

## Character Displacement and Aggression in Two Species of Terrestrial Salamanders

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Two species of plethodontid salamanders (*Plethodon cinereus* and *Plethodon hoffmani*) exhibit character displacement with respect to body size and head morphology in Pennsylvania. In areas of allopatry, the two species do not differ in these traits while in an area of sympatry, *P. cinereus* is smaller (and eats smaller prey) and *P. hoffmani* is larger (and eats larger prey) in body size and head morphology. We tested the hypothesis that this form of character displacement is a consequence of alpha selection, in which natural selection favors increased aggression of sympatric species relative to their allopatric conspecifics. We found little evidence that allomonal response to or aggressive behavior toward heterospecifics differed significantly between allopatric and sympatric populations of either *P. cinereus* or *P. hoffmani*. Thus our data do not support the hypothesis of alpha selection shaping the morphology of the two species in sympatry. However, we found that both allopatric and sympatric populations of *P. cinereus* were significantly more aggressive and significantly less submissive than either allopatric or sympatric populations of *P. hoffmani*. These results suggest either of two conflicting interpretations concerning interspecific competition between the two species. First, the boundary of contact between the two species is static because although *P. cinereus* is aggressively superior, *P. hoffmani* is exploitatively superior (eats larger prey) in competition in areas of sympatry. Alternatively, *P. cinereus* is slowly encroaching on the geographic distribution of *P. hoffmani* because the former species is not only aggressively superior but also exploitatively superior (eats the more profitable, although smaller, soft-bodied prey types). Our results also support inferences drawn from previous research that *P. cinereus* competes strongly when geographically in contact with other confamilial species (e.g., *Plethodon hubrichti*, *Plethodon shenandoah*, juveniles of *Plethodon glutinosus*, and *Eurycea cirrigera*).

CHARACTER displacement occurs when two or more species are similar in some trait(s) when in allopatry but diverge in such trait(s) when in sympatry resulting from selection for reduced interspecific competition (Brown and Wilson, 1956; Levins, 1968). Since Brown and Wilson's (1956) study of character displacement in nuthatches (genus *Sitta*), several studies (e.g., with Darwin's finches: Schluter and Grant, 1984; Schluter et al., 1985) have attempted to discern the evolutionary basis for such divergences (for criteria needed to establish the evolutionary basis for character displacement, see also Schluter and McPhail, 1992). Usually the traits of interest are morphological (body size and characteristics of the head associated with foraging), with the assumption that natural selection has favored reduced competition in sympatry through niche partitioning; that is, divergence of trophic structures in sympatry allows differential interspecific use of prey types, thus reducing exploitative competition for prey.

Adams (2000) and Adams and Rohlf (2000) described a potential case of character displacement between two species of salamanders in the

genus *Plethodon*. One species, *Plethodon cinereus* (red-backed salamander), is widely distributed in forests of eastern North America while the other species, *Plethodon hoffmani* (valley and ridge salamander), occupies a large range within the distribution of *P. cinereus*. With the exception of a small area of sympatry in north-central Pennsylvania, *P. cinereus* is absent from the range of *P. hoffmani* (Highton, 1972). Morphological comparisons of allopatric populations of *P. cinereus* and *P. hoffmani* in south-central Pennsylvania revealed no differences in body size (SVL) or in six measures of head morphology. In sympatry, however, *P. hoffmani* was significantly (about 1.3 times) larger in SVL and significantly (1.2–1.3 times) larger in head characteristics than *P. cinereus*. Thus, there was a shift from the two species being similar in allopatry to *P. hoffmani* increasing and *P. cinereus* decreasing in bodily proportions in sympatry. This morphological divergence of head characters was not just a consequence of differing body sizes in sympatry or of clinal variation. Analyses of head shape revealed that the sympatric morphological divergence was statistically significant

even when the effect of size was held constant (Adams, 2000). Further, the morphological variation was statistically associated with the segregation of food resources along a prey-size axis. Finally, Adams (2000) found evidence for interspecific competition for prey utilization, because both species consumed fewer prey per animal in sympatry than in allopatry, even though the types of prey available did not appear to differ between allopatric and sympatric areas. Such findings are consistent with the hypothesis of character displacement, suggesting an evolutionary cause for the observed sympatric divergence.

This hypothesis was tested by including samples from a second transect, as well as comparing morphology from these transects to that of nearby populations (Adams and Rohlf, 2000). In addition, morphology was quantified using the landmark-based morphometric methods. A pattern of sympatric divergence was confirmed between *P. cinereus* and *P. hoffmani*. Further, the landmark analysis suggested a biomechanical interpretation of this sympatric divergence, as the major anatomical difference between sympatric populations was in the ratio of the squamosal versus the dentary bones of the jaw mechanism. Changes in this ratio were found to be associated with changes in prey acquisition, according to prey size. Adams and Rohlf (2000) found that the species that specialized on large prey appeared to have evolved a faster jaw, and the species that specialized on small prey appeared to have evolved a stronger jaw. Although this result is suggestive of a functional hypothesis, direct observation of jaw biomechanics must be performed to confirm this functional hypothesis.

