

CHARACTER DISPLACEMENT VIA AGGRESSIVE INTERFERENCE IN APPALACHIAN SALAMANDERS

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Abstract. Ecological character displacement occurs when sympatric species compete with one another, resulting in morphological divergence. Theoretically, character displacement can evolve from a number of ecological interactions, such as exploitation, interference, or predation, but most examples describe species competing exploitatively for limiting resources (typically food). Here I report a case of character displacement evolving from aggressive behavioral interference, found in a well-studied system of terrestrial salamanders of the genus *Plethodon*. Using geometric morphometrics, I found parallel shifts in head shape from allopatry to sympatry in both *P. jordani* and *P. teyahalee*, and found significantly greater morphological divergence in sympatry relative to allopatry. Both findings are consistent with ecological character displacement. I also show a significant association between morphology and aggressive behavior, demonstrating a direct link between interference competition and morphology. I present a modified set of the criteria for character displacement that are appropriate for discriminating character displacement via aggressive interference from other possible evolutionary mechanisms. For this example, empirical support satisfying five of the six criteria for character displacement is found. These results provide evidence that morphological variation can be generated by mechanisms other than resource exploitation, which has profound implications for interpreting patterns of biological diversity.

Key words: behavioral interference; character displacement; geometric morphometrics; *Plethodon*.

INTRODUCTION

Understanding the forces that generate and maintain ecological communities has been an active area of research for decades. In many systems, field research has documented the importance and consequences of interspecific competition (reviewed in Schluter [2000a]), though the evolutionary significance of competition is still debated (see, e.g., Gotelli and Graves 1996). In communities where competition for a limiting resource occurs, interspecific resource competition sometimes generates shifts in morphological characters, or character displacement (Brown and Wilson 1956). Here, morphological differences between species are accentuated in sympatry, presumably as a result of interspecific competition (though character convergence can also occur: see Grant [1972], Abrams [1986]). Under this scenario, competing species will not only diverge in morphology, but also in resource use, as there is a causal link between the two. When other explanatory factors such as geographic clines and random chance can be eliminated, sympatric morphological divergence, coupled with resource partitioning, provides strong evidence of exploitative competition (Grant 1975, Arthur 1982, Schluter and McPhail 1992, Taper

and Case 1992). Though much controversy has surrounded the prevalence of ecological character displacement, recent evidence suggests that this evolutionary process may be relatively widespread (Schluter 2000a, b).

Because of its intuitive appeal, documenting examples of character displacement has received considerable attention, and theoretical work has explored the scenarios under which character shifts can and cannot evolve (see, e.g., Arthur 1982, Abrams 1986, Taper and Case 1992). Many theoretical models have shown that both character displacement and character convergence are feasible evolutionary outcomes under a variety of ecological scenarios involving exploitative competition for limiting resources. However, it is also recognized that other species interactions can generate similar patterns (Taper and Case 1992, Schluter 2000a). For instance, mathematical simulations have demonstrated that character divergence can evolve from apparent competition (i.e., shared predators; Abrams 2000), and in some instances from interference interactions (Abrams 1986, Abrams and Matsuda 1994). Though several studies suggest that predation can affect sympatric character divergence (e.g., Chiba 1999, Rundle et al. 2003), most examples of character displacement occur between species that compete exploitatively (nonaggressively) for a limiting resource.

In some biological communities, interference competition is the dominant ecological force describing

