MORPHOLOGY IS DECOUPLED FROM INTERSPECIFIC COMPETITION IN *PLETHODON* SALAMANDERS IN THE SHENANDOAH MOUNTAINS, USA

Erin M. Myers[1,3] and Dean C. Adams[1,2]

[1]*Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA*
[2]*Department of Statistics, Iowa State University, Ames, IA 50011, USA*

ABSTRACT: Interspecific competition plays an important role in structuring ecological communities and generating patterns of phenotypic diversification. In the Shenandoah Mountains of Virginia, strong interspecific competition between *P. cinereus* and *P. shenandoah* shapes the geographic distributions of these species and relegates *P. shenandoah* to sub-optimal habitat. However, while many *Plethodon* salamander communities exhibit phenotypic shifts resulting from interspecific competition, the morphological consequences of competition in this system have not been investigated. We examined head shape variability of *Plethodon cinereus* and *P. shenandoah* to determine whether phenotypic patterns of variation were consistent with the hypothesis of interspecific competition. Across all three mountains where *P. shenandoah* is found, we identified significant species-specific differences in head shape. We also found significant phenotypic shifts between allopatric *P. cinereus* located at lower elevations and sympatric *P. cinereus* located at higher elevations. However, there was no evidence of accentuated phenotypic divergence in the sympatric contact zone between the two species. Thus, while there was evidence of a character shift in *P. cinereus*, patterns of character divergence between species associated with interspecific competition were not found. These observations suggest that morphological variation is decoupled from ecological interactions in this system, and aggressive interactions between the two species do not elicit a phenotypic response as seen in other *Plethodon* communities.

Key words: Character shifts; Competitive exclusion; Morphometrics; Species interactions

INTERSPECIFIC interactions among taxa can have dramatic influences on community and population structuring. As closely related species often require similar resources, competition during co-occurrence, sympatry, can result in a number of outcomes. One potential outcome is to limit niche overlap through ecological character displacement and resource partitioning (Brown and Wilson, 1956). This limitation results in trait differences between species that are greater in sympatry relative to allopatry and a subsequent reduction in resource overlap (Adams, 2004; Losos, 2000). Conversely, if species exhibit too much overlap and an inability to partition the niche, the superior competitor will gain access to more resources relative to the second species, resulting in local extinction of one species from its preferred habitat via competitive exclusion (Jaeger, 1974). While considerable research has documented the existence of character divergence across a wide range of taxa (reviewed in Schluter, 2000), relatively few studies have examined the repeatability of character displacement within replicated communities of the same species (but see Adams et al., 2007; Jastrebski and Robinson, 2004; Losos, 1992).

In recent decades, salamanders of the genus *Plethodon* have been intensively studied to understand how their ecological and behavioral interactions shape population and community dynamics (e.g., Bruce et al., 2000; Hairston, 1980). Across several *Plethodon* communities in the eastern United States, sympatric morphological divergence is a frequent evolutionary response to interspecific competition (Adams, 2004; Adams and Rohlf, 2000; Adams et al., 2007; Jaeger et al., 2002). Further, cranial morphology is associated with a number of ecologically relevant characteristics, including food resource use (Adams, 2000; Maerz et al., 2006) and behavioral aggression (Adams, 2004). Therefore, head shape can be examined as a potential indicator of resource overlap, and associations of head shape with shifts in diet can reveal patterns of character displacement. Alternatively, robustness of cranial morphology is often associated with increased aggres-

[3] CORRESPONDENCE: e-mail, emyers1@iastate.edu

sion, which in turn may suggest patterns of competitive exclusion across the community landscape (Adams, 2004). Finally, salamanders in some adjacent populations have undergone relatively rapid microevolutionary responses to changes within the environment associated with elevation and differentially utilize prey species structured across an altitudinal gradient (Maerz et al., 2006).