Adams (1999) posed two alternative hypotheses to explain the evolutionary basis for the observed morphological divergence of sympatric *P. cinereus* and *P. hoffmani*. First, when range expansions caused the two similar-sized species to come into contact, exploitative (nonaggressive) competition for prey occurred. Natural selection then favored partitioning of resources along a prey-size axis, leading to increased size (in SVL and trophic morphology) by *P. hoffmani* and decreased size by *P. cinereus*. This has led to the presently observed differences in prey sizes ingested by the two species in sympatry (Adams, 2000). Second, when the two species first came into contact, alpha selection (Gill, 1974) through interference (aggressive) competition occurred. Alpha selection acts to enhance the aggressive ability of a species such that it can inhibit or prevent a competing species from gaining access to resources. Thus, the observed partitioning of prey sizes by sympatric *P. cinereus*

and *P. hoffmani* would be only an incidental by-product of natural selection enhancing aggressive abilities through alterations of body size and trophic (also aggressive biting) morphologies of the head. Both of these hypotheses assume that the two species came into contact following geographic range expansion by one or both species.

Although alpha selection has seldom been invoked in studies of character displacement, it is a viable hypothesis to explain the morphological divergence in *P. cinereus* and *P. hoffmani*, for three reasons. First, some populations of *P. cinereus* aggressively defend territories intraspecifically (Gabor and Jaeger, 1995) and perhaps interspecifically against *Plethodon shenandoah* (Griffis and Jaeger, 1998), *Plethodon hubrichti* (Wicknick, 1995), juveniles of *Plethodon glutinosus* (Lancaster and Jaeger, 1995), and *Eurycea cirrigera* (Jaeger et al., 1998). Second, in sympatry, *P. cinereus* appears to have evolved a stronger, more powerful jaw, which may serve to deliver a more intense bite during aggressive encounters, whereas *P. hoffmani* appears to have evolved a faster jaw and, thus, may be able to deliver a faster bite (Adams, 1999). Finally, although, in sympatry, *P. cinereus* ingested smaller prey than *P. hoffmani*, it appeared to shift to the more profitable (sensu Gabor and Jaeger, 1995) lightly armored prey (Collembola), whereas its congener shifted to the less profitable heavily armored prey (Coleoptera; fig. 4 in Adams, 2000).

We performed two laboratory experiments to test for allomonal communication and aggressive behavior between these two species. An allomone is "a chemical substance released by one species that serves as a communicative signal to another species" (Wilson, 1975); Jaeger and Gergits (1979) demonstrated allomonal communication between *P. cinereus* and *P. shenandoah*. We predicted that sympatric *P. cinereus* would respond significantly more intensely to allomones of and be significantly more aggressive toward *P. hoffmani* than would allopatric *P. cinereus* or that sympatric *P. hoffmani* would respond significantly more intensely to allomones of and be significantly more aggressive toward *P. cinereus* than would allopatric *P. hoffmani*. These behavioral responses would be compatible with the hypothesis that alpha selection has shaped the morphology of one or both of the species.

#### MATERIALS AND METHODS

*Collection and maintenance.*—On 11 and 14 May 1998, one of us (DCA) collected salamanders at three localities in Fulton County, Pennsylvania:

McConnellsburg Quadrangle (allopatric *P. cinereus*), Burn Cabins Quadrangle (sympatric location), and Meadow Grounds Quadrangle (allopatric *P. hoffmani*; for more precise locality data, see Adams, 2000). A subset of this collection (10 sympatric and 25 allopatric *P. hoffmani*, 12 sympatric and 25 allopatric *P. cinereus*) was sent during October 1998, in individual containers, to The University of Louisiana at Lafayette for behavioral studies. There, each salamander was placed in a separate Petri dish (14 × 1.5 cm) containing one sheet of filter paper moistened with spring water. The laboratory was maintained at 19–21 C with a 12:12 L:D photoperiod, the salamanders were fed *Drosophila virilis* to satiation every three days, and the chambers were cleaned biweekly until the experiments began (2 June to 11 August 1999 for the allomone tests, 6 September to 11 October 1999 for the aggression tests). Because all of our tests were between species, we did not partition the salamanders by sex.

*Allomone experiment.*—The eight treatments were allopatric *P. cinereus* exposed to presumed allomones of (1) allopatric and (2) sympatric *P. hoffmani*; sympatric *P. cinereus* exposed to allomones of (3) sympatric and (4) allopatric *P. hoffmani*; allopatric *P. hoffmani* exposed to allomones of (5) allopatric and (6) sympatric *P. cinereus*; and sympatric *P. hoffmani* exposed to allomones of (7) sympatric and (8) allopatric *P. cinereus*. We tested each individual twice (e.g., the same allopatric individuals of *P. cinereus* in both treatments 1 and 2), and we randomized the sequence in which these treatments were conducted. Because we had only 10 sympatric *P. hoffmani*, each treatment was replicated 10 times to equalize sample sizes. We randomly chose 10 each of allopatric *P. hoffmani* and *P. cinereus* and of sympatric *P. cinereus* for these replicates. All of the salamanders were adults, but we did not attempt to match snout-vent lengths (SVL) of allomone donors with those of focal animals. Each focal animal was used as an allomone donor in another test.

