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CHARACTER DISPLACEMENT IN POLYPHENIC TADPOLES

DAVID W. PFENNIG[1] AND PETER J. MURPHY
Department of Biology, Coker Hall, CB 3280, University of North Carolina, Chapel Hill, North Carolina 27599-3280
[1]*E-mail: dpfennig@email.unc.edu*

Abstract.—Biologists have long known that closely related species are often phenotypically different where they occur together, but are indistinguishable where they occur alone. The causes of such character displacement are controversial, however. We used polyphenic spadefoot toad tadpoles (*Spea bombifrons* and *S. multiplicata*) to test the hypothesis that character displacement evolves to minimize competition for food. We also sought to evaluate the role of phenotypic plasticity in the mediation of competitive interactions between these species. Depending on their diet, individuals of both species develop into either a small-headed omnivore morph, which feeds mostly on detritus, or a large-headed carnivore morph, which specializes on shrimp. Laboratory experiments and surveys of natural ponds revealed that the two species were more dissimilar in their tendency to produce carnivores when they occurred together than when they occurred alone. This divergence in carnivore production was expressed as both character displacement (where *S. multiplicata*'s propensity to produce carnivores was lower in sympatry than in allopatry) and as phenotypic plasticity (where *S. multiplicata* facultatively enhanced carnivore production in *S. bombifrons,* and *S. bombifrons* facultatively suppressed carnivore production in *S. multiplicata*). In separate experiments, we established that *S. bombifrons* (the species for which carnivore production was enhanced) was the superior competitor for shrimp. Conversely, *S. multiplicata* (the species for which carnivore production was suppressed and omnivore production enhanced) was the superior competitor for detritus. These results therefore demonstrate that selection to minimize competition for food can cause character displacement. They also suggest that both character displacement and phenotypic plasticity may mediate competitive interactions between species.

Key words.—Amphibians, competition, divergent selection, local adaptation, phenotypic plasticity, *Spea.*

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Darwin (1859) first noted that populations of two closely related species are often different (morphologically or behaviorally) where the two species occur together, but are indistinguishable where they occur alone. For example, the ground finches *Geospiza fortis* and *G. fuliginosa* occur singly on the Galapagos islands of Daphne and Hermanos, respectively, and they have almost the same bill size. On islands where these species co-occur, however, *G. fortis* has a substantially larger bill than *G. fuliginosa* (Lack 1947; Grant 1986). This divergence of phenotypes, a pattern termed character displacement by Brown and Wilson (1956), is commonly observed in plants and animals (e.g., Schoener 1970; Eldredge 1974; Fenchel 1975; Kellogg 1975; Schindel and Gould 1977; Roughgarden et al. 1983; Schluter and McPhail 1992; Armbruster et al. 1994; Robinson and Wilson 1994; Adams and Rohlf 2000; Losos 2000).

Evolutionary biologists have long debated why character displacement arises (see Brown and Wilson 1956; Grant 1972, 1994; Diamond et al. 1989; Losos 2000). A leading hypothesis is that character displacement evolves as a means of minimizing competition for resources, especially food. If the ability to procure resources reduces the fitness of individuals in populations that overlap with a close competitor, then those individuals that are the most unlike the other species will experience the least competition and therefore will be favored by natural selection. Consequently, each population will evolve to be less like the other. Divergent selection resulting from competition may be an important force in promoting diversification among coexisting species (Schluter and McPhail 1992; Robinson and Wilson 1994; Schluter 1994; Rundle et al. 2000).

The competition hypothesis is difficult to test because there may be a long time lag between the introduction of a competitor and the evolutionary response of the focal species. For this reason, much of the evidence used to support the hypothesis that competition leads to character displacement is correlational rather than experimental (Grant 1994; Schluter 1996). Moreover, the competition hypothesis has been supported in some instances (Grant 1994), but not others (Grant 1975). Thus, it is difficult to evaluate whether and how resource competition causes character evolution (but see Schluter 1994).