Within *Plethodon*, the species pair of *Plethodon shenandoah* and *P. cinereus* presents a unique opportunity to tease apart the relative importance of aggressive behavior, resource use, and habitat structuring on the distributions of these two species. Both salamanders are similarly sized and are thought to utilize similar ecological niches. Previous work on these species across three mountains within the Shenandoah Mountains (Virginia) suggests that body size and aggressive interactions structure these populations. *P. cinereus* is competitively dominant and excludes *P. shenandoah* from optimal habitat sites, relegating it primarily to the sub-optimal talus near the tops of mountains (Jaeger, 1972). By contrast, *P. cinereus* is found at lower elevations throughout this geographic region (Highton, 1988). These two species occur in sympatry in a narrow zone surrounding the talus, where large-bodied *P shenandoah* are able to compete with *P. cinereus*. The community is unstable, as *P. shenandoah* exhibits source-sink metapopulation structure (Griffis and Jaeger, 1998), and at least one population of *P. shenandoah* was extirpated over the course of a few years due to the combination of interspecific competition and extreme drought (Jaeger, 1970). Those *P. shenandoah* that achieve large body size are able to actively compete with *P. cinereus* outside the talus (Jaeger, 1972). However, environmental factors may also be involved as *P. cinereus* is less tolerant of the dry conditions found in the talus than *P. shenandoah*, though *P. shenandoah* performs equally well in either habitat (Jaeger, 1971). Therefore, competition for limited, optimal habitat and prey items appears critical in structuring these salamander communities.

The repeated interactions of these two species across several mountain tops provide a natural evolutionary experiment to examine the importance of various factors and processes in maintaining and shaping species distributions. Additionally, this distribution provides the opportunity to examine and test for the repeatability of the evolutionary process and outcomes. With this opportunity in mind, we generated several predictions concerning cranial morphology in these species based on our knowledge of the interactions in this system and morphological responses to similar processes in other *Plethodon* communities. First, we predicted that species-specific differences in head shape would be present between the two species, based on work in other *Plethodon* species pairs. Second, consistent with previous studies on other *Plethodon* communities, we predicted that head shape between the two species would be more divergent in sympatry than allopatry in a manner consistent with differential resource use or aggression-related character displacement (displacement of jaw morphologies specialized for different prey types based on jaw length and depth vs. displacement of the more aggressive species to a more robust, deeper morphology, respectively). Finally, we predicted that *P. cinereus* and *P. shenandoah* from the contact zone would exhibit greater morphological divergence as compared to *P. cinereus* located further from *P. shenandoah* at lower elevations down each mountain as a pattern of morphological isolation by distance.

MATERIALS AND METHODS

We obtained 758 adult specimens (522 *Plethodon cinereus* and 236 *P. shenandoah*) from the National Museum of Natural History (Washington, D.C.) from 14 geographic localities in the Blue Ridge Mountains in western Virginia, USA (Fig. 1; Table 1). Three of these localities represented sympatric sites where both species were found. These sites consisted of forest borders and the edges of talus slopes on the three isolated peaks where *P. shenandoah* is known to occur (Hawksbill, Stony Man, and Pinnacle Mountain: [Highton, 1988; Highton and Worthington, 1967; Jaeger, 1970]). Because the exact position for each individual was unknown and the area of sympatry is relatively narrow (<1 km; Jaeger, 1972), all *P. shenandoah* were classified as

Fig. 1.—Location of Shenandoah National Park in the Blue Ridge region of Virginia (B) Geographic locations of salamander populations used in this study. Open circles represent localities of allopatric *P. cinereus*, closed circles represent sympatric locations of *P. shenandoah* and *P. cinereus* on three isolated Mountains in the Shenandoah National Park (P: The Pinnacles, S: Stony Man, H: Hawksbill).

