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COMPLEX SPECIES INTERACTIONS LEAD TO UNPREDICTABLE OUTCOMES IN *PLETHODON*

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ABSTRACT: Evolutionary and ecological theory generates testable predictions concerning the effects of species interactions on ecological, behavioral, and morphological traits. Throughout Ohio, two closely related and ecologically similar salamander species, *Plethodon cinereus* and *P. electromorphus*, occur in similar habitats and in many localities are found in sympatry. Geographic and behavioral patterns previously described between these two species could be the result of interspecific competition, a hypothesis that also predicts distinct patterns of resource use, morphological variation, or both when the two species occur in sympatry. Here we tested these predictions by examining patterns of resource use and morphology in sympatry and compared them to patterns observed in allopatric populations of each species. We found that morphological differences in head shape between species were location-specific, with morphological divergence occurring at some sympatric locations and convergence occurring at others. The degree of food-use overlap was also variable between locations but, in general, the two species used similar food resources.

Key words: Character divergence; Competition; Competitive exclusion; *Plethodon*; Resource partitioning

MANY DIFFERENT ECOLOGICAL PROCESSES influence the biology of species such as parasites and predators (Andrews, 1979; Dick and Platvoet, 2000), environment (Ricklefs, 1987; Pearson and Dawson, 2003; Blackburn and Hawkins, 2004; Smith et al., 2005; Wiens et al., 2006; Wiens, 2007; Tylianakis et al., 2008), stochastic variation (Hubbell, 2001; Rosindell et al., 2012), or competition (Gause, 1934; Connell, 1980). These factors determine what species are found in particular ecological communities and influence patterns of variation in morphological, behavioral, and physiological traits of species (Brown and Wilson, 1956; Hairston, 1983; Dick and Platvoet, 1996). In the temperate forests of North America, terrestrial woodland salamanders fill multiple ecological roles within complex food

webs (Petranka, 1998; Walton et al., 2006; Davenport and Chalcraft, 2012). Studies examining the impact of predator diversity or density on salamanders are few, but suggest that predation may be a dominant force structuring some salamander communities (i.e., *Desmognathus* sp.; Hairston, 1980a) but not others (i.e., *Plethodon*; Hairston, 1980b).

In many salamander communities, the effects of interspecific competition can be profound. For example, interspecific competition has limited the geographic ranges of some competing species (Jaeger, 1970; Hairston, 1980a; Arif et al., 2007; Deitloff, 2011). Additionally, competition has led to a variety of evolutionary outcomes between sympatric species such as sympatric divergence in cranial morphology (*P. cinereus* and *P. hoffmani*: Adams and Rohlf, 2000; Adams, 2004, 2010; Adams et al., 2007; *P. cinereus* and *P. nettingi*: Adams et al., 2007), competitive exclusion (*P. cinereus* and *P. shenandoah*:

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Jaeger, 1971, 1974; Myers and Adams, 2008; *P. cinereus* and *P. hubrichti*: Arif et al., 2007), and enhanced interspecific aggression in sympatry (alpha-selection, *P. jordani* and *P. teyahalee*: Nishikawa, 1987; *P. cinereus* and *P. electromorphus*: Deitloff et al., 2009). Competitive interactions also appear to influence species distributions in some species, as patterns of community composition are consistent with competitive-based models of community assembly (Adams, 2007). On the other hand, the effects of interspecific competition are not ubiquitous, as some studies have demonstrated that resources, especially food, may not be limiting or partitioned among salamander species (Hairston, 1981; Hairston et al., 1987).

In Ohio, the geographic ranges of *Plethodon cinereus* (Green, 1818) and *P. electromorphus* (Highton, 1999) overlap over a broad geographic region (across half of the state); however, at a more fine scale, the two species do not often co-occur in the same geographic locality (Fig. 1 in Deitloff et al., 2008; Deitloff, 2011). When interspecific behavior is examined within sympatric areas, salamanders are more aggressive than salamanders from allopatric locations, suggesting intense competition (Deitloff et al., 2009). Based on these observations, and on patterns observed in other *Plethodon* communities where competition is prevalent (see above), we hypothesize that *P. cinereus* and *P. electromorphus* may be competing for resources due to the lack of co-occurrence generally found across their distributions (Deitloff, 2011) and to the increase in aggression when the two species are found in sympatry (Deitloff et al., 2009). In this study, we examined potential effects of competition in two aspects of the ecological niche of these species: food use and refuge types. We also examined patterns of morphological variation within and among species. We predicted that *P. cinereus* and *P. electromorphus*: (1) partition types of prey eaten, (2) use different types or sizes of cover objects (rocks or logs), and (3) exhibit morphological character displacement of head shape. We also tested the prediction that (4) morphological variation was associated with food use, climate, or behavior.

