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VARIATION IN THE ANTIPREDATOR RESPONSES OF THREE SYMPATRIC PLETHODONTID SALAMANDERS TO PREDATOR-DIET CUES

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ABSTRACT: Organisms may reduce the risk of predation by responding to chemical cues from predators. Recent research shows that many species vary their antipredator response depending on the diet of the predator. We examined the responses of three plethodontid species of salamander (*Plethodon cinereus*, *Eurycea bislineata*, and *Desmognathus ochrophaeus*) to chemical cues from a shared snake predator (*Thamnophis sirtalis*). At the time of the study, *Eurycea bislineata* showed overlap in habitat with *Plethodon cinereus* and *Desmognathus ochrophaeus*, but *Plethodon cinereus* and *Desmognathus ochrophaeus* showed no overlap with one another. Each salamander species was presented with chemical cues from snakes fed *Desmognathus ochrophaeus* (TS_{Do}), *Eurycea bislineata* (TS_{Eb}), and *Plethodon cinereus* (TS_{Pc}). *Plethodon cinereus* avoided both TS_{Pc} and TS_{Eb}, whereas *Eurycea bislineata* avoided only TS_{Eb}. Conversely, *Desmognathus ochrophaeus* did not avoid any cues from the predator, regardless of the diet of the snake. When we analyzed activity data, we discovered that *Plethodon cinereus* showed higher activity levels when exposed to TS_{Pc} than to the other cues. Individual *Eurycea bislineata* did not vary their activity to the three treatments. Lastly, *Desmognathus ochrophaeus*, which did not avoid any of the cues from the predator, were more active in response to TS_{Do} and TS_{Eb} than to TS_{Pc}. These results show that phylogenetically related prey species may employ a variety of antipredator behaviors and suggest that discrimination of predator diet-cues may be linked to the degree of microhabitat overlap among the different prey species at the time of our study. Our study also highlights the importance of using multiple response variables when examining antipredator behavior.

Key words: Chemical cues; *Desmognathus ochrophaeus*; *Eurycea bislineata*; *Plethodon cinereus*; Predator diet; Predator-prey

SOME organisms reduce the risk of predation by responding to predation-related chemicals in their environment (Chivers and Smith, 1998; Kats and Dill, 1998; Weldon, 1990). The use of chemical cues to assess the threat of predation has advantages over other sensory modalities (e.g., visual, auditory, tactile cues) in many environmental contexts (Bradbury and Vehrencamp, 1998; Wilson, 1975). For instance, prey can rely on chemical cues to detect predators when visual cues are obscured or eliminated, such as at night or in turbid aquatic environments (Smith, 1992). In addition, unlike most visual and acoustic stimuli, chemical cues deposited on substrates can convey information to prey in the absence of predators, which may be important if predators show fidelity to certain foraging sites.

An interesting aspect of chemically mediated predator-prey interactions is the occurrence of cross-species antipredator responses. These may occur when prey respond to damage-released cues from heterospecifics (Sullivan et al., 2003) or to cues from individual predators recently foraging on heterospecific prey (Sullivan et al., 2004). Sensitivity to a broad range of predation-related cues may increase the likelihood of survival by increasing the information available from predation events. Cross-species antipredator responses may have evolved as a result of the phylogenetic relatedness and/or ecological relatedness of prey in the diet of a predator (Chivers et al., 1997; Chivers and Mirza, 2001*a*). Phylogenetic relatedness states that cross-species responses are due to the homology of alarm cues among closely related species (e.g., the ostariophysan fishes; Brown et al., 2000; Smith, 1992). Ecological relatedness refers to the recognition of predation-related cues from syntopic members of the same prey guild that may or may not be closely related. Few studies of cross-species antipredator responses exist among terrestrial organisms, although studies suggest that salamanders are capable of responding to predation-related cues from heterospecifics (Chivers et al., 1997; Lutterschmidt et al., 1994; Sullivan et al., 2003).

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Prey sensitivity to chemical cues associated with predation appears to be highly refined, especially with regard to the diet of a predator (Chivers and Mirza, 2001*a*). For example, some prey species increase their antipredator response to individual predators that have recently foraged on conspecific prey (Belden et al., 2000; Madison et al., 1999*a*,*b*; Persons et al., 2001; Venzon et al., 2000). Sensitivity of prey to predator diet has been examined at length in aquatic vertebrates, especially fishes (Brönmark and Pettersson, 1994; Brown et al., 1995; Mathis and Smith, 1993) and larval amphibians (Chivers and Mirza, 2001*b*; Laurila et al., 1997; Wildy et al., 1999; Wilson and Lefcourt, 1993), but has received less attention among terrestrial vertebrates (Madison et al., 1999*a*,*b*; Murray and Jenkins, 1999).

Salamanders belonging to the family Plethodontidae are good models for investigating chemically mediated discrimination of a predator's diet because members of this family respond to chemical cues from predators in laboratory and field trials (Cupp, 1994; Madison et al., 1999*a*,*b*; Maerz et al., 2001; McDarby et al., 1999; Sullivan et al., 2002; Sullivan et al., 2004), and at least one species, *Plethodon cinereus*, is known to discriminate among garter snakes (*Thamnophis sirtalis*) feeding on different prey (Madison et al., 1999*b*; Madison et al., 2002; Murray and Jenkins, 1999; Sullivan et al., 2004). To what degree ecological and phylogenetic relatedness between salamanders influence the discrimination of predator diets is unknown.

