York at Stony Brook.

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