MATERIALS AND METHODS

Collection Methods

Salamanders were obtained during seven collecting trips in 2004 to 2007 from 13 distinct locations in eastern deciduous forests in Ohio. No obvious differences in tree composition, slope, or soils were evident among localities. At each locality, all cover objects were overturned and the boundaries of each locality were delineated by rivers, roads, or nonforested private property (all collection localities were less than 0.2 km² in area). In five localities (A, B, C, D, and E), only *P. cinereus* was obtained while only *P. electromorphus* was found in two localities (F and G). The remaining six localities represented sympatric localities where both species were found (H, I, J, K, L, and M; Table 1). Body size (snout-vent length: SVL) was measured on all salamanders, and only salamanders greater than 31 mm SVL were used in all subsequent analyses (this corresponds to the minimum body size observed for adults of these species: sensu Saylor, 1966). In total, 924 salamanders were used for morphometric quantification (see below). Subsets of these salamanders were used to also examine resource use ($n_{food} = 335$ and $n_{refuge} = 176$) and also to characterize behavior ($n = 136$; sample sizes per species obtained at each locality for each type of data can be found in Table 1).

Resource Use: Food

In total, 335 live specimens ($n_{P. cinereus} = 229$, $n_{P. electromorphus} = 106$) were collected between 0700 h and 1200 h for stomach content analysis. Stomachs were pumped in the field with a 5-ml syringe fitted with 18-gauge rubber tubing and their contents were immediately stored in 70% ethyl alcohol (Fraser, 1976). Following prior authors (Adams and Rohlf, 2000; Maerz et al., 2006), we identified prey items to the level of order except for the phylum Annelida, classes Chilopoda and Diplopoda, and subclass Acarina. Larvae were treated as a single category. We then calculated the number of prey items per stomach for both species at each locality. The quantity of prey items per stomach was low ($n < 5$) and typically whole, intact specimens were encountered. When partial specimens were

encountered, the most conservative estimates were calculated. For example, if a pair of dismembered coleopteran elytra was found, we counted this as a single individual. Data from each allopatric and sympatric locality and for each species were treated separately in all analyses.

We used measures of niche overlap to determine whether sympatric populations of *P. cinereus* and *P. electromorphus* partitioned food resources. First, a food utilization matrix was constructed with rows as species-locality groups, columns as prey categories, and the number of prey items per stomach represented the individual entries of the matrix. From this matrix, pairwise estimates of niche overlap (O_{12} and O_{21}) were obtained using the Pianka index (Pianka, 1973):

$$O_{12} = O_{21} = \frac{\sum_{i=1}^n p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^n (p_{2i}^2)(p_{1i}^2)}}$$

where p_{1i} and p_{2i} are the frequencies of each prey type n for the two species. Values closer to 1.0 indicate a higher degree of resource overlap, whereas values closer to 0.0 indicate more differences in resource use. The significance of the mean overlap measure was then obtained using null-model randomization approaches (Gotelli and Graves, 1996), where entries in the food utilization matrix were randomly shuffled (but retaining row and column totals) and from which random estimates of niche overlap were obtained (see Gotelli and Graves, 1996). The procedure was repeated 10,000 times to generate a random distribution of mean food-use overlap, which was compared to the observed value. Additionally, the range of niche overlap measures between species from the sympatric localities was qualitatively compared to overlap values calculated among allopatric localities, and differences in food use (resource use profiles) between species-locality groups were visualized graphically using correspondence analysis (CA). All niche overlap estimates and null model analyses were conducted with EcoSim (Gotelli and Entsminger, 2007).