To examine how phylogenetic and ecological relatedness among prey contribute to the discrimination of predator diet cues, we studied the anti-predator responses of three sympatric, and seasonally syntopic plethodontid salamanders (Brodie, 1981; MacCullogh and Bider, 1975): red-backed salamanders (*Plethodon cinereus*), northern two-lined salamanders (*Eurycea bislineata*), and Allegheny mountain dusky salamanders (*Desmognathus ochrophaeus*). We exposed individuals of each salamander species to chemical cues from a common predator (garter snakes, *Thamnophis sirtalis*; Hamilton, 1951; Rossman et al., 1996) maintained on diets consisting of each salamander species. At the time of our study, the three salamander species occupied a gradient of habitats from semi-aquatic to fully terrestrial. We predicted that each of the salamander species would be capable of discriminating among snake chemical cues based on the diet of the snake and that the antipredator response of salamanders to predator diet cues would be positively correlated with the degree of microhabitat overlap among the salamander prey species.

Methods

Collection and Maintenance of Study Animals

We collected adult *P. cinereus*, *E. bislineata*, and *D. ochrophaeus* along Bunn Hill Creek in the Binghamton University Natural Area (Broome County, New York) in May 2001. *Desmognathus ochrophaeus* were located beneath rocks within stream margins (some partially submerged in water); *E. bislineata* occupied rock shelters from the stream margin into the adjacent woodlands; and *P. cinereus* occupied terrestrial woodland habitats >20 m from the stream. Salamanders were housed individually in 15-cm diameter petri dishes lined with moistened paper towels at 15 C and maintained on a 15L:9D photoperiod. At the conclusion of the experiment, each salamander was released to its respective capture site.

We collected three adult female *T. sirtalis* from the Binghamton University Nature Preserve (Broome County, New York) in May 2001 and housed them individually in 38-l glass aquaria with crumpled paper towels for cover and water provided *ad libitum*. Snakes were housed separately from salamanders, were given access to direct sunlight, and were maintained at ambient temperature (approximately 25 C) and 15L:9D photoperiod.

Collection of Predator Cues

We maintained the three adult female *T. sirtalis* on: *P. cinereus* (TS_{Pc}), *E. bislineata* (TS_{Eb}), or *D. ochrophaeus* (TS_{Do}) for 2 wk. For collection of stimuli, we fed each snake six salamanders in one sitting and then immediately transferred the snakes to 4-l beakers and covered the beakers with cheesecloth. After 72 h, we returned snakes to their home aquarium and rinsed each beaker with 200 ml of distilled water. The rinses were passed through a 0.45-μm filter to remove solid particles, rapidly frozen in liquid nitrogen,

and stored in a freezer until use. Previous research has shown that salamanders respond to snake rinse that has been frozen using this method in the laboratory and field (Sullivan et al., 2002). Before using the predator stimulus in behavioral trials, we thawed each aliquot and diluted it with an equivalent volume of distilled water. Although only one garter snake was used for each treatment, previous research has shown that the response of *P. cinereus* to snake chemical cues does not appear to be specific to individual *T. sirtalis* (Madison et al., 1999a; Madison et al., 2002). Therefore, we assumed that any treatment differences were a result of snake diet and not of individual differences in snake chemistry.

Experimental Protocol

To examine salamander responses to the different predator diet stimuli, we modified the experimental methodology from Madison et al. (1999*a*,*b*). In brief, we placed two filter paper semicircles on opposite sides of a 15-cm petri dish while maintaining a 3-mm gap between each semicircle. We used a 10-ml tuberculin syringe to add 1.5 ml of a predator diet treatment to one side and water to the other. The location of each treatment dish and its orientation (right or left) and each subject (species) were randomly distributed on an 8×7 grid on the floor of our test room. Fifty-four different salamanders (18 of each species) were tested each night for six nights. Species and treatments were randomly stratified over the six nights so that six salamanders of each species were exposed to each of the three treatments per night for a total of 36 replicates per treatment per species. We transferred each salamander from its home dish to the assigned experimental dish with a cotton swab and then placed a 15-mm collar of gray paper around the dish to visually isolate each salamander. After all salamanders were distributed (approximately 15 min), the lights were turned off and the trial was recorded for 60 min in complete darkness with a video camera sensitive to infrared light. Conducting trials in total darkness eliminates visual biases and forces salamanders to select substrates using only nonvisual cues. We began recording trials at 2400 h each night because *P. cinereus* are most responsive to snake diet at this time and do not discriminate among snake diets during the day.

Data Collection and Statistical Analyses

For each laboratory trial, we recorded the side occupied by each salamander every 3 min for 1 h including the initial position. If a salamander straddled the 3-mm gap, the side with more than half of the individual was considered the occupied side. We chose this criterion, instead of the location of the sensory organs, because conceivably an individual could "freeze," an antipredator response shown by red-backed salamanders (Brodie et al., 1974; Madison et al., 1999*a*), when it detects a predator cue on one of the filter papers. In such a scenario, the sensory receptors of red-backed salamanders can be over the predator substrate and therefore show a "preference" for the predator side, but the body of the individual may be predominantly on the control side, indicating a more accurate negative response to the alarm substance. We added the number of times each salamander was located on the substrate with the predator diet treatment out of 21 total observations. We considered a salamander that was located on the treatment substrate $\leq$10 times out of 21 observations as "avoiding" the treatment and $\geq$11 times as being "attracted" to the treatment. Laboratory responses of red-backed salamanders tend to be bimodally distributed as described in Madison et al. (1999*a*) and Sullivan et al. (2003), so we used the Chi-square goodness-of-fit test to determine whether the number of salamanders that avoided the treatments differed significantly from random expectation (Sokal and Rohlf, 1995).