TABLE 1.—Description of geographic localities (sites) used in this study. The mountain, species found, sample size, elevation, latitude, and longitude are provided. Species codes are as follows: C = *P. cinereus*; S = *P. shenandoah*.

| Site type	Mountain	Species	Sample size	Elev. (ft)	Latitude	Longitude
Sympatry	Hawksbill	C, S	57, 97	3560–3650	Various localities near summit	Various localities near summit
Allopatry	Hawksbill	C	53	3270	38° 34′ 43″ N	78° 22′ 38″ W
Allopatry	Hawksbill	C	32	3000	38° 33′ 38″ N	78° 23′ 18″ W
Allopatry	Hawksbill	C	23	2750	38° 34′ 26″ N	78° 21′ 00″ W
Allopatry	Hawksbill	C	24	2650	38° 33′ 18″ N	78° 21′ 57″ W
Allopatry	Hawksbill	C	22	2000	38° 33′ 27″ N	78° 20′ 00″ W
Sympatry	The Pinnacles	C, S	91, 74	3100–3540	38° 37′ 57″ N	78° 19′ 37″ W
				3150	38° 37′ 50″ N	78° 20′ 02″ W
Allopatry	The Pinnacles	C	26	3220	38° 37′ 07″ N	78° 20′ 28″ W
Allopatry	The Pinnacles	C	33	3680	38° 37′ 40″ N	78° 19′ 54″ W
Allopatry	The Pinnacles	C	35	2250	38° 37′ 52″ N	78° 17′ 47″ W
Allopatry	The Pinnacles	C	27	1700	38° 38′ 43″ N	78° 20′ 27″ W
Sympatry	Stony Man	C, S	64, 65	3430	38° 35′ 53″ N	78° 22′ 47″ W
				3440	38° 36′ 10″ N	78° 22′ 09″ W
				3220	38° 36′ 20″ N	78° 22′ 02″ W
				3400	38° 36′ 03″ N	78° 22′ 25″ W
Allopatry	Stony Man	C	21	3020	38° 30′ 39″ N	78° 24′ 33″ W
Allopatry	Stony Man	C	14	1490	38° 36′ 45″ N	78° 23′ 43″ W
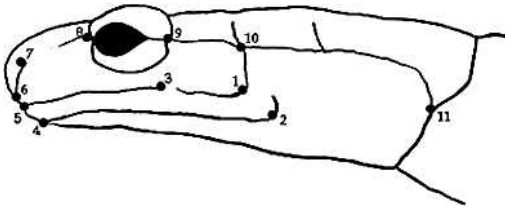
Fig. 2.—Positions of 11 landmarks used in this study. All landmarks were digitized from the left-lateral view of the skull (modified from Adams, 2004).

sympatric. Conclusively allopatric populations of *P. shenandoah* are essentially absent. The remaining 11 localities were single-species allopatric sites of *P. cinereus* located further from the contact zone on each of the three mountains (Fig. 1; Table 1). We used specimens from five allopatric localities on Hawksbill Mountain, four allopatric localities on The Pinnacles, and two allopatric localities on Stony Man Mountain.

For all specimens, we quantified head shape to assess patterns of morphological variation across species and localities. We chose to measure head shape because previous studies in *Plethodon* have demonstrated that patterns of variation in head shape were related to interspecific interactions in some communities (e.g., Adams, 2004; Adams and Rohlf, 2000; Adams et al., 2007; Arif et al., 2007). Landmark-based geometric morphometric methods were used to quantify head shape (Adams et al., 2004; Rohlf and Marcus, 1993). For this approach, we first obtained digital images of the left-lateral side of each head using a Nikon DXM-1200 digital camera, mounted on a Nikon SMZ 1500 stereomicroscope. We then digitized the location of 11 biologically homologous landmarks from the skull and jaw of each specimen (Fig. 2) using TPSDIG (Rohlf, 2004). Variation in the position of the mandible relative to the skull was standardized by rotating the mandible of all specimens to a fixed angle relative to the skull (Adams, 1999). Nonshape variation was then removed using a generalized Procrustes analysis (GPA: Rohlf and Slice, 1990), which superimposes specimens to a common coordinate system after accounting for differences in position, orientation, and scale. Partial warp scores (Bookstein, 1991) and standard uniform components (Rohlf and Bookstein, 2003)

were then generated from the aligned specimens, and head shape was represented by the set of principal component scores from all principal component axes that expressed variation. These 18 shape variables (partial warp scores and uniform components) were then used to assess patterns of morphological variation using standard multivariate statistics.