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species interactions. One of the best-studied examples of interference competition is found in *Plethodon* salamander communities in the southern Appalachian Mountains. Here, *Plethodon teyahalee* inhabits lower elevations, and members of the *P. jordani* complex inhabit higher elevations (Hairston 1949, 1951, Highton and Henry 1970, Highton and Peabody 2000). There is wide overlap between *P. metcalfi* and *P. teyahalee* in the Balsam Mountains (Balsams), but in the Great Smoky Mountains (Smokies) *P. jordani* replaces *P. teyahalee* altitudinally, with a narrow sympatric zone found in some parts of the range (Highton and Henry 1970). This pattern suggests that interspecific competition is more intense in the Smokies than in the Balsams (Hairston 1951, 1973). In a now classic series of long-term manipulative field experiments, Hairston (1980a) demonstrated that removal of one or the other species from experimental plots produced a faster and larger increase in abundance of the remaining species in the Smokies, supporting the hypothesis of more intense interspecific competition in the Smokies. In subsequent experiments (Hairston 1980b, 1983), transplanting animals from one location to another revealed that salamanders from the Smokies had a greater impact on salamanders from the Balsams, irrespective of which species was local or introduced. Because this affect was independent of transplant location, and also of local resources, it was proposed that aggressive interference, not resource exploitation, was the mechanism driving species interactions (Hairston 1983). This suggested that the competitive abilities of salamanders in the Smokies were heightened as a result of α selection (Gill 1974), a nonexploitative means of one species gaining competitive advantage over another. Behavioral experiments tested this hypothesis directly (Nishikawa 1985a, 1987), confirming that aggressive interactions (particularly of *P. teyahalee*) were heightened in the Smokies as a result of interference (Nishikawa 1987). Finally, when food resources were investigated, neither prey nor foraging microhabitats were partitioned in sympatry (Hairston et al. 1987), nor were food resources a limiting factor affecting salamander abundance (Hairston 1981). Taken together, these results show that competition was more intense in the Smokies, and provide strong evidence that the competition is mediated by interference, rather than exploitation (Hairston et al. 1987).

The field and laboratory experiments of Hairston and colleagues provide compelling evidence of interspecific interference competition between *P. jordani* and *P. teyahalee*. An unexplored question, however, is whether or not these competitive interactions affect morphology. In other species pairs of *Plethodon*, competitive interactions for food resources are significantly associated with differences in head morphology (Adams 2000, Adams and Rohlf 2000). Because aggressive interference between *P. jordani* and *P. teyahalee* in the Smokies is largely mediated by biting (Nishikawa

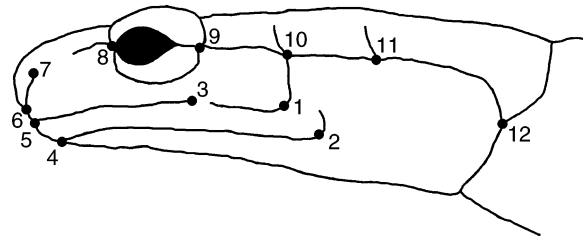


FIG. 1. Positions of 12 landmark locations used in this study. All landmarks were digitized from the left-lateral view of the skull. A total of 600 specimens were used in this study.

1985a), I hypothesize that populations with heightened aggression are more distinct morphologically than populations where aggression is reduced. Additionally, I hypothesize that there is a direct association between aggressive behavior and head morphology: a necessary requirement for selection to operate on morphology as a result of behavioral aggression. I examine both of these hypotheses using museum-based collections and geometric morphometric methods.

METHODS

A total of 600 adult specimens (289 *P. jordani* and 311 *P. teyahalee*) from 14 populations were obtained from the National Museum of Natural History (Washington, D.C., USA) and the Museum of Vertebrate Zoology (Berkeley, California, USA). Of these, 509 specimens from eight sympatric populations were collected from the same geographic locations as those used in prior ecological and behavioral studies (Hairston 1951, 1980a, b, 1983, Nishikawa 1985a, b, 1987). The collection localities included Heintooga Ridge, Keport Prong, and Taywa Creek in the Smokies; and Courthouse Creek in the Balsams. An additional 91 specimens were also obtained from six neighboring allopatric sites above and below the sympatric sites in the Smokies. Finally, a subset of the specimens from the Museum of Vertebrate Zoology had been used in previous behavioral studies (Nishikawa 1985a, b, 1987), allowing the direct comparison of morphology and aggressive behavior.

To quantify head morphology (shape) I used landmark-based geometric morphometric methods (Rohlf and Marcus 1993, Adams et al. 2004). First, digital images of the left-lateral side of the head were obtained from each specimen using a Nikon DXM-1200 high-resolution digital camera mounted to a Nikon SMZ-1500 stereomicroscope (Nikon Instruments, Inc., Melville, New York, USA). The x, y coordinates of 12 anatomical landmarks from the skull and jaw (Fig. 1) were then recorded from each image using TPSDIG (Rohlf 2001). From these, a set of shape variables were generated, after the effects of non-shape information (position, orientation, and scale) had been mathematically held constant. This was accomplished through a generalized Procrustes analysis (GPA; Rohlf and Slice

1990) followed by a thin-plate spline analysis (Bookstein 1991). The separate subset method (Adams 1999) was used to allow for the simultaneous analysis of the skull and mandible. With this approach, shape variables were generated separately for the skull and mandible using standard techniques, and then combined to form a data set representing the shape of the entire head for use in multivariate analyses (e.g., Adams and Rohlf 2000, Rüber and Adams 2001).