Resource Use: Refuge Sites (Cover Objects)

Estimates of refuge sites used by each species were obtained through an assessment of cover object use. At each sympatric locality, we collected salamanders and recorded what type of cover object each utilized (rock, log, bark, leaves). Because rocks and logs were the most common cover objects, we included only these types of cover objects ($n_{rocks} = 134$; $n_{logs} = 28$). In addition, because rocks were the most common cover types, we also measured their greatest length and width (to the nearest centimeter). We then tested whether the rocks with multiple salamanders underneath ($n_{rocks} = 11$) were larger than rocks with only one salamander underneath ($n_{rocks} = 123$) using a t -test. For the remainder of the analyses, we included only cover objects that had one salamander (*P. cinereus*: $n_{rocks} = 114$, $n_{logs} = 19$; *P. electromorphus*: $n_{rocks} = 9$, $n_{logs} = 5$). With these data we tested whether *P. cinereus* and *P. electromorphus* used different types of cover objects using the Pianka index of niche overlap as described above. We tested whether the two species used differently sized rocks using a t -test. While some studies have found an association between salamander size and cover object size (Mathis, 1990; Hickerson et al., 2004), other studies have not confirmed this pattern (Gabor, 1995; Faragher and Jaeger, 1997). To determine whether this was the case in our system, we used correlation analysis to compare rock size and SVL of the salamanders found under those rocks.

Morphology

Cranial morphology was quantified using geometric morphometric methods (Rohlf and Marcus, 1993; Adams, 2004). We quantified head shape for a total of 924 specimens from all localities (Table 1). First, we imaged the left-lateral side of each head using a Nikon DXM-1200 digital camera mounted on a Nikon SMZ1500 stereomicroscope or a Nikon D70 digital camera. From each image we digitized 10 biologically homologous landmarks from the skull and jaw (Fig. 1A) using TPSDIG2 (Rohlf, 2006). 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).

TABLE 1.—Location information for localities used in this study. Locality is referred to throughout the manuscript by the letter shown (A through M). Column headings beginning in *n* list samples sizes from each locality for each type of data that was collected; SVL = snout-vent length; food represents food type and quantity data; morph represents morphological data; covobs represents cover-object type and size data; PLS represents partial-least-squares analysis for food-use and morphological data; behav08 and behav09 represents morphological and behavioral comparisons using behavior data from Deitloff et al., 2008, and Deitloff et al., 2009, respectively. For sympatric localities, the first number represents the sample size of *P. cinereus* from that locality and the second number represents the sample size of *Plethodon electromorphus*. Coordinates are based on the WGS84 datum.

Locality	Locality type	Latitude	Longitude	<i>n</i> _{SVL}	<i>n</i> _{food}	<i>n</i> _{morph}	<i>n</i> _{covobs}	<i>n</i> _{PLS}	<i>n</i> _{behav08}	<i>n</i> _{behav09}
A	Allopatry <i>P. cinereus</i>	39°48'16"N	81°52'12"W		21	23		20		
B	Allopatry <i>P. cinereus</i>	40°07'54"N	82°36'53"W		22	49		21		
C	Allopatry <i>P. cinereus</i>	40°46'04"N	80°43'37"W	102	21	131		18	20	24
D	Allopatry <i>P. cinereus</i>	41°03'58"N	80°57'45"W			3				
E	Allopatry <i>P. cinereus</i>	41°22'01"N	81°03'44"W		21	61		17		
F	Allopatry <i>P. electromorphus</i>	40°00'11"N	81°43'03"W		19	36		17		
G	Allopatry <i>P. electromorphus</i>	40°09'04"N	81°35'02"W	105	9	156		8	19	24
H	Sympatry	40°10'01"N	82°15'28"W	58, 28	22, 17	147, 62		20, 15		25, 24
I	Sympatry	40°11'27"N	82°26'38"W		22, 3	37, 3		18, 3		
J	Sympatry	40°21'05"N	82°08'21"W	17, 4	14, 2	16, 4	17, 4	13, 2		
K	Sympatry	40°26'48"N	81°25'45"W	17, 5	16, 4	16, 5	17, 5	15, 4		
L	Sympatry	40°46'04"N	80°43'33"W	46, 2	8, 1	44, 8	46, 2	8, 1		
M	Sympatry	40°49'48"N	80°49'19"W	79, 6	42, 23	89, 34	79, 6	39, 21		

Specimens were then optimally aligned using a Generalized Procrustes Analysis (GPA; Rohlf and Slice, 1990), and size-standardized shape variables were obtained as partial warp scores from the thin-plate spline (Bookstein, 1991) and the two uniform components (Rohlf and Bookstein, 2003).