To examine patterns of morphological variation on each mountain, we performed separate two-factor multivariate analyses of variance (MANOVA), with species and geographic locality as the main effects. No interaction term was included in these models because on each mountain, specimens of *P. shenandoah* were from contiguous populations that could not be accurately designated as allopatric or sympatric geographic localities and were thus only categorized as sympatric. Therefore, to test for sympatric character divergence, we compared the observed morphological differentiation between sympatric populations of both species to the differences between allopatric *P. cinereus* and sympatric *P. shenandoah*. For this comparison we used residual randomization to determine whether there was significant morphological divergence between sympatric and allopatric populations of *P. cinereus* (see Adams and Collyer, 2007; Collyer and Adams, 2007). Unlike standard randomization where individuals are shuffled among groups, residual randomization accounts for population differences and differences due to other model effects and shuffles residual values from this model. Thus, when multiple factors are present in a model, residual randomization is superior to the standard approach, as it does not conflate variation due to main effects (e.g., differences among populations) with the error variation among individuals (see discussions in Adams and Collyer, 2007; Collyer and Adams, 2007; Freedman and Lane, 1983; Gonzalez and Manly, 1998).

For the residual randomization procedure, we first calculated the observed morphological differentiation between sympatric and allopatric *P. cinereus* (D_{obs}) as the Euclidean distance between least squares means from each of the mountain-specific MANOVA models described above. A reduced MANOVA containing only the species factor was then performed, and predicted values and

TABLE 2.—Multivariate analysis of variance for sources of head shape variation for (a) Hawksbill Mountain, (b) The Pinnacles, (c) Stony Man Mountain.

Source	Pillai's trace	Exact F	df	P
(a) Hawksbill Mountain				
Species	0.542	18.696	18, 284	<0.0001
Locality	0.841	3.233	90, 1440	<0.0001
(b) The Pinnacles				
Species	0.3458	7.7238	18, 263	<0.0001
Locality	0.7672	3.5069	72, 1064	<0.0001
(c) Stony Man Mountain				
Species	0.5752	10.7568	18, 143	<0.0001
Locality	0.7407	4.7050	36, 288	<0.0001

residuals were calculated. Residuals from the reduced model were then randomly assigned to predicted values to reconstruct "random" phenotypic values, and from these values the random differentiation (D_{rand}) between sympatric and allopatric P. cinereus was estimated. This procedure was repeated 9999 times, and the proportion of random differentiation values (D_{rand}) that exceeded the observed morphological differentiation (D_{obs}) was treated as the significance of the effect (see Collyer and Adams, 2007). Finally, using a similar procedure, we determined whether the observed morphological divergence between P. cinereus and P. shenandoah in sympatry was significantly greater than that found between P. shenandoah and allopatric populations of P. cinereus. By comparing morphological differences between species in the contact zone to differences between allopatric populations, we could assess the extent to which the patterns observed in sympatry were the result of clinal or geographic variation. Finally, morphological patterns were visualized through a principal components analysis (PCA) of shape, where locality means were projected on PC axes. Thin-plate spline deformation grids were generated to graphically describe patterns of shape variation (see Adams, 2004). All statistical analyses were performed in R (R Development Core Team, 2006).