To assess morphological divergence in the Smokies between species (*P. jordani* vs. *P. teyahalee*), and between sites (allopatry vs. sympatry), a two-way MANOVA with interaction was performed on the combined data. A separate MANOVA was also performed on each transect. Head shape variation was then examined graphically along the first two axes of a principal components analysis (PCA) to facilitate anatomical description of any implied morphological changes. To assess the hypothesis that populations with heightened aggression were more distinct morphologically than populations where aggression was reduced, two statistical tests were performed. First, sympatric populations of both species were randomly paired with one another, and their morphological divergence (Euclidean distance among group means) was compared to the morphological divergence between randomly paired allopatric populations using a sign test (for similar approaches see: Schluter and McPhail 1992, Adams and Rohlf 2000). This procedure preserves the morphological covariance within-populations, and thus assesses only the between-population divergence relative to chance. For the second procedure, the observed difference between sympatric and allopatric divergence (D) was calculated. Specimens were then randomly assigned to one of the four groups, and the difference score was recalculated. The proportion of randomly generated difference scores (of 9999) that was greater than the observed difference score was treated as the significance level of the observed value (see, e.g., Adams and Rohlf 2000). This procedure therefore assesses between-population divergence against differing patterns of within-population covariance as generated by chance, providing a complementary test of observed divergence vs. chance expectation. Comparisons between the species in the Balsams and Smokies were performed using this second procedure. Finally, a multivariate association method (two-block partial least squares; see Rohlf and Corti [2000]) was used to examine the covariation between morphology and aggressive behavior.

RESULTS

Examining head shape variation in the Smokies, a two-way MANOVA revealed significant differences between species (exact $F = 4.59$, $df = 18, 315$, $P < 0.0001$), between sites (exact $F = 11.46$, $df = 18, 315$, $P < 0.0001$), and a significant interaction between species and site (exact $F = 2.15$, $df = 18, 315$, $P =$

0.0047). These results suggest that both species exhibited a significant morphological shift from allopatry to sympatry, a pattern consistent with ecological character displacement. Subsequent multiple comparisons revealed that the degree of morphological divergence between sympatric populations was significantly greater than between allopatric populations (sympatry $D = 0.079$, allopatry $D = 0.016$, random $P = 0.0001$), and that none of the randomly paired allopatric populations exhibited greater morphological divergence than found between sympatric populations (sign test, $N = 9$, $P = 0.0019$). These findings are also consistent with the hypothesis of ecological character displacement. When each transect was analyzed separately using MANOVA, a nearly identical pattern was revealed ($P < 0.0001$ for MANOVAs with sympatry $D >$ allopatry D [random $P = 0.0001$] for post hoc multiple comparisons). This indicated that the sympatric divergence was not geographically isolated, but was more consistent across populations. This finding, coupled with those from the randomly paired allopatric population analysis, strongly suggest that the character shift evolved in situ, reducing the possibility that geographic clines were responsible for the observed pattern (see Losos 2000).

When morphological variation was examined visually, both the morphological shift from allopatry to sympatry, and the greater sympatric morphological divergence, were biologically interpretable (Fig. 2). Comparing head shape between allopatric and sympatric populations revealed that both species displayed a relative elongation of the lower jaw in sympatry, coupled with a relative expansion of the posterior region of the jaw and head. Therefore, both species exhibited a parallel morphological shift of increased robustness in sympatry relative to allopatry. The greater difference between sympatric populations was also evident, as morphological variation of the two species in allopatry overlapped considerably, but was distinct for the species in sympatry (Fig. 2). Additionally, *P. teyahalee* displayed the most morphological change from sympatry to allopatry, and was extremely robust in its head shape characteristics. Comparisons of the morphological divergence from allopatry to sympatry supported this visual observation, showing greater divergence for *P. teyahalee* ($D = 0.099$) than for *P. jordani* ($D = 0.087$). This increased robustness in sympatric *P. teyahalee* was also consistent with behavioral observations, which demonstrated that *P. teyahalee* in the Smokies is highly aggressive (Nishikawa 1987).