We used multivariate analysis of variance (MANOVA) to assess variation in head shape with species, environment type (allopatry or sympatry), and species \times environment interaction as factors. We then compared the degree of phenotypic divergence in sympatry to what was expected based on differences between allopatric localities. For this, we first obtained the phenotypic means for each species-locality group and calculated the Euclidean distance between *P. cinereus* and *P. electromorphus* for each of the six sympatric localities. We then obtained the phenotypic divergence between species for all possible pairings of allopatric localities and compared the observed divergence values in each sympatric locality to the distribution of phenotypic divergence values among the allopatric localities to determine whether sympatric morphological divergence was within the range for allopatric localities. In a MANOVA, the numerical df are related to the number of variables. In this study, the number of shape variables was 16. For the overall

model df, numerical df are calculated as (no. of groups \times [no. of levels of Factor 1 – 1] – [no. of levels of Factor 2 – 1]) \times no. of variables. In our analysis, the overall model df = (4 \times [2 – 1] – [2 – 1]) \times 16 = 32. For each factor, the df is calculated as the (no. of levels of each factor – 1) \times no. of variables. For our analysis, each factor df = (2 – 1) \times 16 = 16.

Associations Among Morphology and Food Use, Climate, and Behavior

We used two-block partial least squares (PLS) analysis (Rohlf and Corti, 2000) to examine the association between head shape and food use (for those specimens for which both data types were available; Table 1). Then we obtained 19 climatic variables (Appendix) from the WORLDCLIM data set (Hijmans et al., 2005) using the software DIVA-GIS (Hijmans et al., 2004) and quantified the multivariate relationship between mean head-shape and climate across localities using two-block PLS (all specimens that were used for the head shape analyses were also used for this analysis; Table 1). Further, we assessed the association between head shape and behavior using two-block PLS (Table 1). For this analysis, we used a subset of specimens for which both morphology and behavior had been quantified. We had previously recorded aggressive and submissive behaviors for other studies (Deitloff et