We also estimated the relative effect of each predator diet treatment on the activity of each salamander species through time. Comparisons of activity levels were made among the different diet cue treatments. We measured activity during five consecutive intervals of 12 min by counting the number of times that individuals crossed the 3-mm gap separating the treatments. To test for the effects of salamander species, snake diet, and time on activity, we conducted a 3-way, repeated-measures ANOVA with night of the trial as a blocking variable. We then conducted post-hoc multiple comparison tests using Tukey's HSD when main effects were significant.

TABLE 1.—Chi-square goodness-of-fit comparisons of the number of salamanders of three species that avoided or were attracted to the chemical cues from *Thamnophis sirtalis* fed *Plethodon cinereus* (TS_{Pc}), *Eurycea bislineata* (TS_{Eb}), or *Desmognathus ochrophaeus* (TS_{Do}).

Species	Treatment	No. of salamanders		χ^2	P
		Avoided	Attracted		
Plethodon cinereus	TS_{Pc}	26	10	7.11	0.008
	TS_{Eb}	24	12	4.00	0.045
	TS_{Do}	22	14	1.78	0.182
Eurycea bislineata	TS_{Pc}	18	18	0.00	1.000
	TS_{Eb}	25	11	5.44	0.020
	TS_{Do}	20	16	0.44	0.505
Desmognathus ochrophaeus	TS_{Pc}	20	16	0.44	0.505
	TS_{Eb}	18	18	0.00	1.000
	TS_{Do}	20	16	0.44	0.505

To test the hypothesis that the activity of test salamanders would be correlated with the degree of microhabitat overlap among heterospecifics species, we ranked the hypothetical risk represented by the heterospecific diets based on the degree of microhabitat overlap. For red-backed salamanders, TS_{Do} represented the lowest risk because there was essentially no habitat overlap between red-backed and dusky salamanders at the time of the study, and the TS_{Eb} treatment represented the greatest risk because two-lined salamanders occupied terrestrial and aquatic habitats with similar frequencies. For dusky salamanders, TS_{Pc} represented the lowest risk, and TS_{Eb} represented the greatest risk for reasons stated above. Because two-lined salamanders occupied aquatic and terrestrial habitats, we used a finer spatial scale to assign hypothetical risk values. We assigned TS_{Pc} the highest value because 43% of the two-lined salamanders used in this study were found under the same cover rocks as *P. cinereus*, whereas no *E. bislineata* were found cohabiting with dusky salamanders, so we predicted that snakes preying on *P. cinereus* may represent a greater threat to two-lined salamanders. We used these ranks in Spearman rank order correlation tests to determine whether activity responses (mean of the five time intervals) were correlated positively with the degree of microhabitat overlap between the test species and the species used in each snake diet. STATISTICA data analysis software was used for all statistical analyses (StatSoft, Inc., 2001).

RESULTS

Red-backed salamanders significantly avoided TS_{Pc} and TS_{Eb}, but were indifferent to TS_{Do} (Table 1). Two-lined salamanders avoided TS_{Eb}, but were indifferent to both TS_{Pc} and TS_{Do} (Table 1). Lastly, dusky salamanders did not avoid any of the diet treatments from the predator (Table 1).

Repeated-measures ANOVA showed significant main effects of trial day, predator diet, time interval, and species on salamander activity (Table 2). There were also significant time × diet, time × species, and species × diet interactions (Table 2). When considering overall activity for all treatments combined, two-lined salamanders were most active (Tukey's HSD: *E. bislineata* versus *D. ochrophaeus*, $P < 0.001$; *E. bislineata* versus *P. cinereus*, $P < 0.001$), red-backed salamanders were least active (Tukey's HSD: *P. cinereus* versus *D. ochrophaeus*, $P < 0.001$),

TABLE 2.—Repeated-measures analysis of activity for each salamander species exposed to three predator diet treatments (TS_{Pc}, TS_{Eb},TS_{Do}) during five 12-min time intervals. Trial day was used as a blocking variable.

Factor	SS	df	MS	F	P
Trial day	849.34	5	169.87	5.33	<0.001
Species	24,649.30	2	12,324.65	386.75	<0.001
Predator diet	195.93	2	97.97	3.07	0.048
Species × Predator diet	538.26	4	134.57	4.22	0.002
Error	9878.88	310	31.87		
Time	11,189.38	4	2797.34	388.73	<0.001
Time × trial	456.25	20	22.81	3.17	<0.001
Time × species	6365.95	8	795.74	110.58	<0.001
Time × diet	138.28	8	17.28	2.40	0.014
Time × species × predator diet	134.23	16	8.39	1.17	0.289
Error	8923.11	1240	7.20		