We fed *D. virilis* to each allomone donor in its home Petri dish on day 0 so that fecal pellets would be produced by day 5. On day 1, we moved the salamander to a new Petri dish containing one sheet of dampened (spring water) filter paper. On day 5, we removed the soiled filter paper and rolled it into a cylinder. These cylinders then became the allomone sources for the focal animals to be tested on day 5.

On day 1, we placed each focal animal into a Nunc bioassay dish (24 × 24 × 2 cm; Cole-Parmer Co.) lined with damp (spring water) pa-

per towels. On days 2 and 4, it was fed *D. virilis*. Because five days are sufficient for *P. cinereus* to establish a territory (Wise and Jaeger, 1998), we conducted the allomone detection test on day 5. We placed the focal animal under a habituation cup (9 × 1 cm) on a randomly chosen side of the chamber for 15 min, placed the allomone source in the center of the chamber, released the focal animal, replaced the chamber's lid, and observed the salamander's behavior for 15 min. We recorded (from 1000–1400 h) number of nose taps (chemoinvestigation: Dawley and Bass, 1988), and total seconds spent in the all-trunk raised (ATR) threat posture (Jaeger, 1984; Jaeger and Schwarz, 1991), in the flat submissive posture (Jaeger, 1984), and touching the allomone source.

Because each focal animal was tested twice, the same observer recorded data both times to control for interobserver bias. To analyze the data, we used the nonparametric, two-tailed Wilcoxon signed ranks test (for related data: Siegel and Castellan, 1988) to compare treatments 1 versus 2, 3 versus 4, 5 versus 6, and 7 versus 8. We also used the nonparametric, two-tailed Wilcoxon-Mann-Whitney test (for independent samples: Siegel and Castellan, 1988) to compare treatments 1 versus 4, 2 versus 3, 5 versus 8, and 6 versus 7. Because each data set was used twice in statistical comparisons, we reduced alpha to 0.025.

*Aggression experiment.*—The randomized treatments were allopatric resident of *P. cinereus* with intruding (1) allopatric and (2) sympatric *P. hoffmani* and (3) surrogate control; sympatric resident of *P. cinereus* with intruding (4) sympatric and (5) allopatric *P. hoffmani* and (6) surrogate; allopatric resident of *P. hoffmani* with intruding (7) allopatric and (8) sympatric *P. cinereus* and (9) surrogate; sympatric resident of *P. hoffmani* with intruding (10) sympatric and (11) allopatric *P. cinereus* and (12) surrogate. Each resident was tested three times in random sequence in treatments 1–3, 4–6, 7–9, or 10–12. The surrogate was a piece of moist paper towel rolled to approximately the same size as a salamander; its function was to occupy the space that would otherwise be occupied by the intruder and as an object toward which behavioral displays could be directed in control tests (Gabor and Jaeger, 1995). Each treatment was replicated 10 times using the same salamanders as in the allomone experiment above; however, no salamanders were paired in the aggression experiment that had been allomonally paired in the allomone experiment. Also, the same individuals were used both as residents and intrud-

ers, but only individuals unfamiliar with each other were paired in these aggression tests.

On day 1, we placed a resident salamander into a bioassay dish (as above) and placed a future intruder into an identical chamber. Both were fed *D. viridis* on days 2 and 4, and the test was conducted on day 5 (0900–1330 h). We placed the resident salamander under a habituation cup on one randomly selected side of its chamber and placed the intruder under another cup on the opposite side of the resident's chamber. Both animals were handled equally by allowing each to walk into a plastic tube ( $9 \times 1$  cm), moving the tube to the position of the habituation cup, and allowing each to exit the tube, at which time the cup was placed over the salamander. After 15 min, we released both salamanders from their cups and recorded their behavior patterns for 15 min. For both resident and intruder, we recorded the total number of nose taps and bites, and the total seconds spent in the ATR threat posture, the submissive flat posture, touching the opponent (time awarded to the salamander that initiated the touch), and edge behavior. "Edge" occurred when the salamander roamed the periphery of the chamber while pressing its snout against the walls or in the crevice between the lid and walls of the chamber; this was interpreted as a salamander's attempt to escape or a way of avoiding the opponent (Wise and Jaeger, 1998). Because each salamander was tested in three treatments, one of us recorded the behavior of a particular salamander in each of those treatments, to avoid interobserver bias.

We compared statistically each set of three treatments using the Friedman two-way analysis of variance by ranks test (related data: Siegel and Castellan, 1988) with  $\alpha = 0.05$ . When Friedman's test yielded a significant difference, we employed the posthoc multiple comparison procedure (Siegel and Castellan, 1988) to locate pairwise significant differences. We also compared the behavior patterns of residents and intruders in treatments 1, 2, 4, 5, 7, 8, 10, and 11 using the two-tailed Wilcoxon signed ranks test, with  $\alpha = 0.05$ .

## RESULTS

*Allomone experiment.*—Allopatric *P. cinereus*, sympatric *P. cinereus*, and allopatric *P. hoffmani* did not significantly differ in responses to presumed allomones of allopatric versus sympatric members of the other species (Table 1). Sympatric *P. hoffmani* showed a significant difference for only one response variable, spending more time in the submissive flat posture when in the pres-

ence of allomones of allopatric *P. cinereus* compared to those of sympatric *P. cinereus* (Table 1).