RESULTS

Using MANOVA, we found significant differences between species and between localities on all three mountains (Table 2). There was significant morphological divergence between allopatric and sympatric populations of P. cinereus on all three mountains ($D_{Hawksbill} = 0.0189$, $P_{rand} = 0.0014$; $D_{Hawksbill} = 0.0138$, $P_{rand} = 0.0136$; $D_{hawksbill} = 0.0262$, $P_{rand} = 0.0001$). However, the observed morphological divergence between the two species in sympatric localities was not significant (Table 3). Further, when the observed sympatric divergence was examined relative to allopatric populations, in most cases the observed differentiation was not greater than that found by comparing allopatric P. cinereus to sympatric P. shenandoah (Table 3). Not surprisingly, none of the sympatric morphological differences were significantly greater than these allopatric values when examined using residual randomization (Table 3). Taken together, these results reveal that there were significant differences in cranial morphology between allopatric and sympatric P. cinereus, but the observed differentiation between the two species in sympatry did not exceed levels found between allopatric populations of P. cinereus as compared to P. shenandoah.

TABLE 3.—Results from residual randomization procedures for divergence comparisons of P. shenandoah morphology to P. cinereus morphology across Hawksbill, The Pinnacles, and Stony Man Mountains. Values represent the Euclidean distance between least squares means for the populations of P. cinereus versus P. shenandoah. Levels of allopatry refer to geographic localities further from the contact zone of the two species (see Table 1).

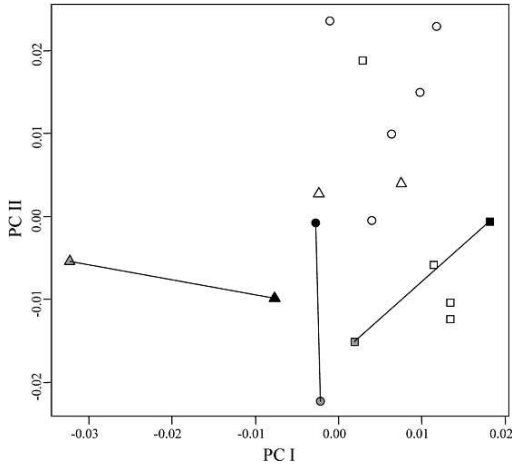| | Hawksbill | | The Pinnacles | | Stony Man | |
| | P. shenandoah | | P. shenandoah | | P. Shenandoah | |
P. cinereus	D	P_{rand}	D	P_{rand}	D	P_{rand}
Sympatry	0.02905	0.6891	0.02392	0.3381	0.03126	0.8621
Allopatry 1	0.03449	0.9034	0.01940	0.1195	0.05314	0.9998
Allopatry 2	0.03357	0.791	0.02174	0.2463	0.03907	0.8325
Allopatry 3	0.03490	0.157	0.02463	0.4666		
Allopatry 4	0.03490	0.8119	0.03816	0.9834		
Allopatry 5	0.04565	0.9959				

FIG. 3.—Principal components (relative warp) plot of least squares means for each locality. Localities from Hawksbill Mountain are displayed as circles, localities from Pinnacle Mountain are displayed as squares, and localities from Stony Man Mountain are displayed as triangles. Open symbols represent allopatric *P. cinereus* localities, black symbols represent sympatric *P. cinereus* localities, and gray symbols represent *P. shenandoah* localities. Sympatric *P. cinereus* and *P. shenandoah* localities from each mountain are connected with solid lines.