To establish a direct link between sympatric morphological divergence and levels of aggressive interference, I examined the covariation between head shape and aggressive behavior (lunge, snap, bite) for a subset of specimens used in the earlier behavioral studies (Nishikawa 1985a, b). Using a two-block partial least-squares analysis I found a significant correlation between head shape and aggressive behavior ($r = 0.469$, $t = 3.19$, $df = 53$, $P = 0.003$). This analysis revealed

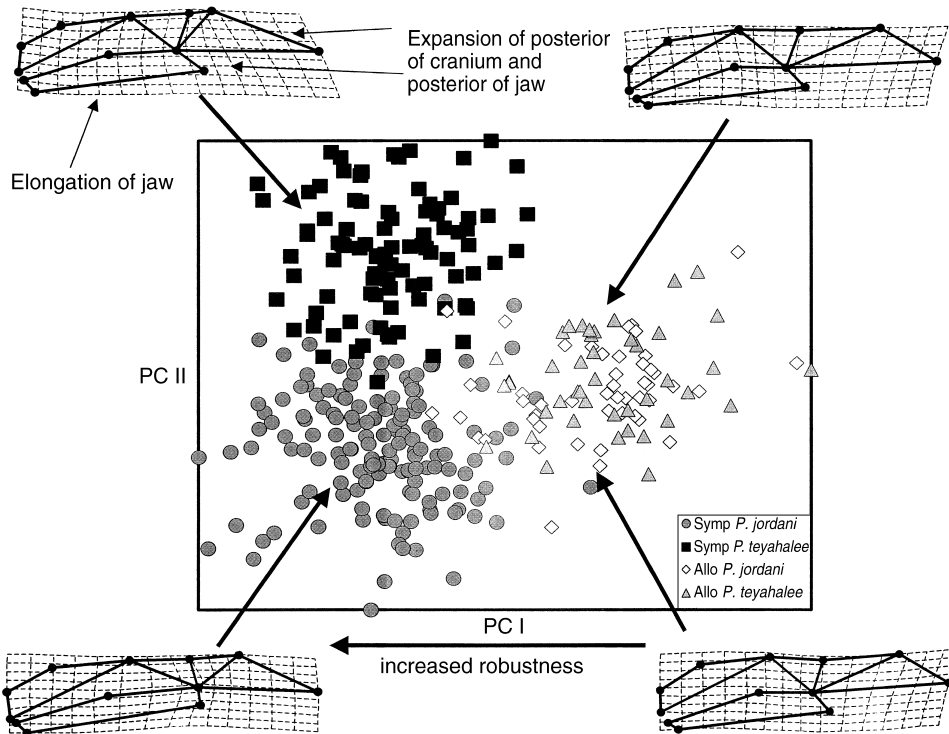


FIG. 2. Plot of the first two axes of a principal components analysis of head shape for sympatric and allopatric populations of *P. jordani* and *P. teyahalee* from the Smokies. Variation along PC1 corresponds to intraspecific differences between allopatric and sympatric populations, while variation along PC2 corresponds to interspecific differences between *P. jordani* and *P. teyahalee*. For intraspecific comparisons, head shape becomes more robust in sympatry. This morphological shift is more pronounced for *P. teyahalee*, which is considerably more robust in sympatry. Thin-plate spline representations of the average specimen for each population are exaggerated by a factor of 2 to emphasize the observed differences in head shape among populations.