We found that allopatric and sympatric *P. cinereus* did not differ significantly in responses to allomones of allopatric *P. hoffmani* (treatments 1 vs 4):  $P = 0.124$  for ATR,  $P = 0.456$  for flat,  $P = 0.176$  for touch, and  $P = 0.124$  for nose taps (Table 1). Allopatric and sympatric *P. cinereus* also showed no significant differences toward allomones of sympatric *P. hoffmani* (treatments 2 vs 3):  $P = 0.176$  for ATR,  $P = 0.140$  for flat,  $P = 0.038$  ( $\alpha = 0.025$ ) for touch, and  $P = 0.370$  for nose taps. Allopatric and sympatric *P. hoffmani* showed only one significant difference toward allomones of allopatric *P. cinereus* (treatments 5 vs 8):  $P = 0.003$  for flat, and  $P = 0.062$  for touch, and  $P = 0.289$  for nose taps (statistic not computed for ATR because of few responses). Allopatric and sympatric *P. hoffmani* showed no significant differences toward allomones of sympatric *P. cinereus* (treatments 6 vs 7):  $P$  not computed for ATR,  $P = 0.197$  for flat,  $P = 0.264$  for touch, and  $P = 0.370$  for nose taps.

*Aggression experiment.*—Allopatric residents of *P. cinereus* showed a significant difference in times spent in the threat posture (ATR) across treatments 1–3 (Table 2). Pairwise multiple comparison tests found these residents to be significantly more threatening toward sympatric *P. hoffmani* than toward the surrogate control ( $P < 0.05$ ) but found no significant differences in ATR toward allopatric versus sympatric *P. hoffmani* or between allopatric *P. hoffmani* and the surrogate. These residents showed no significant differences among treatments for the submissive flat posture, edge behavior, touching, nose taps, or bites.

Sympatric residents of *P. cinereus* exhibited a significant difference in times spent in the flat posture across treatments 4–6 (Table 2), but pairwise multiple comparison tests found no significant differences among any combination of treatments. These residents showed no significant differences among treatments for any other behavior.

Allopatric residents of *P. hoffmani* showed no significant differences among treatments 7–9 for any behavior pattern, and sympatric residents of *P. hoffmani* also exhibited no significant differences among treatments 10–12 for any behavior (Table 2).

When we compared *P. cinereus* as residents and *P. hoffmani* as intruders (Table 3), allopatric residents spent significantly more time in the ATR posture than did sympatric intruders and they spent significantly more time touching the

TABLE 1. ALLOMONE EXPERIMENT. Response of allopatric and sympatric individuals of *P. cinereus* and *P. hoffmani* to allomonal cues of allopatric and sympatric individuals of the opposite species. Treatment numbers are in parentheses. NT = nose taps.

Focal animal	Allomone source						P
	Allopatric <i>P. hoffmani</i> (1)			Sympatric <i>P. hoffmani</i> (2)			
Allopatric <i>P. cinereus</i>	Mean	Median	Range	Mean	Median	Range	
ATR (s)	71.6	6.0	0-340	186.4	28.0	0-863	0.1954
Flat (s)	193.1	16.0	0-900	213.7	157.0	0-716	0.8204
Touch (s)	175.7	91.0	0-664	411.1	432.0	0-838	0.1640
NT (number)	2.9	1.5	0-12	6.1	3.5	0-18	0.1290
Sympatric <i>P. cinereus</i>	Allopatric <i>P. hoffmani</i> (4)			Sympatric <i>P. hoffmani</i> (3)			P
	Mean	Median	Range	Mean	Median	Range	
ATR (s)	12.8	0.0	0-73	46.0	0.0	0-172	0.3126
Flat (s)	142.2	34.0	0-900	73.6	33.0	0-439	0.9102
Touch (s)	387.2	358.5	0-884	211.6	159.5	0-754	0.1094
NT (number)	2.3	1.0	0-7	6.9	2.5	0-34	0.1954
Allopatric <i>P. hoffmani</i>	Allopatric <i>P. cinereus</i> (5)			Sympatric <i>P. cinereus</i> (6)			P
	Mean	Median	Range	Mean	Median	Range	
ATR (s)	6.6	0.0	0-66	27.4	0.0	0-274	—*
Flat (s)	166.9	85.5	5-563	245.5	78.5	0-900	0.5566
Touch (s)	201.0	111.0	0-799	341.4	226.0	0-844	0.4610
NT (number)	3.6	2.5	0-10	2.3	1.5	0-7	0.3828
Sympatric <i>P. hoffmani</i>	Allopatric <i>P. cinereus</i> (8)			Sympatric <i>P. cinereus</i> (7)			P
	Mean	Median	Range	Mean	Median	Range	
ATR (s)	2.1	0.0	0-21	92.8	0.0	0-837	—*
Flat (s)	566.2	699.5	45-900	181.9	64.5	0-849	0.0020**
Touch (s)	116.2	0.0	0-868	223.8	16.0	0-837	0.6250
NT (number)	1.1	0.0	0-8	3.3	0.0	0-25	0.6250

\* Pvalue not computed because of small sample size.  
 \*\* Significant difference at alpha = 0.025.

opponent than did allopatric intruders. Sympatric residents spent significantly more time in ATR than did sympatric intruders and significantly less time in edge behavior than did allopatric intruders.