Species that respond to competitors through polyphenism, the existence of environmentally cued alternative phenotypes in a population (West-Eberhard 1989), provide a direct method to evaluate the role of competition in promoting character change. If the production of phenotypic alternatives is influenced by competitors, such a mechanism could enable the facultative expression of a phenotype more unlike the competitor's. A causal link can then be established experimentally between the presence of heterospecific competitors and character change if, by removing (or adding) competitors, the polyphenic species differentiates (or fails to differentiate) into an alternative morph that resembles the competitor (e.g., see Pfennig 1992a; Maret and Collins 1997). Furthermore, such competitively induced polyphenism may eventually lead to a pattern of character displacement, where different inherited tendencies to adopt each alternative phenotype may become fixed in sympatry versus in allopatry with heterospecifics. Fixation may occur because selection should become increasingly effective at producing a particular phenotype as that phenotype becomes increasingly common in the population (West-Eberhard 1989). Polyphenic species, therefore, may be ideal for evaluating whether and how resource competition leads to character displacement.

We sought to explore the possible role of resource competition in promoting character displacement using Plains spadefoot toads (*Spea bombifrons*) and New Mexico spade-

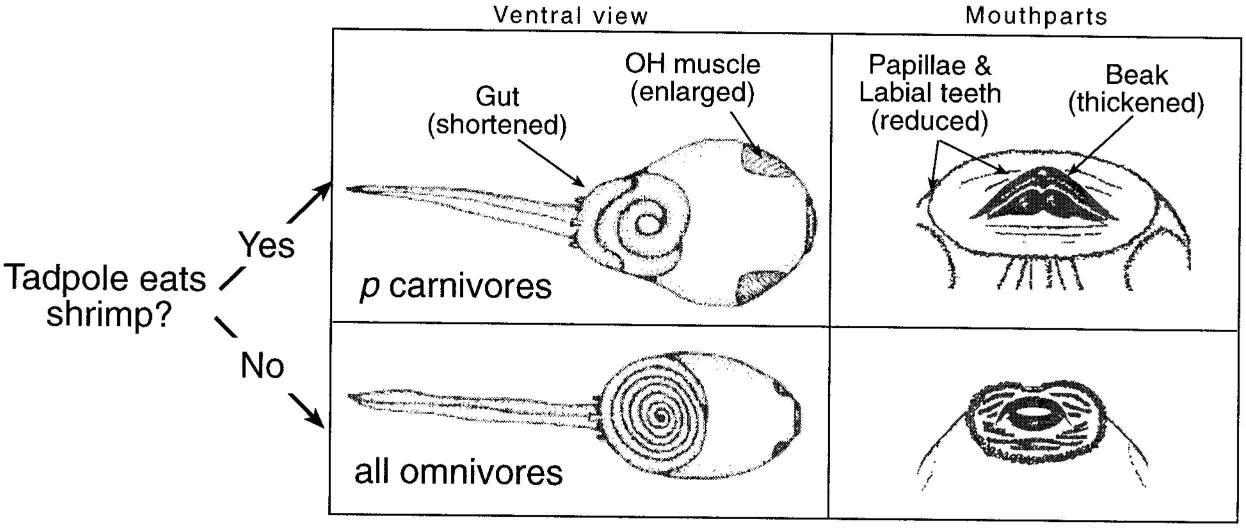

FIG. 1. Spadefoot toad tadpoles are born as omnivores, but if a young omnivore ingests shrimp, a reversible switch causes a fraction, *p*, to change into a distinctive carnivore morph tadpole.

foot toads (*S. multiplicata*). As illustrated in Figure 1, typical omnivorous tadpoles of both species may assume a distinctive carnivore phenotype following ingestion of anostracan fairy shrimp (Pomeroy 1981; Pfennig 1990, 1992a,b). This plasticity is maintained evolutionarily, in part, as an adaptation to spatial and temporal variation in pond drying times (Pfennig 1990, 1992a). Carnivores are favored in highly ephemeral pools, where shrimp are most abundant and where the carnivore's rapid growth and development increase the chance that tadpoles will metamorphose before the pond dries (Pfennig 1990, 1992a). Omnivores, conversely, are favored in longer lasting pools, because they tend to achieve metamorphosis in better condition (Pfennig 1992a).

Polyphenism in *Spea* appears to have a heritable basis. Although heritability of carnivore production has not been measured, certain families are more likely than others to produce carnivores when reared under common conditions (Pfennig and Frankino 1997; Pfennig 1999). This variation among families suggests that polyphenism in *Spea* has a heritable basis capable of responding to selection.