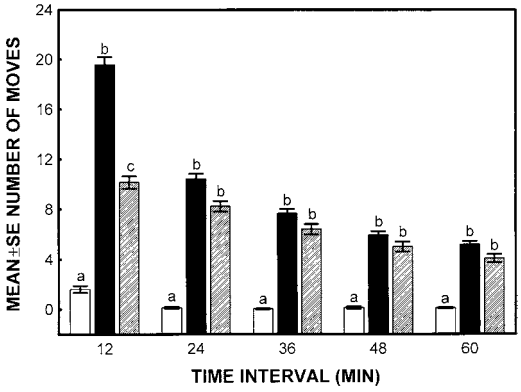


FIG. 1.—Overall activity scores for *Plethodon cinereus* (□), *Eurycea bislineata* (■), and *Desmognathus ochrophaeus* (▨) obtained by combining the responses to the different snake diet treatments. Activity scores are the average number of times that individual salamanders crossed the midline of test dishes at 12-min intervals. Letters indicate significant differences among responses to predator diet treatments at each time interval using Tukey's HSD paired comparisons with α adjusted for multiple comparisons.

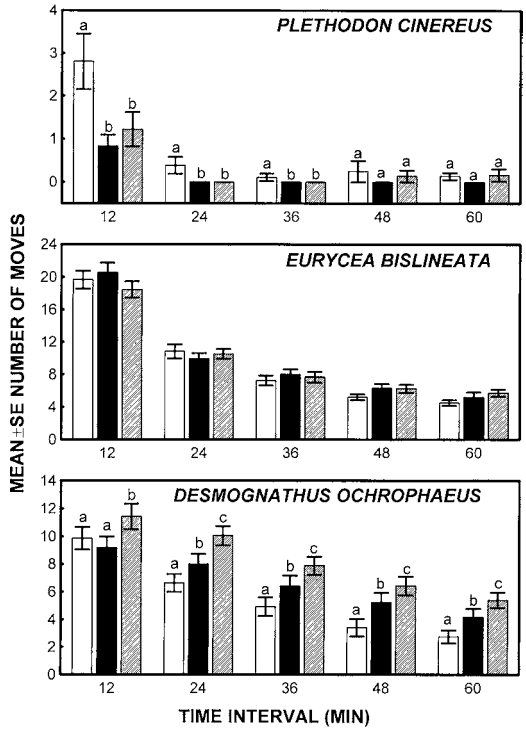


FIG. 2.—Separate activity scores of three salamander species exposed to chemical cues from *Thamnophis sirtalis* fed *Plethodon cinereus* (□), *Eurycea bislineata* (■), or *Desmognathus ochrophaeus* (▨). Activity scores are the average number of times that individual salamanders crossed the midline of test dishes at 12-min intervals. Letters indicate significant differences among responses to predator diet treatments at each time interval using Tukey's HSD paired comparisons with α adjusted for multiple comparisons.

and activity levels for all species decreased over time (Fig. 1). The difference in activity between two-lined salamanders and dusky salamanders was driven primarily by differences during the first time interval, after which their activity was similar (Fig. 1). In addition, prey species tended to exhibit higher activity levels when exposed to snakes feeding on conspecifics. During the first three time intervals, red-backed salamanders were more active when exposed to TS_{Pc} relative to TS_{Eb} and TS_{Do}. Red-backed salamanders did not distinguish between TS_{Eb} and TS_{Do} with relative changes in activity (Fig. 2). Dusky salamanders were significantly more active when exposed to TS_{Do} versus the other diet treatments, and maintained activity differences between snakes fed heterospecific salamanders throughout the trial. In addition, their response to TS_{Eb} was intermediate to TS_{Do} and TS_{Pc} (Fig. 2). The activity level of two-lined salamanders was equivalent among the different diet treatments (Fig. 2).

The overall activity (combined for all time intervals) was not correlated significantly with the degree of habitat overlap with prey for red-backed salamanders ($r = -0.153$; $P = 0.200$), dusky salamanders ($r = 0.164$; $P = 0.169$), or two-lined salamanders ($r = -0.047$; $P = 0.696$).

DISCUSSION

Our results showed that all three salamander species performed antipredator behaviors when they were exposed to chemical cues from predators. Our results are consistent with previous studies that show that salamanders respond to damage-released cues (Chivers et al., 1997; Lutterschmidt et al., 1994; Sullivan et al., 2003) and predator diet cues (Madison et al., 1999; Sullivan et al., 2004). However, the lack of association between avoidance and activity among these species, such that differential avoidance between any two species was not necessarily accompanied by a difference in activity, was unexpected. As such, this work revealed an important caveat regarding conclusions about antipredator responses obtained from single traits. Had we considered

avoidance or activity response only, our interpretations of these data would be much different and the ability of some of these species to discriminate and differentially respond to predator diet cues would not have been detected. It is likely that the range of responses used by these salamanders are species specific and could be influenced by microhabitat selection, familiarity with other members of the salamander community, and fluctuating levels of predation risk (Chivers et al., 1997).

Our study does not provide conclusive evidence supporting the phylogenetic relatedness hypothesis. While the observed antipredator responses to predation-related cues from conspecifics are consistent with this hypothesis, the responses to cross-species cues are not. For example, red-backed salamanders and two-lined salamanders belong to the sub-family, Plethodontinae, whereas dusky salamanders belong to the sub-family Desmognathinae. Based on the hypothesis that homology of the chemical cues exists among more closely related species, we would predict test salamanders to respond more strongly to cues from snakes fed prey from the same sub-family. Instead, we see that two-lined salamanders do not appear to respond to cues from predators foraging on red-backed salamanders (same sub-family), and dusky salamanders differentially respond to TS_{Eb} versus TS_{Pc}, although both of these prey species belong to the same subfamily.