When *P. hoffmani* was resident and *P. cinereus* was intruder (Table 4), allopatric residents spent significantly less time in ATR, significantly more time in submissive flat posture, significantly less time touching the opponent, and exhibited significantly fewer nose taps than did either the allopatric or sympatric intruders. Sympatric residents also spent significantly less time in ATR and significantly more time in flat than did either the allopatric or sympatric intruders. The sympatric residents also exhibited significantly fewer nose taps than did allopatric intruders.

Although *P. cinereus* (both as residents and intruders) occasionally bit opponents, *P. hoffmani* (as residents and intruders) never bit opponents (Tables 3-4). Counting each individual only once, no matter how many times it engaged in biting, we found that six individuals of

*P. cinereus* performed bites and 14 did not, whereas none of the 20 *P. hoffmani* bit. Thus, *P. cinereus* was significantly more likely to bite a congeneric opponent than was *P. hoffmani* (Fisher's exact test,  $P = 0.0101$ ).

DISCUSSION

Interspecific competition has long been thought to be a pervasive influence on species distributions (Levins, 1968), and much of the empirical support for this concept has derived from knowledge of the interactions among species of salamanders in the genus *Plethodon* (summarized by Hairston, 1987). Species-pairs of *Plethodon* are frequently distributed in patterns of contiguous allopatry with narrow areas of sympatry along contact zones. For example, *P. cinereus* completely surrounds all three populations of *P. shenandoah* (the Shenandoah salamander) on mountaintops in Shenandoah National Park, Virginia. As a consequence of interspecific territoriality by *P. cinereus* (Griffis and Jaeger, 1998), the Shenandoah salamander has

TABLE 2. AGGRESSION EXPERIMENT. Comparison of responses of resident individuals to the presence of allopatric and sympatric intruders of the opposite species, and the surrogate control. Treatment numbers are in parentheses. NT = nose taps.

Resident	Intruder						Control			P
	Allopatric <i>hoffmani</i> (1)			Sympatric <i>hoffmani</i> (2)			Surrogate (3)			
Allopatric <i>P. cinereus</i>	Mean	Median	Range	Mean	Median	Range	Mean	Median	Range	
ATR (s)	152.8	52.5	0–524	264.9	244.0	0–880	19.0	9.0	0–62	0.0111**
Flat (s)	225.0	128.0	0–900	175.8	76.0	0–900	130.6	31.0	0–900	0.0839
Edge (s)	43.6	0.0	0–202	49.2	0.0	0–373	113.1	116.0	0–251	0.1409
Touch (s)	74.7	1.5	0–587	8.4	0.0	0–50	5.0	0.0	0–24	0.3406
NT (number)	3.4	4.5	0–7	5.2	0.0	0–39	0.8	0.0	0–4	0.2019
Bite (number)	0.0	0.0	0–0	0.2	0.0	0–2	0.0	0.0	0–0	0.3679
Sympatric <i>P. cinereus</i>	Intruder						Control			P
	Sympatric <i>hoffmani</i> (4)			Allopatric <i>hoffmani</i> (5)			Surrogate (6)			
	Mean	Median	Range	Mean	Median	Range	Mean	Median	Range	
ATR (s)	176.3	91.5	0–530	166.5	56.0	0–675	50.9	42.5	0–153	0.3679
Flat (s)	296.3	274.5	0–665	192.4	174.0	0–493	144.9	52.0	0–900	0.0161**
Edge (s)	76.1	0.0	0–292	47.6	0.0	0–237	102.8	0.0	0–494	0.3311
Touch (s)	69.3	2.0	0–388	10.3	0.0	0–70	7.3	0.0	0–49	0.1078
NT (number)	2.4	1.0	0–9	2.4	1.0	0–9	3.0	2.0	0–7	0.8777
Bite (number)	0.0	0.0	0–0	0.3	0.0	0–2	0.0	0.0	0–0	0.1353
Allopatric <i>P. hoffmani</i>	Intruder						Control			P
	Allopatric <i>cinereus</i> (7)			Sympatric <i>cinereus</i> (8)			Surrogate (9)			
	Mean	Median	Range	Mean	Median	Range	Mean	Median	Range	
ATR (s)	0.0	0.0	0–0	0.0	0.0	0–0	0.0	0.0	0–0	—*
Flat (s)	606.2	645.0	75–900	588.1	626.0	169–853	439.2	485.0	107–854	0.7408
Edge (s)	22.5	0.0	0–206	90.2	60.0	0–284	77.1	86.5	0–170	0.0718
Touch (s)	0.0	0.0	0–0	1.2	0.0	0–12	0.0	0.0	0–0	0.3679
NT (number)	0.3	0.0	0–3	0.1	0.0	0–1	0.5	0.0	0–3	0.7788
Bite (number)	0.0	0.0	0–0	0.0	0.0	0–0	0.0	0.0	0–0	—*
Sympatric <i>P. hoffmani</i>	Intruder						Control			P
	Sympatric <i>cinereus</i> (10)			Allopatric <i>cinereus</i> (11)			Surrogate (12)			
	Mean	Median	Range	Mean	Median	Range	Mean	Median	Range	
ATR (s)	8.4	0.0	0–84	14.7	0.0	0–83	68.7	0.0	0–514	0.0970
Flat (s)	600.3	691.0	37–900	469.7	433.0	0–900	411.3	273.0	56–900	0.9155
Edge (s)	113.5	13.0	0–432	155.4	149.5	0–415	130.1	36.0	0–570	0.9661
Touch (s)	22.5	0.0	0–147	13.9	0.0	0–59	9.2	0.0	0–62	0.6271
NT (number)	0.3	0.0	0–3	0.3	0.0	0–3	1.7	0.0	0–7	0.2319
Bite (number)	0.0	0.0	0–0	0.0	0.0	0–0	0.0	0.0	0–0	—*

\* P-value not computed because of small sample size.