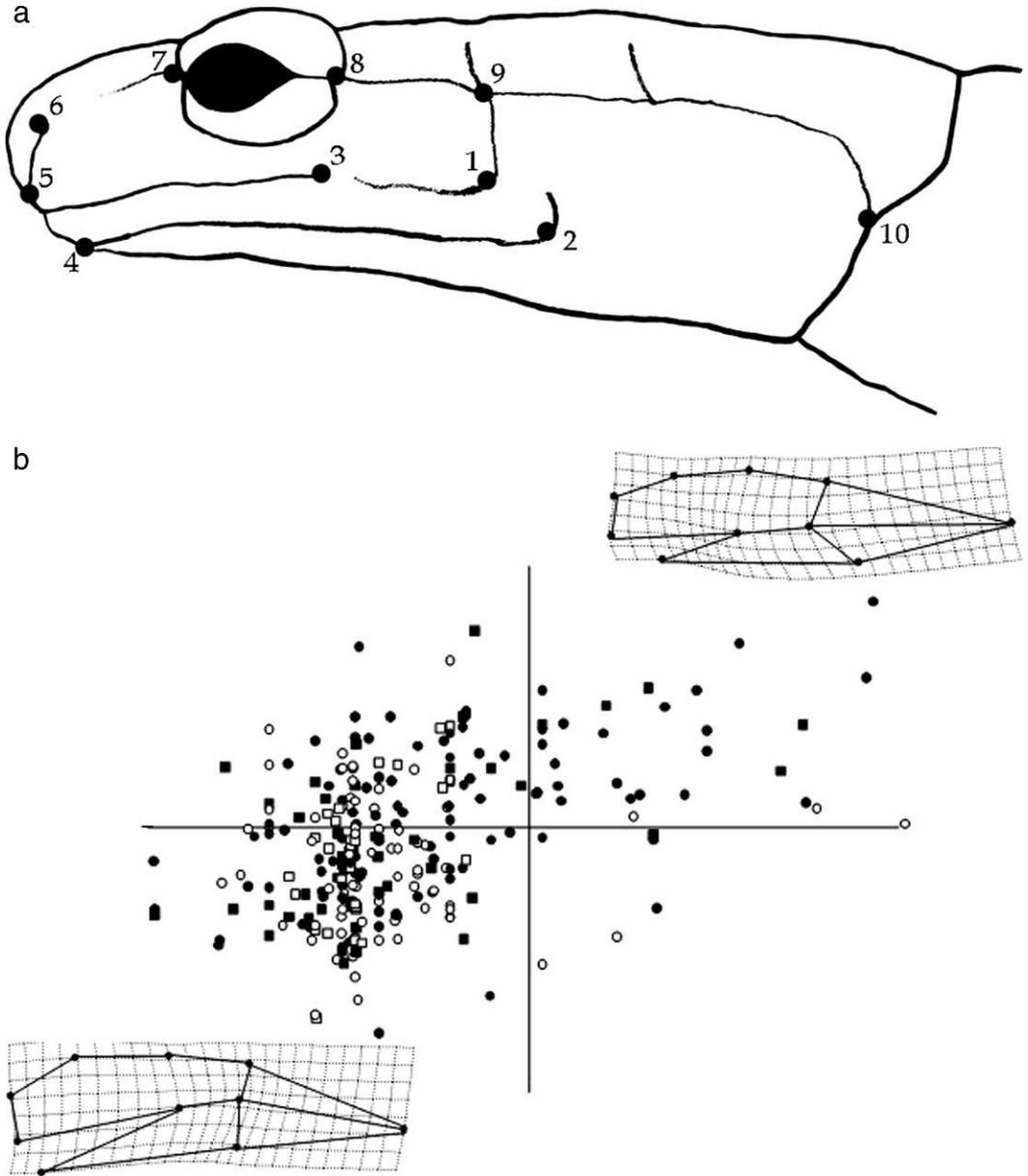


FIG. 1.—(a) Positions of 10 landmarks used in this study. All landmarks were digitized from the left-lateral view of the head (adapted from Adams, 2004). (b) Multivariate association of head shape and food utilization. The X-axis represents food use and the Y-axis represents morphology (extremes illustrated by using thin-plate spline). Open circles represent allopatric *Plethodon cinereus*, closed circles represent sympatric *P. cinereus*, open squares represent allopatric *P. electromorphus*, and closed squares represent sympatric *P. electromorphus*. Individuals represented towards the left, lower end consumed more prey from Acarina and Coleoptera but few prey from Annelida; individuals shown in the right, upper area consumed fewer prey from Acarina and Coleoptera and more prey from Annelida.

TABLE 2.—Pairwise food-use overlap and morphological divergence between species of *Plethodon* for each sympatric locality and all possible pairs of allopatric localities. None of the pairwise overlap values for sympatric localities were outside of the range of overlap values for pairs of allopatric locations. For morphology, divergence at I and K were greater than divergence for all allopatric pairs (denoted by °), and divergence at H and M were less than allopatric pairings (denoted by †). Food-use data were not collected for D; L was excluded from food-use overlap due to low sample size.

Sympatric locality	Food-use overlap	Divergence	Allopatric localities	Food-use overlap	Divergence
H	0.95	0.011 [†]	A and F	0.65	0.036
I	0.45	0.047 [°]	A and G	0.55	0.029
J	0.8	0.042	B and F	0.99	0.029
K	0.87	0.062 [°]	B and G	0.9	0.035
L		0.035	C and F	0.43	0.030
M	0.73	0.018 [†]	C and G	0.48	0.042
			D and F		0.025
			D and G		0.030
			E and F	0.98	0.022
			E and G	0.9	0.033
Average	0.76	0.036		0.74	0.031
Range	0.45–0.95	0.011–0.063		0.43–0.99	0.022–0.042

al., 2008, 2009). To understand the association between head shape and behavior, we examined all behaviors simultaneously as well as separately for each individual behavior. All statistical analyses were performed in JMP Version 7 (SAS Institute Inc., 2007), or R 2.10.1 (R Development Core Team, 2010). All specimens were deposited in the Cleveland Museum of Natural History.

RESULTS

Resource Use: Food Use and Refuge Sites

Some specimens either did not contain any prey items in their stomachs or the prey items were too digested to identify ($n = 48$); therefore, we had stomach content data for 287 salamanders (Table 1). The most commonly found prey items in the diets of *P. cinereus* and *P. electromorphus* were Hymenoptera, Acarina, and Coleoptera. Interestingly, at all sympatric locations, Collembola was found in stomachs of *P. cinereus*, but was not found in the stomachs of *P. electromorphus*. Overall, the two species displayed significantly greater niche overlap than was expected by chance ($O = 0.52$; $P < 0.0001$). When we compared overlap values in areas of sympatry versus all pairwise combinations of allopatric localities, we found that the overlap values of sympatric localities were all within the range of the paired allopatric localities but that overlap was variable between sympatric localities

(Table 2). Correspondence analysis revealed that overlap in food use was variable but was generally high at most sympatric localities.