We feel that the balance of the behavioral data supports ecological relatedness rather than phylogenetic relatedness as the primary mechanism contributing to the observed pattern of antipredator responses. Even though the total activity of salamanders was not correlated with the degree of habitat overlap among prey, the overall responses do appear to be consistent with habitat overlap among test species. Red-backed salamanders respond to both TS_{Pc} and TS_{Eb} which we would predict given that red-backed and two-lined salamanders are seasonally syntopic, so a predator foraging on each species could represent an equivalent threat. The lack of response to TS_{Do} could be due to minimal exposure to dusky salamanders during this time of year, and so may not represent the same level of predation risk. Dusky salamanders exhibited a gradient of activity from TS_{Do} (highest) to TS_{Pc} (lowest), which also is consistent with the degree of habitat overlap among these species. Two-lined salamanders did not differentially respond to snakes fed heterospecific salamanders, but given that two-lined salamanders are likely to encounter red-backed and dusky salamanders because of their overlapping distributions at our study site, it seems plausible that two-lined salamanders are responding to all three snake-diet cues with an increase in activity. Without a treatment to assess baseline activity levels, we can only speculate that this is the case until further studies are conducted.

The results of this study show clear differences in the responses of three confamilial salamanders to predators maintained on different diets, and suggest factors that may contribute to the discrimination of predator diet cues including seasonal movements and fluctuations in predation pressure (e.g., MacCullogh and Bider, 1975). Based on our observations, it seems likely that phylogenetic and ecological relatedness work in concert to produce individuals capable of cue fine-scale discrimination of predator cues. A study of these confamilial prey species throughout the year may detect shifting antipredator behaviors as implicated in previous work showing that seasonal distributions and climatic factors may influence antipredator responses (Hileman and Brodie, 1994; Rohr et al., 2003).

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THE ROLE OF MUSCLE MASS AND TOOTH NUMBER IN ECOLOGICAL CHARACTER DISPLACEMENT BETWEEN *PLETHODON CINEREUS* AND *P. HOFFMANI* (CAUDATA: PLETHODONTIDAE)

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Evidence for ecological character displacement must include correlation between the morphological character in question and the function of that character in the organisms' environment. Examination of the cranial skeletons and jaw components of sympatric populations of *Plethodon cinereus* and *Plethodon hoffmani* correlate well with the sympatric shift in diet in these two species relative to their respective allopatric populations. This hypothesized relationship between cranial features and diet is consistent with ecological character displacement. A biomechanical model predicts a stronger, slower jaw in sympatric *P. cinereus* and a faster, weaker jaw in *P. hoffmani* relative to their respective allopatric populations. Inherent in this model is the assumption that no differences in the jaw muscles exist. Here we test this assumption using data on jaw muscle mass and tooth number in sympatric and allopatric populations of *P. cinereus* and *P. hoffmani*. Our findings indicate significant differences between species, but no consistent pattern of character displacement in these structures. We discuss the consistency of our data with the previously proposed biomechanical model and alternative hypotheses.

Key words: Character displacement; Dentition; Jaw muscle; *Plethodon*

CHARACTER displacement, or the modification of a characteristic (morphological or behavioral) due to interaction with a species occupying a similar ecological niche is one of the oldest and strongest concepts supporting the theory of natural selection (Arthur, 1982; Brown and Wilson, 1956; Darwin, 1859; Schluter, 2000). Examples of reproductive character displacement (characteristics under sexual selection) are thought to be more common than ecological character displacement (characteristics associated with resource acquisition or defense). Indeed, few examples of ecological character displacement have been studied in a thorough and convincing manner (see Losos, 2000; Schluter, 2000). A convincing argument for the occurrence of ecological character displacement requires evidence of a relationship between the apparent morphological change and the ecological function of the morphological characters in question (Arthur, 1982; Grant, 1975). Furthermore, other factors that might explain the morphological variation (sexual selection, clinal variation, chance, alpha selection, etc.) must be ruled out. The best supported examples of ecological character displacement examined

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multiple aspects of the biology of the organisms involved. Notable examples include beak shape in Darwin's Finches (*Geospiza* sp.: Grant, 1986; Schluter and Grant, 1984), bill size (and mating call) in Rock Nut-hatches (*Sitta* sp.: Grant, 1975) and body shape in three-spinned sticklebacks (*Gasterosteus* sp. Schluter and McPhail, 1992).

Evidence for character displacement between the salamanders *Plethodon cinereus* and *Plethodon hoffmani* is observed in general cranial shape and especially in features of the jaw bones (Adams, 2000; Adams and Rohlf, 2000). Furthermore, an ecological correlate for this character displacement was identified (Adams, 2000). Prey ingestion is partitioned when these two species occur in sympatry, and is associated with the change in head shape and jaw components (Adams and Rohlf, 2000). Additionally, a behavioral test for alpha selection as an alternative to ecological character displacement between these two species found no behavioral evidence for this alternative (Jaeger et al., 2002). Thus, all data (ecological, behavioral, and morphological) are consistent with the hypothesis of ecological character displacement.