Within a species, resource competition plays an important role in influencing the likelihood of each morph being produced. In *S. multiplicata*, previous research (Pfennig 1992a) indicates that there is disproportionately severe competition among members of the same morph. Competition within morphs arises because food types used by carnivores and omnivores (shrimp and detritus, respectively) are potentially limiting in natural ponds (Pomeroy 1981). Evidence of intramorph competition comes from manipulations in natural ponds in which the frequency of each morph was altered. When each morph was overrepresented (i.e., when its frequency was increased), that morph was significantly smaller at metamorphosis than when it was underrepresented (Pfennig 1992a). In response, tadpoles tended to switch to the underrepresented morph. These results demonstrate that conspecific *Spea* with similar phenotypes are more likely to compete for food than are conspecifics with dissimilar phenotypes.

Field surveys suggest that interspecific resource competition may also influence carnivore production within both *Spea* species. In ponds where *S. bombifrons* and *S. multiplicata* co-occur, most carnivores are *S. bombifrons*, even if *S. bombifrons* is more rare (Simovich 1985), indicating that the species differ in their tendency to adopt the carnivore phenotype. Moreover, the presence of heterospecific competitors may influence carnivore production in these species, creating an opportunity to study the ecological causes of character displacement.

This study addressed four questions. First, has the tendency to express the carnivore phenotype in either species diverged evolutionarily between sites in sympatry and in allopatry with the other species? In other words, has there been character displacement in propensity to express the carnivore morphology? Second, does either species facultatively influence the developmental decisions of the other species? In particular, when the two species are reared together, is carnivore production in *S. bombifrons* enhanced, but suppressed in *S. multiplicata*? Third, is resource competition the selective basis of character change in response to heterospecifics? Finally, what is the proximate basis of any competitive differences that might exist between the two species?

METHODS

Field Surveys

We first asked whether *S. multiplicata* is more likely to adopt the carnivore phenotype in allopatry than in sympatry with *S. bombifrons*. To test this, we sampled carnivores and omnivores from nine ponds near Portal, Arizona, with a handheld dip net (locations of ponds in Pfennig 1990). Five ponds were high-elevation (~ 1650 m), pure-species ponds (i.e., ponds in which *S. multiplicata* was the only *Spea* species present); the remaining four ponds were lower-elevation (~ 1200 m), mixed-species ponds (i.e., ponds in which both *Spea* species were present). *Spea bombifrons* does not live above about 1500 m elevation in southeastern Arizona (Simovich

1985), and this species had been present in the mixed-species ponds and absent in the pure-species ponds for at least the past 20 years (Pomeroy 1981; Simovich 1985). Moreover, other than the presence of *S. bombifrons*, ponds were similar in ecological characteristics (e.g., pond drying times, fairy shrimp density, tadpole density; Pfennig 1992a). Because tadpoles of the two species are difficult to distinguish morphologically and may hybridize and produce viable F_1 hybrid female offspring (Simovich 1985), we employed protein electrophoresis to classify tadpoles as *S. bombifrons*, *S. multiplicata*, or F_1 hybrids (Simovich and Sassaman 1986).

Our response measures were the overall proportion of tadpoles that were carnivores in each pond and the proportion of *S. multiplicata* that were carnivores in each mixed-species pond. Using these data, and two-tailed Mann-Whitney tests, we asked two questions. First, did the overall proportion of carnivores differ in mixed and pure-species ponds? Second, was the proportion of *S. multiplicata* that developed into carnivores in mixed-species ponds less than that in pure-species ponds?

Experiment 1: When Reared under Common Conditions, Do Tadpoles from Pure- and Mixed-Species Ponds Differ in Propensity to Express the Carnivore Phenotype?

The field surveys indicated that fewer *S. multiplicata* carnivores were produced in mixed-species ponds than in pure-species ponds (see Results). These differences in carnivore production could be due to genetic differences between sympatric and allopatric populations, where populations in allopatry have a higher inherent propensity to express the carnivore morphology. Alternatively, these differences could be attributable to phenotypic plasticity, where *S. bombifrons* facultatively suppresses carnivore production in *S. multiplicata* in mixed-species ponds. In this experiment, we used a common-garden design to determine if the propensity to express the carnivore morphology varies between sympatric and allopatric *S. multiplicata* populations. In Experiment 2 (see below), we evaluated the phenotypic plasticity hypothesis.