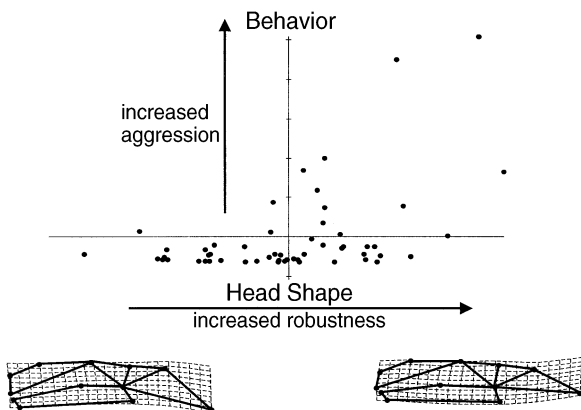


FIG. 3. Correlation plot of head shape versus aggressive behavior for a subset of specimens used in earlier behavioral studies (Nishikawa 1985a, b). The x-axis is head shape, and the y-axis is aggression. The significant correlation reveals that animals that are more robust in their cranial morphology are also more aggressive (bite more frequently and perform more gape displays). Thin-plate spline representations are exaggerated by a factor of 3 to emphasize the observed differences in head shape.

that salamanders with more robust jaws and heads also exhibited more aggression, and performed more bites and gape displays during behavioral trials than less aggressive salamanders (Fig. 3). Consistent with earlier findings (Hairston 1980b), *P. teyahalee* was more aggressive than *P. jordani* (*P. teyahalee* bite \bar{X} = 6.1, gape \bar{X} = 4.5; *P. jordani* bite \bar{X} = 5.4, gape \bar{X} = 2.4). This observed link between cranial robustness and aggressive behavior is consistent with field observations of territoriality and aggression in *Plethodon*, and suggests that increased robustness of the jaw and head may incur a fitness advantage in individuals that are more aggressive during territorial encounters.

Finally, to examine the broader morphological relationships between *P. teyahalee* and the *P. jordani* complex, I compared morphological divergence between sympatric *P. jordani* and *P. teyahalee* in the Smokies to morphological divergence between sympatric *P. metcalfi* and *P. teyahalee* in the Balsams. There were significant differences in overall head shape between populations (Wilks' Λ = 0.1101, F = 29.54, df = 18, 488, P << 0.0001), and the degree of morphological divergence between populations in the Smokies was significantly greater than between populations in the Balsams (Smokies D = 0.079, Balsams D =

0.032, random $P = 0.0001$). This was consistent with ecological and behavioral findings, which demonstrated both enhanced competition and heightened aggression in salamanders from the Smokies.

DISCUSSION

The data presented here identify significant morphological divergence between sympatric *P. jordani* and *P. teyahalee*, which is directly associated with aggressive behavior. This pattern is consistent with the hypothesis of ecological character displacement. Several studies have shown that behavioral modulation (e.g., niche partitioning) can be associated with character displacement (e.g., Pacala and Roughgarden 1985), but these patterns were also associated with a shift in resource use. Thus, it is unclear whether exploitative competition was responsible for the behavioral and morphological shifts, or if behavioral interactions were responsible for morphological differences and exploitative resource segregation (for explicit behavioral tests of these differing hypotheses see, e.g., Jaeger et al. [2002]). In a recent study, habitat segregation via aggressive interactions was associated with character displacement in body size (Melville 2002). Therefore, for some systems, it is possible that interspecific interference generates and/or maintains morphological character displacement.

My results, coupled with prior research on this system (e.g., Hairston 1980a, b) indicate that interspecific aggressive interference is responsible for the competitive interactions of *P. jordani* and *P. teyahalee*, and that this behavioral interference is directly associated with, and likely responsible for character displacement in cranial morphology. To rigorously demonstrate this however, alternative explanations must be eliminated. For character displacement via resource competition, one must show that (1) chance is ruled out as an explanatory factor; (2) other explanatory variables (e.g., body size, geographic clines) are eliminated; (3) there is independent evidence of competition for resources; (4) there is an association between morphology and resource use; (5) the morphological traits have a genetic basis; and (6) the resource bases among populations are qualitatively similar (Schluter and McPhail 1992). When character displacement arises from aggressive interference however, not all of these criteria apply, and so a modified set of criteria must be used (criteria have been proposed for other mechanisms, such as apparent competition [Schluter 2000a]). For such cases, I propose the following criteria: (1) chance is ruled out as an explanatory factor; (2) other explanatory variables (e.g., body size, geographic clines) are eliminated; (3) there is independent evidence of competition via aggressive interference; (4) there is an association between morphology and aggressive behavior; and (5) the morphological traits have a genetic basis. The last criterion, (6) comparing levels of aggression among populations, requires two alternative