\*\* Significant difference at alpha = 0.05.

been confined to dry refugia of talus (Jaeger, 1970) with a narrow zone of sympatry at the talus-deep soil interface (Jaeger, 1980). Thus, *P. cinereus* apparently has been successful in displacing *P. shenandoah* from its favored deep soil habitat (Jaeger, 1971, 1972). *Plethodon cinereus* also surrounds *P. hubrichti* (Peaks of Otter salamander) in the Blue Ridge Mountains of Virginia, where sympatry occurs in a zone 50–150 m wide (Wicknick, 1995). Based on laboratory studies of interspecific aggression and field studies of competitive release, Wicknick (1995) concluded that the two species are about equal-

ly successful as competitors. Thus, these two species may have a static contact boundary. Hairston (1980) found that different populations of *P. glutinosus* and *P. jordani* (cf. *P. glutinosus* complex and *P. jordani* complex in Highton and Peabody, 2000) have either narrow areas of sympatry, attributed to strong interspecific competition, or broad areas of sympatry, attributed to relaxed competition. Nishikawa (1985) suggested that alpha selection has occurred in populations of *P. glutinosus* under conditions of intense interspecific competition. These cases of both allopatry and sympatry among species of

TABLE 3. AGGRESSIVE INTERACTIONS. Behavioral interactions between residents of *P. cinereus* and intruding *P. hoffmani*. In treatments 1 and 5, the intruders were from an allopatric population; in treatments 2 and 4, the intruders were from a sympatric population.

Resident	Behaviors	Treatment	Mean		Median		Range		P
			Resident	Intruder	Resident	Intruder	Resident	Intruder	
Allopatric <i>P. cinereus</i>	ATR (s)	1	152.8	66.4	52.5	0.0	0-524	0-664	0.2367
		2	264.9	94.6	244.0	20.0	0-880	0-421	0.0367**
	Flat (s)	1	225.0	495.6	128.0	544.0	0-900	1-900	0.1141
		2	175.8	400.6	76.0	387.5	0-900	0-900	0.0858
	Edge (s)	1	43.6	90.6	0.0	0.0	0-202	0-479	0.3441
		2	49.2	134.3	0.0	68.0	0-373	0-551	0.1730
	Touch (s)	1	74.7	0.0	1.5	0.0	0-587	0-0	0.0431**
		2	8.4	22.0	0.0	0.0	0-50	0-112	0.3452
	Nose Tap (number)	1	3.4	0.7	4.5	0.0	0-7	0-7	0.1361
		2	5.2	1.7	0.0	0.0	0-39	0-13	0.3430
Bite (number)	1	0.0	0.0	0.0	0.0	0-0	0-0	—*	
	2	0.2	0.0	0.0	0.0	0-2	0-0	—*	
Sympatric <i>P. cinereus</i>	ATR (s)	4	176.3	11.4	91.5	0.0	0-530	0-100	0.0464**
		5	166.5	28.3	56.0	0.0	0-675	0-204	0.1159
	Flat (s)	4	296.3	499.8	274.5	405.5	0-665	84-900	0.1688
		5	192.4	395.0	174.0	371.0	0-493	0-780	0.1141
	Edge (s)	4	76.1	142.5	0.0	49.5	0-292	0-529	0.4990
		5	47.6	180.4	0.0	162.5	0-237	0-443	0.0173**
	Touch (s)	4	69.3	44.0	2.0	0.0	0-388	0-375	0.4990
		5	10.3	0.0	0.0	0.0	0-70	0-0	0.1797
	Nose Tap (number)	4	2.4	1.2	1.0	0.0	0-9	0-6	0.1682
		5	2.4	0.4	1.0	0.0	0-9	0-3	0.1400
Bite (number)	4	0.0	0.0	0.0	0.0	0-0	0-0	—*	
	5	0.3	0.0	0.0	0.0	0-2	0-0	0.1797	

\* Pvalue not computed because of small sample size.  
 \*\* Significant difference at alpha = 0.05.

*Plethodon* suggest that this genus provides numerous situations in which character displacement may have occurred.

We hypothesized that alpha selection is the evolutionary factor that has shaped the morphological character displacement that Adams (2000) and Adams and Rohlf (2000) found between allopatric and sympatric populations of *P. cinereus* and *P. hoffmani*. This hypothesis led to several predictions.

First, sympatric *P. cinereus* would respond significantly more intensely to allomones of *P. hoffmani* than would allopatric *P. cinereus*. Our data lend no support to this prediction, because neither allopatric nor sympatric *P. cinereus* demonstrated any significant discrimination between allomones of the allopatric or sympatric congener.