For the common-garden experiment, we sampled breeding pairs of *S. multiplicata* from nine ponds near Portal, Arizona. Three ponds were high-elevation (~ 1650 m), pure-species ponds and six were lower-elevation (~ 1200 m), mixed-species ponds. Ponds were separated by at least 3 km but no more than 27 km; given evidence of reduced migration in *Spea*, there was probably negligible gene flow between populations in different ponds. Ponds were similar ecologically except for the presence or absence of *S. bombifrons*. After capture, pairs spawned in separate 10-L water-filled plastic boxes. Five days after the tadpoles hatched, four to 10 groups of eight full siblings from each sibship were chosen randomly, and each group was placed into a separate rearing tank. In this and all following experiments, rearing tanks (28 × 18 × 10 cm) were filled with 6 L of dechlorinated tap water and placed in the same room. Tanks containing tadpoles from different sibships and ponds were interspersed and randomized by location in the rearing room. Tadpoles were fed live Anostracan fairy shrimp (*Thamnocephalus* and *Streptocephalus* spp.) throughout the experiments ad libitum. At 2 weeks posthatching, tadpoles were scored as being omnivores or carnivores by characterizing the shape of the head and mouthparts (e.g., see Fig. 1). Morph assignments were unambiguous and made without a priori knowledge of pond origin. These experiments involved 2056 *S. multiplicata* tadpoles from 58 sibships (22 from allopatric sites and 36 from sympatric sites).

For the analysis, we first calculated the proportion of tadpoles that developed into carnivores in each tank and subsequently sibship. A pond mean in carnivore production was determined from all resident sibships. We used a two-tailed Mann-Whitney test to determine if the mean proportion of carnivores produced by *S. multiplicata* in ponds in sympatry with *S. bombifrons* differed from *S. multiplicata* in allopatric ponds.

Experiment 2: Does the Presence of Heterospecifics Influence the Developmental Decisions of Individual Tadpoles to Express the Carnivore Phenotype?

We next used laboratory experiments to answer two questions regarding facultative changes in polyphenism. First, does the presence of heterospecifics affect the overall production of carnivore morphs? Second, do heterospecifics decrease the propensity to become a carnivore in one species, but increase the propensity to become a carnivore in the other species? To address these questions, we compared the likelihood of tadpoles assuming the carnivore phenotype when raised with conspecifics only versus when raised with both conspecifics and heterospecifics.

We collected four amplectant pairs each of *S. bombifrons* and *S. multiplicata* during July 1999 at a pond near Portal, Arizona. One week after the tadpoles hatched from spawning boxes, we randomly assigned groups of eight similarly sized larvae from each sibship to the following three treatment categories: (1) *S. bombifrons* only ($n = 60$ replicate tanks); (2) *S. multiplicata* only ($n = 60$ replicate tanks); or (3) four *S. bombifrons* and four *S. multiplicata* ($n = 60$ replicate tanks). The original four sibships for both species were equally represented in the mixed- and pure-species treatment categories, and tankmates differed in snout-vent length (SVL) by no more than 5%. Tadpoles were placed in rearing tanks and fed live fairy shrimp ad libitum, with treatments interspersed and randomized by location (see experiment 1). The experiment was ended after 6 days (13 days posthatching), because carnivores are unlikely to be produced thereafter (Pfennig 1992a). At termination, one person scored all of the tadpoles as either omnivores or carnivores as in experiment 1, without a priori knowledge of each tank's treatment. These data provided us with the observed proportion of pure- and mixed-species tanks that produced a carnivore.

To assess whether carnivore production differed in mixed- and pure-species tanks, we computed the expected number of carnivores in mixed-species tanks by assuming that the two species did not interact to produce carnivores. We then compared this expected number of carnivores with the actual number observed in the mixed-species tanks by using a chi-square goodness-of-fit test. Calculating the expected number of carnivores in the mixed-species tanks required obtaining a per larva probability of carnivore production, rather than a per tank probability, because mixed-species tanks contained four rather than eight tadpoles of each species. Based on p_j, the per tank probability of carnivore production for each species j (i.e., the number of tanks with carnivores divided by the total number of tanks [no more than one carnivore was produced per tank]), the per larva probability, O_j, was calculated as follows (see Pfennig and Collins 1993):

$$O_j = 1 - \sqrt[8]{1 - p_j}. \tag{1}$$

We then used O_j to calculate E, the overall expected probability of a carnivore morph developing in mixed-species tanks:

$$E = 1 - \prod_{j=1}^{s} (1 - O_j)^{N_j}, \tag{2}$$

where s was the number of species per tank (two) and N_j the number of larvae from species j (four). Finally, the expected number of mixed-species tanks with carnivores was the product of E and the number of tanks (60).