Although character displacement has acted upon head shape in general in these species, the sympatric anatomical differences could be simplified to differences in the ratio of two bones: the squamosal and the dentary (Adams and Rohlf, 2000). Adams and Rohlf found significant differences in this ratio, and using simple biomechanical equations, hypothesized that these differences may be associated with the evolution of a stronger jaw in *P. cinereus* and a faster jaw in *P. hoffmani*. This hypothesis must be tested using functional morphological methods (e.g., kinematic studies) or by establishing a link between the jaw structure and performance. Inherent in jaw mechanics is jaw muscle function. An important assumption of the hypothesis of Adams and Rohlf (2000) is that there are no systematic differences in the muscles associated with jaw closure between allopatric and sympatric populations within species. Differences in muscle mass relate directly to power. So, two animals with an equivalent squamosal:dentary ratio but with different sized muscles would have bites of equivalent speed but of different power (Josephson, 1975). Here we present results of jaw mass measurements on sympatric and allopatric populations of *P. cinereus* and *P. hoffmani* in a test of the biomechanical hypotheses of Adams and Rohlf (2000).

Another important feature of jaw function that has been shown to vary with diet is tooth number and morphology (fish, Blabber et al., 1994; Lewis et al., 1999; primates, Ungar, 1998; amphibians, Regal, 1966; Wake and Wurst, 1979). While there is some evidence for intrafamilial variation in salamander tooth number with diet and season, data on interpopulation differences in tooth number in salamanders is limited (Coss, 1974; Highton, 1962; Stewart, 1958; Townsend et al., 1998). No previous study on teeth of the small species of Plethodontidae has simultaneously compared data on prey choice. Adams (2000) found that *P. cinereus* shift from a diet consisting of a broad range of prey sizes in allopatry to a diet of mainly smaller prey types when in sympatry with *P. hoffmani*. Likewise, the diet of *P. hoffmani* is restricted to prey of larger size classes when sympatric with *P. cinereus*. The morphometric data indicate differences in jaw element structure coincident with this diet shift and we predicted a change in tooth number as well.

The biomechanical hypothesis of Adams and Rohlf (2000), assuming equivalent muscle mass in sympatry and allopatry, predicts that *P. hoffmani* adopts a faster but weaker jaw in sympatry relative to allopatric populations, and field surveys indicate a coincident shift from a broad range of prey size to larger prey items. Here we test the hypothesis that a shift toward larger prey items requires an increased muscle mass to facilitate handling of larger prey by sympatric *P. hoffmani*. Likewise, in *P. cinereus*, the biomechanical model, assuming no change in jaw muscle mass, predicts a stronger but slower jaw, and field data indicate a shift in sympatry to small prey items relative to allopatric populations. We test the hypothesis that a shift toward smaller prey items by sympatric *P. cinereus* requires less muscle power relative to allopatric populations of *P. cinereus*. Further, given the scarcity of data on interpopulational variation on plethodontid dentition, we test the null hypothesis that tooth number is not affected by this shift in resource use in either species.

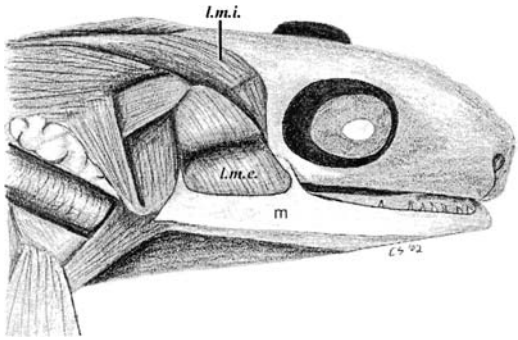


FIG. 1.—Illustration of the jaw muscles of *Plethodon cinereus*. *l.m.i.* = levator mandibularis internus, *l.m.e.* = levator mandibulae externus, m = mandible.

MATERIALS AND METHODS

Individuals used in this study are the same as those used in the behavioral assay of Jaeger et al. (2002), which were collected in Fulton County, Pennsylvania. Salamanders were anesthetized by placing Oragel© (Del Pharmaceuticals Inc.) on their heads for 5–10 min followed by sacrificing by cervical dislocation. Snout–vent length (SVL) was measured using digital calipers and recorded for each animal while anesthetized prior to sacrifice. Animals were fixed in chilled Davidson's solution (Shaw and Battle, 1957) for 24 h, rinsed in tap water for 8 h, and dehydrated through an ethanol series to 70% ethanol. We used 57 animals for the experiment (10 sympatric and 18 allopatric *P. hoffmani*, 11 sympatric and 18 allopatric *P. cinereus*).

Muscle power is proportional to cross-sectional area of a muscle. Measurement of this variable is not practical because it does not mean "area of the muscle at its widest point"; instead it means the cumulative area of all muscle fibers in the muscle at their widest points. We employed another measure of muscle power: i.e., muscle mass (Josephson, 1975; Keynes and Aidley, 1991). The two branches of the *levator mandibulae* (Fig. 1), the *l. m. externus* (*l.m.e.*) and the *l. m. internus* (*l.m.i.*), were removed from both right and left sides, uniformly patted dry on tissue paper, and weighed using a Sartorius MC210 P analytical balance (Denver Instruments Inc.). An average of the mass of the left and right muscles of each salamander was used for statistical analysis. The lower jaw was removed from each animal and the number of teeth on the dentary, vomer and the maxillary arcade (maxillae and premaxillae, Townsend et al., 1998) were observed under a dissecting microscope.