Next, sympatric *P. hoffmani* would respond significantly more intensely to allomones of *P. cinereus* than would allopatric *P. hoffmani*. Our data lend only partial support for this prediction. Sympatric *P. hoffmani* spent significantly more time in the flat submissive posture than did allopatric conspecifics in response to allo-

mones of allopatric *P. cinereus* (treatments 5 vs 8). However, no such discrimination was exhibited for ATR, touch, or nose taps.

Furthermore, sympatric residents of *P. cinereus* would be significantly more aggressive toward intruding *P. hoffmani* than would allopatric *P. cinereus*. Our data gave no support for this prediction. Allopatric, not sympatric, *P. cinereus* was more aggressive toward the sympatric congener than toward the surrogate control. Sympatric *P. cinereus* showed a significant difference in times spent in the submissive flat posture across treatments 4-6, but this result may be spurious because posthoc multiple comparison tests failed to detect any significant differences.

Finally, alternatively to the previous prediction, sympatric residents of *P. hoffmani* would be significantly more aggressive toward intruding *P. cinereus* than would allopatric conspecifics. Our data provide no support for this prediction, because neither allopatric nor sympatric *P. hoffmani* responded significantly differently to intruding *P. cinereus* relative to the surrogate control.

Thus, the data from our two experiments pro-

TABLE 4. AGGRESSIVE INTERACTIONS. Behavioral interactions between residents of *P. hoffmani* and intruding *P. cinereus*. In treatments 7 and 11, the intruders were from an allopatric population; in treatments 8 and 10, the intruders were from a sympatric population.

Resident	Behaviors	Treatment	Mean		Median		Range		P
			Resident	Intruder	Resident	Intruder	Resident	Intruder	
Allopatric <i>P. hoffmani</i>	ATR (s)	7	0.0	181.8	0.0	148.0	0-0	0-520	0.0180**
		8	0.0	223.7	0.0	151	0-0	0-858	0.0180**
	Flat (s)	7	606.2	103.0	645.0	78.5	75-900	0-274	0.0069**
		8	588.1	79.4	626.0	55.0	169-853	0-256	0.0051**
	Edge (s)	7	22.5	195.0	0.0	163.5	0-206	0-700	0.0630
		8	90.2	214.1	60.0	69.0	0-284	0-786	0.2135
	Touch (s)	7	0.0	64.1	0.0	46.0	0-0	0-180	0.0117**
		8	1.2	97.2	0.0	66.5	0-12	0-267	0.0180**
	Nose Tap (number)	7	0.3	6.0	0.0	5.5	0-3	0-13	0.0178**
		8	0.1	6.1	1.0	0.0	0-1	0-13	0.0116**
	Bite (number)	7	0.0	0.1	0.0	0.0	0-0	0-1	—*
		8	0.0	0.5	0.0	0.0	0-0	0-3	0.1797
Sympatric <i>P. hoffmani</i>	ATR (s)	10	8.4	216.0	0.0	156.0	0-84	0-709	0.0180**
		11	14.7	280.8	0.0	185.0	0-83	0-874	0.0117**
	Flat (s)	10	600.3	156.7	691.0	48.5	37-900	0-604	0.0109**
		11	469.7	81.3	433.0	65.0	0-900	1-255	0.0166**
	Edge (s)	10	113.5	128.4	13.0	42.0	0-432	0-546	0.9999
		11	155.4	189.3	149.5	54.0	0-415	0-729	0.9528
	Touch (s)	10	22.5	77.6	0.0	56.5	0-147	0-190	0.1282
		11	13.9	57.3	0.0	29.5	0-59	0-182	0.0924
	Nose Tap (number)	10	0.3	3.6	0.0	1.5	0-3	0-16	0.0585
		11	0.3	7.2	0.0	5.0	0-3	0-21	0.0116**
	Bite (number)	10	0.0	0.2	0.0	0.0	0-0	0-1	0.1573
		11	0.0	0.0	0.0	0.0	0-0	0-0	—*

\* P-value not computed because of small sample size.

\*\* Significant difference at alpha = 0.05.

vide little support for the hypothesis of alpha selection as a factor shaping the character displacement exhibited by *P. cinereus* and *P. hoffmani*. We cannot reject the alternative hypothesis of prey niche partitioning through exploitative competition (Adams, 2000) as a more likely explanation (although yet to be tested by competitive release experiments) causative of morphological character displacement between these two species.

However, our data from the aggression experiment (interaction behaviors) showed that both allopatric and sympatric individuals of *P. cinereus* were significantly more aggressive and less submissive than either allopatric or sympatric individuals of *P. hoffmani*. When individuals of allopatric *P. cinereus* were residents, they were significantly more threatening (ATR) than sympatric intruders and significantly more likely to "touch" than allopatric intruders. When individuals of sympatric *P. cinereus* were residents, they also were significantly more threatening than sympatric intruders and spent significantly less time in edge ("escape") than allopatric intruders. As intruders, allopatric and sympatric

individuals of *P. cinereus* were significantly more threatening and less submissive (flat) than both allopatric and sympatric residents of *P. hoffmani*, and significantly more likely to "touch" than allopatric residents of *P. hoffmani*. Also, significantly more individuals of *P. cinereus* attacked (bit) opponents than did *P. hoffmani*. Our general impression during this experiment was that *P. cinereus* is a very active and aggressive species, whereas *P. hoffmani* is a very lethargic species (e.g., cf. frequencies of nose taps in Tables 3-4).