Given that the presence of heterospecifics increased the production of carnivores, we sought to determine if this enhancement was caused by a change in carnivore production in *S. bombifrons, S. multiplicata,* or both species. To compare carnivore production in each species separately, we first ascertained the number of carnivores of each species in mixed-species tanks by using protein electrophoresis to identify species-specific alleles (see Field Surveys above). We then asked whether each species' propensity to produce carnivores when with heterospecifics was different than their propensity in pure-species tanks. Because only four tadpoles of each species were present in mixed tanks, we calculated E_j, the expected probability of carnivore production for each species j, from O_j, determined for pure-species tanks above:

$$E_j = 1 - (1 - O_j)^4. \tag{3}$$

The expected number of mixed-species tanks with carnivores for each species was then the product of E and the total number of tanks (60). We used a separate chi-square goodness-of-fit test for *S. bombifrons* and *S. multiplicata* to determine whether the observed numbers of mixed-species tanks with and without carnivores differed significantly from the expected numbers.

Experiment 3: Is Divergence between Species in Carnivore Production Related to Competitive Differences between Species?

Next, we sought to ascertain the possible selective basis for why competing species differ more in expression of polyphenism when they occur together than when occur alone. Based on the outcomes of the field surveys and the previous experiments, we tested two hypotheses: (1) *S. bombifrons* carnivores are competitively superior to *S. multiplicata* carnivores, because *S. bombifrons* outcompete *S. multiplicata* for shrimp prey; and (2) *S. multiplicata* omnivores are competitively superior to *S. bombifrons* omnivores, because *S. multiplicata* outcompete *S. bombifrons* for detritus.

We collected 10 amplectant pairs each of *S. bombifrons* and *S. multiplicata* from a July 1999 breeding chorus near Apache, Arizona (31°40′N, 109°08′W). Two days after the tadpoles hatched from pairs in spawning boxes, we placed all *S. bombifrons* and *S. multiplicata* tadpoles into separate wading pools (two 1.93-m diameter pools per species) that had been filled 20 cm deep with dechlorinated water. Tadpoles were fed live fairy shrimp and rabbit chow ad libitum. When the tadpoles were seven days old, we randomly selected 45 carnivores and 120 omnivores of each species and conducted a separate interspecific competition experiment for each morph.

In the carnivore competition experiment, we randomly assigned similarly sized carnivores of each species to the following two treatments: (1) a pure-species group, in which each carnivore was reared with a single conspecific carnivore (N = 10 tanks for each species); and (2) a mixed-species group, in which each carnivore was reared with a single heterospecific carnivore (N = 25 tanks). All carnivores were measured for initial SVL, and tankmates differed in initial SVL by no more than 5%. We also recorded the starting orbitohyoideus (OH) muscle width of each carnivore. The OH is the primary abductor muscle of the buccal cavity (Satel and Wassersug 1981), and more extreme carnivores have a larger OH:SVL ratio (Pfennig 1992b).

To distinguish between the two species, we used a 26-gauge hypodermic needle to inject a fluorescent green or orange elastomer (Northwest Marine Technology, Inc., Shaw Island, WA) into the dorsal tail membrane of each tadpole in all tanks. Once injected, the material formed an inert strip (approximately 1 mm wide by 5 mm long) visible under ultraviolet light. The marking procedure did not affect larval mortality.

Carnivores were reared under similar conditions as in experiments 1 and 2, but the feeding regime was modified. Each tank received 10 large (total length = 30 mm) fairy shrimp once a day and 0.1 g of crushed rabbit chow every three days. Pulverized rabbit chow closely approximates in form and nutrition the organic detritus on which spadefoot tadpoles feed in natural ponds (Pfennig et al. 1991). The carnivores' diet was restricted, because all shrimp and chow had been consumed from each tank before they were fed again. We ended the experiment seven days after it started so that all tadpoles could be measured before metamorphosis. For each carnivore, we recorded final SVL and width of the OH muscle.