Visualizing morphological differences among population means using principal components analysis (PCA) revealed that the two major axes of variation (PC1 and PC2) corresponded with a separation of *P. shenandoah* with low scores and *P. cinereus* with higher values (Fig. 3). PC2 also corresponded with population type. Sympatric populations from both species generally clustered together while there was considerable diversity among allopatric populations, indicating head shape differences among these populations. Unfortunately, individual loadings from PCA are not interpretable when geometric morphometric shape data are used, because each shape variable cannot be described independently (see Adams and Rosenberg, 1998; Rohlf, 1998). Therefore, interpretation of anatomical differences along principal component directions is accomplished through visualizing shape differences using, thin-plate spline deformation grids. With this approach, we found that *P. shenandoah* had a flat and compressed cranial region relative to mean cranial shape (Fig. 4). In addition, *P. shenandoah* exhibited compression throughout the posterior region of the head, and the lower jaw
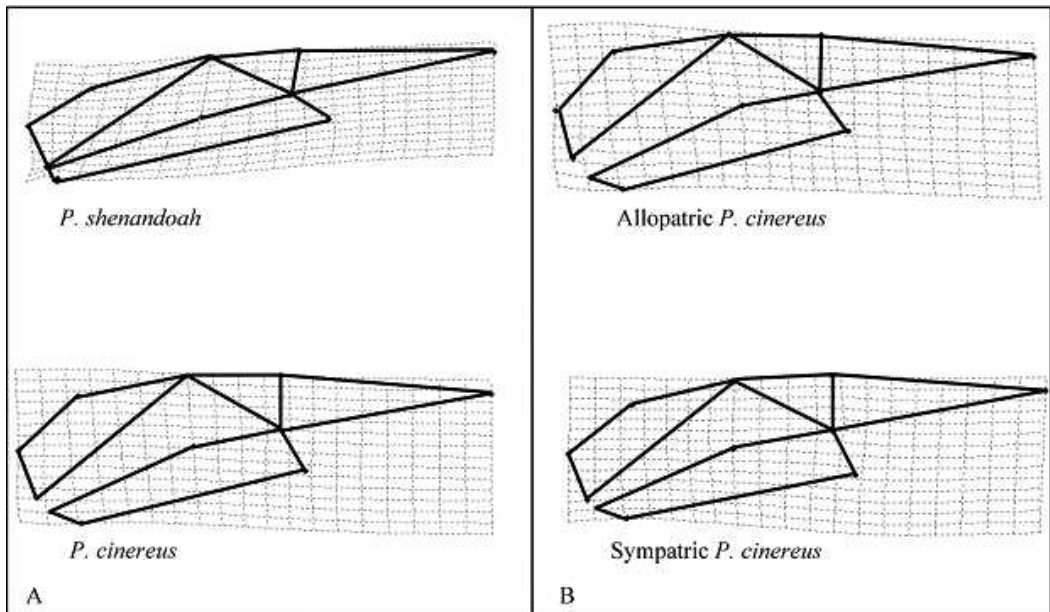

FIG. 4.—Thin-plate spline deformation grids depicting head shape differences between (A) species means for *P. cinereus* and *P. shenandoah*, and (B) head shape differences between allopatric and sympatric *P. cinereus*. Deformation grids are accentuated by a factor of 5 to facilitate visual interpretation of differences.

(Fig. 4). By contrast, *P. cinereus* displayed a relative expansion of the head in all directions creating a longer, deeper bodied cranial region (Fig. 4). However, while the lower jaw was deeper in the dorsal-ventral direction, it was relatively shorter as compared to the lower jaw of *P. shenandoah*. When we compared populations of *P. cinereus*, there were morphological differences between sympatric and allopatric populations, consistent with the PCA and MANOVA results. Allopatric individuals of *P. cinereus*, which were found at lower elevations, exhibited relative expansion in most regions of the head, and particularly in the frontal region (Fig. 4). Sympatric individuals of *P. cinereus*, which were found at higher elevations, displayed more of an average head depth (neither expanded nor depressed), but the posterior region of the lower jaw was relatively expanded (Fig. 4).

DISCUSSION

Evolutionary ecologists have long considered competitive interactions between closely related species important determinants of community composition and a major cause of phenotypic diversification. In the eastern United States, many *Plethodon* salamander communities exhibit phenotypic evolutionary responses to competition, where morphological differences between species are enhanced in sympatry and are associated with resource partitioning or enhanced aggressive behavior (e.g., Adams, 2000, 2004). In Virginia, the distribution of the wide-ranging *P. cinereus* completely surrounds that of the geographically-restricted *P. shenandoah*, and both laboratory and field studies have indicated that interspecific competition is critical in structuring these geographic distributions (Griffis and Jaeger, 1998; Jaeger, 1971, 1972). While the behavioral interactions of these species have been well documented, we explored whether patterns of morphological variation correlate with the observed competitive interactions.