Rocks with more than one salamander underneath were not larger than rocks with only one salamander ($X_I = 478.87$; $X_{>I} = 675.92$; $t = 1.57$; $P = 0.14$). For rocks and logs with one individual underneath, we did not find an overall difference between species in the use of rocks versus logs ($O = 0.94$; $P = 1.0$). Furthermore, the two species did not differ in the size of rocks used ($\bar{X}_c = 479.1$; $X_e = 475.8$; $t = 0.045$; $P = 0.96$). We found no correlation between SVL and rock size ($r^2 = 0.001$; $P = 0.69$) for rocks with one salamander underneath.

Morphology

We found significant phenotypic differentiation in head shape between species (Wilk's $\lambda = 0.87$, $F_{32,1808} = 8.53$, $P < 0.0001$) and between environments (Wilk's $\lambda = 0.87$, $F_{16,904} = 8.55$, $P < 0.0001$), as well as a significant species \times environment interaction (Wilk's $\lambda = 0.90$, $F_{16,904} = 6.17$, $P < 0.0001$). When comparing divergence in head shape at each sympatric locality to divergence of paired allopatric localities, we found that divergence in two sympatric localities (I and K) was greater than in any of the paired allopatric localities. Further, in two localities (H and M) divergence was less than any of the allopatric pairs, while in two other localities (J and L)

divergence fell within the range of the allopatric pairs (Table 2). Sympatric localities varied greatly in the divergence of head shape between *P. cinereus* and *P. electromorphus*, both in the amount of phenotypic divergence (Table 2) as well as in its direction in morphospace (as revealed by principal components analysis). Similar to the pattern of diet, morphological differentiation in sympatry was locality-specific.

Associations Among Morphology and Food Use, Climate, and Behavior

Two-block PLS revealed that head shape was significantly associated with food utilization in *P. cinereus* and *P. electromorphus* ($r = 0.46$; $P = 0.0015$; Fig. 1B). In general, individuals from all species-locality groups are found across the entire PLS plot, with the exception of allopatric *P. electromorphus* (F and G), which is slightly restricted along the food-use axis (X-axis; Fig. 1B). In addition, head-shape change described above is linked with food-use differences: individuals with longer lower jaws and shorter posterior regions of the skull tend to eat more prey from Acarina and Coleoptera and fewer prey from Annelida than do individuals with shortened lower jaws and expanded posterior regions of the skull (other prey types showed no strong trends with head shape; Fig. 1B).

We also tested whether head shape was associated with climate and found no association between those variables ($r = 0.72$; $P = 0.29$). In addition, head shape was not associated with behavior when all the behaviors (all trunk raised, flattened posture, biting, and edging) were tested as one matrix in either of the previous behavior studies (Deitloff et al., 2008: $r = 0.49$, $P = 0.56$; Deitloff et al., 2009: $r = 0.40$, $P = 0.38$). However, when behaviors were tested separately, we found that all trunk raised (ATR) during the 2009 data (Deitloff et al., 2009) was associated with head shape ($r = 0.39$; $P = 0.04$), but all other associations between behavior variables and head shape were not significant (results not shown).

DISCUSSION

Previous work examining pattern and process of ecological characteristics of *Plethodon*

species have shown that competition between species is important in shaping many communities (Jaeger, 1970; Hairston, 1980a; Adams, 2007; Arif et al., 2007; Deitloff, 2011). Despite this, we did not find support for our first prediction that *P. cinereus* and *P. electromorphus* exhibited resource partitioning of food types in sympatry as compared to food use in allopatry. In contrast to our prediction, these two species overlap significantly in diet. When sympatric localities were examined individually, we found that variability existed in the amount of food-use overlap between localities, but this variability was within the range of differences seen in paired allopatric localities. Our second prediction, that *P. cinereus* and *P. electromorphus* partitioned cover objects in sympatry, was also not supported. Thirdly, we examined morphological differences between the species in allopatric and sympatric localities and found that, in general, character displacement did not occur. Interestingly, we found variability in the amount of morphological divergence between sympatric localities: at some sympatric locations *P. cinereus* and *P. electromorphus* exhibited morphological character divergence in head shape, but at other sympatric localities morphological convergence occurred. Furthermore, we found evidence in this study that morphology correlates with food use and with aggressive behavior (e.g., ATR) but not with climate (overall for all localities). Thus, our results reveal that *P. cinereus* and *P. electromorphus* exhibit morphological character divergence at some sympatric locations and that morphology is associated with aggressive behavior in these species.