We used analysis of covariance (ANCOVA) to assess differences in muscle mass and tooth counts among allopatric and sympatric populations of the two species while holding the effects of body size (SVL) constant (Sokal and Rohlf, 1995). First we examined whether the relationship between SVL and each variable (*l.m.e.* and *l.m.i* muscle mass, number of dentary, maxillary, and vomerine teeth) was consistent among populations (i.e., homogeneity of slopes test). For those variables where the relationships were consistent, we proceeded with the ANCOVA. Additionally, we performed pairwise multiple comparisons (Tukey-Kramer tests) on the size-adjusted means for each variable to determine which populations differed from one another for which traits. We predict that with the shift toward larger prey in sympatry, *P. hoffmani* will exhibit larger jaw muscle mass and no change in tooth number (null hypothesis) relative to allopatric *P. hoffmani* populations. For *P. cinereus*, we predict that the shift to smaller prey in sympatry will be coincident with a decrease in jaw muscle mass and no change in dentition is predicted (null hypothesis) relative to allopatric *P. cinereus*.

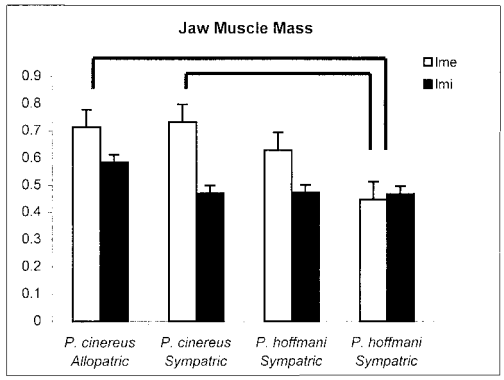
RESULTS

Using homogeneity of slopes tests, we found that the relationship between SVL and each of the variables was consistent among populations (dentary: $F = 0.60$, $P > 0.62$; maxillary: $F = 0.137$, $P > 0.26$; vomer: $F = 0.139$, $P > 0.26$; *l.m.e.*: $F = 0.77$, $P > 0.51$; *l.m.i.*: $F = 0.101$, $P > 0.40$). Therefore, all variables covaried with size in a concordant fashion for all populations. Further comparisons among populations for each variable revealed significant differences for three variables: dentary tooth number, premaxillary tooth number, and *l.m.e.* muscle mass (Table 1). Inspection of the adjusted group means revealed that, in all cases, differences between species were greater than differences between populations within the same species (Fig. 2). Further, multiple comparison tests for the three variables revealed that in no case were intraspecific

TABLE 1.—Overall results of ANCOVA on size adjusted means for each variable. Pop = population, Muscles are: *l.m.e.* = levator mandibulae externus, *l.m.i.* = levator mandibulae internus. * indicates significance at $\alpha = 0.05$.

Variable	Covariate	df	SS	MS	*F*	*P*
Tooth Number						
Dentary	Pop	3	796.01	265.34	3.63	0.0188*
	Svl	1	1234.97	1234.97	16.91	0.0001*
Premaxillary	Pop	3	718.87	239.96	2.88	0.045*
	Svl	1	178.28	178.28	2.14	0.1497
Vomerine	Pop	3	72.76	24.25	1.88	0.1442
	Svl	1	58.03	58.03	4.51	0.0387*
Muscle Mass						
l.m.e.	Pop	3	0.674	0.224	5.09	0.0037*
	Svl	1	1.076	1.076	24.38	0.0001*
l.m.i.	Pop	3	0.128	0.043	0.84	0.4771
	Svl	1	0.641	0.641	12.66	0.0008*

A.



B.

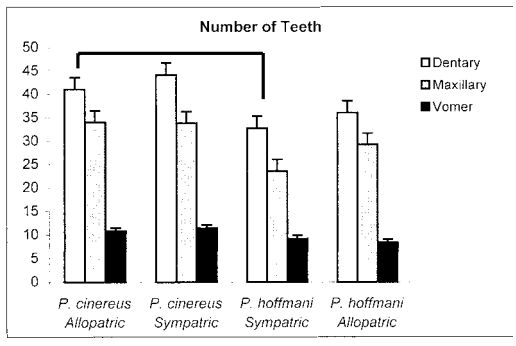


FIG. 2.—Comparison of least square means of muscle mass (A) and tooth number (B) data for sympatric and allopatric populations of *Plethodon cinereus* and *P. hoffmani* (Bracketed pairs are significantly different for Tukey-Kramer pairwise comparisons).

differences (sympatry vs. allopatry) significantly greater than expected by chance (Table 2). Therefore, our data suggest that differences in muscle mass and tooth number between species far outweigh differences between allopatric and sympatric populations within species. For *P. cinereus* and *P. hoffmani*, mean tooth numbers for dentary, premaxillary, and vomerine teeth respectively are: 45.8, 35.9, 11.8 and 31.7, 26.0, 8.1. Our data agree with previous studies indicating that *P. cinereus* is smaller than *P. hoffmani* in snout–vent length (41.7 mm and 46.0 mm respectively).