In this study, we examined head shape variability of *P. cinereus* and *P. shenandoah* to determine whether phenotypic patterns of variation were consistent with the hypothesis of interspecific competition. Using specimens from 14 geographic localities across the three mountain peaks where *P. shenandoah* occurs, we identified significant differences in head shape between the two species. Further, on each mountain we found significant phenotypic shifts between allopatric *P. cinereus* (located at lower elevations) and sympatric *P. cinereus* (located at higher elevations). However, in the contact zone between the two species, we found no evidence of accentuated phenotypic divergence, and sympatric phenotypic differences were not greater than those found when comparing allopatric *P. cinereus* to *P. shenandoah*. Therefore, while there was evidence for a character shift in *P. cinereus*, patterns of character divergence between species were not found.

Our analysis of phenotypic differences between localities revealed that the largest phenotypic signal in this system was found between *P. cinereus* from lower and higher elevations; a pattern consistent across all three mountains (Table 2 and Results). Previous researchers have shown a similar phenotypic pattern in Pennsylvania and New York, where adjacent upland and lowland populations of *P. cinereus* differed significantly in head shape (Maerz et al., 2006). These morphological differences were also associated with differential utilization of food resources between localities. In examining the anatomical differences observed in our study (Fig. 4), we found that the patterns between low elevation and high elevation *P. cinereus* were quite similar to those found between upland and lowland *P. cinereus* in Pennsylvania and New York (Maerz et al., 2006). In addition, food utilization was qualitatively similar at both high-elevation localities on Hawksbill Mountain (Jaeger, 1972) and upland localities in Pennsylvania and New York (Maerz et al., 2006). These observations are consistent with the hypothesis that morphological differences between populations may result from dietary shifts and local adaptation to differences in prey availability between high elevation and low elevation localities. We emphasize, however, that this is a tentative hypothesis, as no data on prey availability or food use at lower elevation localities is currently available. Future ecological surveys will allow a more rigorous test of this hypothesis.

Interestingly, while there is strong ecological and behavioral evidence of interspecific competition between *P. cinereus* and *P. shenandoah* (e.g., Jaeger, 1971), we found no phenotypic divergence in cranial morphology associated with this competition. This result was somewhat surprising, as several other *Plethodon* communities maintained by competitive interactions also exhibit consistent sympatric character divergence resulting from this competition (e.g., Adams, 2000; Adams and Rohlf, 2000; Adams et al., 2004). However, such consistent patterns are not universally the case. For instance, in some *Plethodon* communities, sympatric character divergence is consistently observed, but adaptation to the local environment results in differences in how that divergence is phenotypically expressed (Adams et al., 2007). In other communities, morphological convergence, rather than divergence, has been identified (Arif et al., 2007). However, in all of these studies, there were clear phenotypic shifts associated with community dynamics. When compared to these previous findings, the results of our study are quite distinct, as there does not appear to be any phenotypic shift associated with interspecific competition between *P. cinereus* and *P. shenandoah*. Because shifts have previously been detected in *P. cinereus*, this suggests that either *P. shenandoah* cannot modify its morphology to limit competition possibly due to limited genetic variability for this trait, or that it is not possible for these two species to partition the niche and utilize different resources thus constraining morphological evolution. If this is the case, a lack of morphological character displacement may not be surprising. This pattern lends strength to the argument that competitive exclusion is operating in this system (Jaeger, 1974). Rather than exhibit a morphological character shift, these species have utilized an ecological displacement such that the talus represented a refuge from competition for *P. shenandoah* that *P. cinereus* cannot invade. Thus, this observation suggests that competitive exclusion shapes the population structure of these two species and response to ecological factors shapes morphological differences within the species for *P. cinereus*.

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