Our study reveals a complex pattern of morphological, behavioral, and resource use variation across the landscape, wherein these two potentially competing species are similar in some phenotypic attributes in some geographic localities but not in others. Several ecological mechanisms could explain this pattern, such as differences in the level of interspecific aggression or utilization of resources across the landscape which could generate a mosaic of selection pressures at different localities. Other *Plethodon* communities display variation in the degree of resource overlap between coexisting species,

with some species partitioning prey items when found in sympatry (e.g., *P. cinereus* and *P. hoffmani*: Adams, 2000; Adams and Rohlf, 2000) while other species do not (e.g., Hairston, 1983). In addition, the species studied here do not consistently partition ecological resources when they come into contact. These factors alone may not be sufficient to determine species co-existence in *Plethodon* communities.

Differences in the local climatic environment, or other historical or contingent processes, may also play a role in generating the distinct patterns of morphological differences observed here. Our analysis of climatic characteristics revealed that climatic variation was not associated with patterns of morphological variation across localities. Nevertheless, the broad-scale climatic characteristics used in this study may not account for environmental differences observed at finer spatial scales that may be associated with morphological differences (e.g., Jastrebski and Robinson, 2004; Berner et al., 2008). In addition, historical processes could also contribute to these patterns, such as the time since the northwest expansion of both species into their current ranges in Ohio after the retreat of the Wisconsin glaciation (Highton, 1999). From an evolutionary standpoint, the contact areas studied here may be relatively new and, thus, the time for these communities to reach equilibrium may have been insufficient. If this scenario is the case, the contemporary patterns we observed provides a snapshot of the evolutionary process and may show inconsistent patterns across localities, despite the fact that similar ecological processes may be occurring. Interestingly, other *Plethodon* systems show similar context-specific responses to ecological interactions across localities (Adams et al., 2007), and our work suggests that such historical contingency may be more prevalent in *Plethodon* more broadly.

Contrary to previous research, where interspecific competition in *Plethodon* salamanders has resulted in similar patterns of morphological evolution across localities in some species (Adams and Rohlf, 2000; Adams, 2010; but see Adams et al., 2007), the patterns observed in this study reveal that the morphology of *P.*

cinereus and *P. electromorphus* is divergent in some sympatric areas but convergent in others. Further, our findings suggest that the interplay between biotic and abiotic factors varies from locality to locality, resulting in a mosaic pattern of phenotypic and behavioral variation across the landscape. Interspecific competition in *Plethodon* salamanders has resulted in similar patterns of morphological evolution across localities in some species (Adams and Rohlf, 2000; Adams, 2010; but see Adams et al., 2007). Our results, therefore, provide an interesting counterexample in that the morphological shifts observed at different sympatric locations are not consistent in this system. This leads to further questions about what factors at each sympatric locality contribute to these differing outcomes.

The distribution, persistence, behavior, and morphological patterns of *Plethodon* salamanders used in this and past studies suggest that these communities respond in complex ways to various ecological pressures. These results suggest that the interplay between distinct selective forces of interspecific interactions and adaptation to local environmental conditions has resulted in unique evolutionary outcomes in different sympatric localities. Alternatively, we are observing populations that are still changing and adjusting to environmentally new conditions during the time since the last glacial period.

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APPENDIX

Climatic Variables (WORLDCCLIM database: Hijmans et al., 2005)

Abbreviation	Climatic variable
Bio1	Annual mean temperature
Bio2	Mean diurnal temperature range (mean of monthly maximum temperature minus mean minimum temperature)
Bio3	Isothermality (BIO2/BIO7°100)
Bio4	Temperature seasonality (standard deviation of monthly temperature)
Bio5	Max temperature of warmest month
Bio6	Min temperature of coldest month
Bio7	Temperature annual range (BIO5-BIO6)
Bio8	Mean temperature of wettest quarter
Bio9	Mean temperature of driest quarter
Bio10	Mean temperature of warmest quarter
Bio11	Mean temperature of coldest quarter
Bio12	Annual precipitation
Bio13	Precipitation of wettest month
Bio14	Precipitation of driest month
Bio15	Precipitation seasonality (coefficient of variation)
Bio16	Precipitation of wettest quarter
Bio17	Precipitation of driest quarter
Bio18	Precipitation of warmest quarter
Bio19	Precipitation of coldest quarter