From an ecological perspective, the present geographic distributions of these two species (*P. hoffmani* embedded within the range of *P. cinereus* with few areas of sympatry) suggest four hypotheses. First, the geographic boundary between the two species is static and will remain in equilibrium under present environmental conditions. This hypothesis might hold if the two species are not engaging in interspecific competition (either through exploitation or interference). Second, the boundary is static because the two species are competitive but equally so, as in the presumed relationship between



*P. cinereus* and *P. hubrichti* (Wicknick, 1995). Third, *P. hoffmani* is competitively superior and is slowly expanding into the range of *P. cinereus*. Finally, *P. cinereus* is competitively superior and is slowly expanding into the range of *P. hoffmani*, as in the relationship between *P. cinereus* and *P. shenandoah* (Griffis and Jaeger, 1998).

We reject the first hypothesis because Adams (1999, 2000) found that the foraging success of both species was reduced in areas of sympatry compared to areas of allopatry, suggesting that interspecific competition for prey occurs. The second hypothesis cannot be rejected at this time. Although *P. cinereus* appears to be the more aggressive species (our data), *P. hoffmani* may balance this by superiority in exploitative competition. Adams (2000) found that *P. hoffmani* ingested significantly larger prey than sympatric *P. cinereus*, which may translate into the former species gaining more utilizable energy per unit of foraging effort. Walls and Jaeger (1987) suggested that larvae of *Ambystoma maculatum* and *A. talpoideum* coexist in ponds as a result of a trade-off between exploitative superiority of the former species and aggressive superiority of the latter species.

We consider the third hypothesis to be unlikely. Even if *P. hoffmani* is superior in exploitative (foraging) competition, this superiority would have to overwhelm the aggressive superiority of *P. cinereus*. Kaplan (1977) tested congeneric pairs of *P. cinereus* and *P. shenandoah* in the laboratory and found the latter to be superior in rate of prey capture. However, in the forest, *P. cinereus* is still able to exclude *P. shenandoah* from favorable deep soil habitats through interspecific territoriality (Griffis and Jaeger, 1998). The densities of the two species also make this hypothesis unlikely. At our research sites, allopatric populations of *P. cinereus* attain higher densities than those of allopatric *P. hoffmani* (DCA, unpubl. data). Fraser (1976) found that *P. hoffmani* responded more negatively to increased density than did *P. cinereus*. Thus, for the third hypothesis to be correct, *P. hoffmani* would need to expand its range into an area of *P. cinereus* at higher densities, which seems unlikely.

The fourth hypothesis cannot be rejected and has strong support from available data. Not only was *P. cinereus* more likely to bite in pairwise contests than was *P. hoffmani* in our experiment, but it apparently can deliver a more powerful bite than its sympatric congener (Adams, 1999). In addition, *P. cinereus* may be equal or superior in exploitative competition for prey; Adams (2000) found that both species ingested Collembola (a profitable prey type) in areas of allopa-

try, but in sympatry this prey type was deleted from the diet of *P. hoffmani* but not from that of *P. cinereus*. Thus, one might infer that the morphological character displacement found by Adams and Rohlf (2000) is a consequence of *P. cinereus*, in sympatry, sequestering smaller but more profitable prey types, thus forcing *P. hoffmani* to specialize on larger but less profitable prey types (sensu Gabor and Jaeger, 1995).

We tentatively draw the following two conclusions. First, alpha selection is not a significant factor in the evolution of character displacement between *P. cinereus* and *P. hoffmani*. Data supporting this conclusion are somewhat paradoxical, however. *Plethodon cinereus* is superior to *P. hoffmani* in aggressive encounters, yet *P. hoffmani* is the larger of the two species in sympatry. Both theory (e.g., Maynard Smith and Parker, 1976) and empirical data for *P. cinereus* (Townsend and Jaeger, 1998) suggest that aggressive superiority usually is awarded to the larger individual in pairwise asymmetric contests. In our research, however, this does not appear to be the case.

Second, either *P. cinereus* is aggressively superior to its congener and, thus, may be expanding its geographic distribution into the range of *P. hoffmani*, or the boundary of contact between the two species is static because, although *P. cinereus* is aggressively superior, *P. hoffmani* may be exploitatively superior during foraging. Distinguishing between these two scenarios will require a competitive release experiment in areas of sympatry. If *P. cinereus* is exploitatively superior in interspecific competition, then removing this species from experimental plots should result in *P. hoffmani* ingesting significantly more small prey (e.g., Collembola) than it does in control plots where *P. cinereus* has not been removed. Alternatively, if *P. hoffmani* is exploitatively superior, then removing this species from experimental plots should result in *P. cinereus* ingesting significantly more large prey (e.g., Coleoptera) than in control plots. Such an experiment should differentiate between our two scenarios. If *P. cinereus* is both aggressively superior (our data) and a better exploiter of prey than *P. hoffmani*, then *P. cinereus* should be displacing *P. hoffmani* geographically. If *P. cinereus* is aggressively superior but *P. hoffmani* is a better exploiter of prey, than the boundary of contact between the two species may be static because of a competitive trade-off between the species.

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