expectations, because interspecific behavioral interference can evolve from one of two mechanisms. When interspecific aggression evolves from misidentification of intraspecific aggression (Tinbergen 1935, Lorenz 1966), levels of aggression should be similar between allopatric and sympatric populations. However, when interference evolves as a result of α selection (selection for enhanced competitive abilities [Gill 1974, Hairston 1980a]), intraspecific aggression and interspecific aggression are not equivalent. In such cases, levels of aggression should be higher in sympatric regions where interspecific competition is intense vs. sympatric regions where interspecific competition is minimal (the intensity of competition can be assessed independently through transplant and removal experiments, or through the estimation of the competitive effects of each species on the other [competition coefficients; see, e.g., Hairston 1980a, b, 1983]).

In this study, intraspecific morphological shifts from allopatry to sympatry were observed for both species, and significant sympatric morphological divergence was identified in the Great Smoky Mountains. Chance and body size patterns were eliminated as possible explanations of this pattern (criteria 1 and 2), and the consistent morphological pattern found in multiple transects ruled out the possibility that geographic clines were a possible explanation (criterion 2). I further found that morphology was significantly associated with aggressive behavior (criterion 4). Prior ecological and behavioral studies (Hairston 1980a, b, 1981, 1983, Nishikawa 1985a, 1987, Hairston et al. 1987) provide independent evidence of behavioral interference (criterion 3), and show that aggression in sympatric regions with interspecific competition is greater than in sympatric regions without interspecific competition (criterion 6). Taken together, this evidence addresses five of the six criteria for character displacement, providing strong support that ecological character displacement via aggressive interference may be a causal mechanism explaining current morphological differences between sympatric populations in the Smokies. Only evidence of the genetic basis of the morphological traits is lacking.

The fact that increased sympatric morphological divergence was observed with increased aggression suggests that greater morphological divergence was associated with stronger interspecific interaction. This finding is somewhat counterintuitive, and is in opposition to what is expected under exploitative resource competition, where theory predicts that the selective forces generating ecological character displacement serve to reduce interspecific competition, not enhance it. However, the difference may lie in the fact that, under interference competition, the morphological traits under selection are those used directly in aggressive encounters. In sympatry, those individuals that are more aggressive, and have increased robustness of the jaw and head, may incur a fitness advantage during

aggressive encounters. Thus, one can envision a competitive arms race, where those individuals with more robust jaws and skulls are more aggressive, thereby enhancing the competitive interactions.

One question not addressed is what ecological pressures lead to the initiation of α selection. A likely scenario is that the observed interference competition is mediated through territoriality, and territorial aggression has been enhanced as a result of α selection. Both species have fixed home ranges (Nishikawa 1990), and these home ranges are largely exclusive of the home ranges of rivals, supporting the hypothesis that both species are territorial. The exclusivity of most home ranges (Nishikawa 1990), the fact that most laboratory behavior encounters ended in aggression (Nishikawa 1985a, 1987), and the observation that many animals in natural populations had injuries caused by other salamanders (Nishikawa 1990) all suggest that both species actively defend territories through aggression. Taken together, this evidence supports the hypothesis that interference competition is mediated through territoriality, and territorial aggression has been enhanced as a result of α selection.

Identifying morphological patterns generated by interspecific competition is an important means of understanding the evolutionary consequences of species interactions. While morphological patterns generated from exploitative competition are well understood, little is known about the effects that interference competition may have on morphology (but see Melville 2002). Further, theoretical models have shown that character divergence is a mathematical possibility (Abrams 1986, Abrams and Matsuda 1994), but have not fully explored the full spectrum of ecological interactions that generate interference between species (e.g., what occurs when intraspecific and interspecific interference are not equal?) In this study, I identified an example of ecological character displacement as a result of aggressive behavioral interference. These results provide evidence that morphological variation can be generated and maintained by mechanisms other than resource exploitation, a finding that has profound implications for interpreting and understanding patterns of biological diversity. It further emphasizes that the best approach to understanding the evolutionary consequences of interspecific interactions is a pluralistic one, where diverse data types are brought together to address the same ecological hypothesis. With this approach, strong inference can be made, and the morphological effects of competition can be better understood.

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