DISCUSSION

Previous results examining the ecological interactions of *Plethodon cinereus* and *P. hoffmani* demonstrate that character displacement occurs in the general cranial features of each species, especially the shape of the jaw bones (Adams and Rohlf, 2000). Further, this pattern of change in cranial features was correlated with a change in diet indicating ecological character displacement resulting from niche partitioning. Our data on muscle mass and tooth number do not show a pattern of character displacement. However the muscle mass data can be used in the biomechanical

TABLE 2.—Least Squares adjusted mean values for number of dentary teeth, and mass (mg) of the levator mandibulae externus (*l.m.e.*).

LS Means	Allopatric *P. hoffmani*	Sympatric *P. hoffmani*	Sympatric *P. cinereus*	Allopatric *P. cinereus*
l.m.e.	0.448	0.630	0.733	0.714
Dentary	36.1	32.8	44.2	41.1

model of Adams and Rohlf (2000) to test for differences in jaw closing force between sympatric and allopatric populations of *Plethodon cinereus* and *P. hoffmani*. The model of jaw function, based on lever mechanics using the ratio of the two components of the jaw, the squamosal and dentary, predicts a faster, weaker jaw in *P. cinereus* and a stronger, slower jaw in *P. hoffmani*. The model, $F_i l_i = F_o l_o$ and $v_o l_i = v_i l_o$, predicts that contraction force (F_i) and velocity (v_i) of the muscle and closing force (F_o) and velocity (v_o) of the jaw (skeletal elements and muscle) are at equilibrium (given l_o = dentary length and l_i = squamosal length). Using the bone lengths from Adams and Rohlf (2000) and muscle mass reported herein, we can solve for jaw closing force. For sympatric *P. cinereus*, F_o = 0.501 * 0.733 or F_o = 0.367. For sympatric *P. hoffmani*, F_o = 0.376 * 0.630 or F_o = 0.237. The new data incorporating a measure of muscle mass verifies the prediction of Adams and Rohlf (2000), which was based on the assumption of equivalent muscle mass, where they predicted a stronger bite force for sympatric *P. cinereus* relative to sympatric *P. hoffmani*. Given the intrinsic properties of vertebrate skeletal muscle, velocity of contraction is assumed to be equal (Josephson, 1975; Keynes and Aidley, 1991). We stress however that functional morphological (i.e., kinematic) studies (e.g., Maglia and Pyles, 1995; Deban, 1997) must be performed to confirm these predictions, and to establish a direct link between the predicted differences in bite force due to structural differences in the jaw, and foraging activities of the two species in sympatry.

Our data on tooth number indicate an interspecific difference, with *P. cinereus* having more dentary teeth than *P. hoffmani*. Data on interspecific variation in tooth number in plethodontids is limited but some general descriptions of size, number, and shape are available. For vomerine teeth, our numbers agree with those reported by Highton (1962) for six populations of *P. cinereus* from various regions of the eastern United States. Our numbers for teeth of *P. cinereus* agree with those reported for maxillary + premaxillary, dentary, and vomerine teeth of specimens collected in Virginia (Townsend et al., 1998), and for premaxillary + maxillary reported in Coss (1974, collection sites unreported). We are unaware of any tooth counts reported for *P. hoffmani*. Coss (1974) included discussion of the teeth of *P. hoffmani* in his study but did not present any data.

One important source of variation not included in this study is tooth shape, especially involving the relative sizes of the lingual and labial cusps of the bicuspid teeth of Plethodontidae. Previous work indicates a large amount of seasonal, sexual, and inter- and intra-specific variation in tooth shape (Coss, 1974; Townsend et al., 1998). Wake and Wurst (1979) for caecilians and Coss (1974) and Regal (1966) for salamanders described variation in tooth size and shape, suggesting possible variation with diet, especially between aquatic and terrestrial species. Previous work has also suggested that in several salamander species, especially small plethodontids, teeth are important in aggressive interactions and in courtship rituals (see Coss, 1974; Stewart, 1958; Wake and Deban, 2000). Our data are consistent with this hypothesis. Jaeger et al. (2002) examined aggressive behavior of allopatric and sympatric populations of *P. cinereus* and *P. hoffmani*, and found that both allopatric and sympatric populations of *P. cinereus* were more aggressive than populations of *P. hoffmani*. These findings did not support the hypothesis that interspecific competition between *P. cinereus* and *P. hoffmani* was driven by behavioral aggression (via alpha-selection), and they therefore concluded that ecological character displacement via exploitative competition remains a viable interpretation for the observed sympatric morphological divergence. With respect to our findings, differences in tooth number were species specific, with *P. cinereus* having more dentary teeth than *P. hoffmani*. When coupled with aggression, we find that the more aggressive species in sympatry (*P. cinereus*) also has more dentary teeth. Therefore, our dental data are consistent with the hypothesis that teeth in small plethodontids may be more important for aggressive behavior than for feeding (see e.g., Wake and Deban, 2000). Future work should more thoroughly explore this possibility.

In summary, general skeletal features of the cranium but not jaw muscles of *P. cinereus* and *P. hoffmani* are altered in sympatry. Given the confirmation of a shift in diet in sympatry

(Adams, 2000) and the predictions of the biomechanical model of Adams and Rohlf (2000), the diet shift in sympatry has resulted in character displacement in jaw bones but not jaw muscles. Species specific differences are apparent in dentary tooth number between *P. cinereus* and *P. hoffmani*, but no pattern of character displacement is recognized.

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