In the omnivore competition experiment, we assigned two similarly sized omnivores to one of four treatments: (1) a pure-species/shrimp diet group, in which each tadpole was reared with a conspecific and fed exclusively live fairy shrimp (N = 20 tanks for each species); (2) a mixed-species/shrimp diet group, in which each was reared with a heterospecific and fed exclusively live fairy shrimp (N = 40 tanks); (3) a pure-species/detritus diet group, in which each was reared with a conspecific and fed exclusively pulverized rabbit chow (N = 40 tanks for each species); and (4) a mixed-species/detritus diet group, in which each was reared with a heterospecific and fed exclusively pulverized rabbit chow (N = 40 tanks). All omnivores were measured for initial SVL, and tankmates differed initially by no more than 5%.

Omnivores were reared under the same conditions as carnivores, with the exception of treatment diet. In shrimp treatments, during the first three days tanks received 20 ml of water containing approximately 100 small fairy shrimp (total length < 10 mm). After day 3, when the omnivores increased in size, tanks received 10 large (total length = 30 mm) fairy shrimp daily. In detritus treatments, tanks received 0.1 g of crushed rabbit chow every three days. Both diets were restrictive: all shrimp and rabbit chow had been consumed from tanks before the next feeding. We ended the experiment 13 days after it started and recorded the final SVL of each omnivore. Omnivores from mixed-species tanks were scored using protein electrophoresis to determine species identity (see Field Surveys above).

For both the carnivore and omnivore competition experiments, the statistical analysis consisted of contrasting change in SVL of tadpoles when reared with conspecifics versus that of the same species when reared with a heterospecific. Change in SVL was an appropriate measure to assess the effects of competition, because larval growth in amphibians is highly sensitive to competition (Wilbur 1977; Semlitsch and Caldwell 1982). Moreover, larval growth rate appears to be under strong directional selection in *Spea*, with greater growth rates being favored for two reasons. First, rapid larval growth is essential for tadpoles to metamorphose from the highly ephemeral ponds in which *Spea* breed (Pfennig 1990, 1992a). Second, larval growth rate correlates positively with post-metamorphic longevity in *Spea* (Pfennig et al. 1991).

For the carnivore competition analysis, we also contrasted the OH muscle of individuals reared with conspecifics versus that for individuals of the same species reared with a heterospecific. Width of the OH muscle is a plastic trait in *Spea* and increases or decreases depending on how many shrimp the tadpole ingests (the more shrimp a tadpole ingests, the larger the OH: Pfennig 1990). To control for differences among individuals in overall body size (SVL), we used the OH:SVL ratio to contrast carnivores reared with conspecifics versus those reared with a heterospecific. Both the change in SVL and the OH:SVL data were arcsine-square-root transformed before analysis to meet the assumptions of parametric statistical procedures and analyzed using two-tailed unpaired *t*-tests.

Experiment 4: Are Competitive Differences between Species Related to Differences in Foraging Behavior?

Finally, we sought to elucidate a proximate mechanism by which differences in competitive abilities might arise. We tested the following two hypotheses: (1) *S. multiplicata* larvae are less active and, thus, are less efficient shrimp foragers than *S. bombifrons* larvae; and (2) *S. bombifrons* larvae spend less time grazing for food and, thus, are less efficient detritivores than *S. multiplicata* larvae.

To test the first hypothesis regarding shrimp foraging, we asked whether *S. bombifrons* and *S. multiplicata* tadpoles differed in mean capture and handling of a single large fairy shrimp. Second, we asked if such differences in capture time were due to species-specific differences in the ability to sense or perceive a shrimp in their environment or species-specific differences in activity levels (i.e., all else being equal, a more active tadpole should be more likely to encounter a shrimp than a less active tadpole). We conducted two separate experiments to address the above questions.

First, we placed 32 similarly sized, satiated omnivores of both species in separate cups filled with 450 ml of dechlorinated water. We then put into each cup three large fairy shrimp (total length = 30 mm). An observer then censused the cups at least once every hour between 0700 h and 2200 h and recorded the time from the start of the experiment to when the first shrimp disappeared. We then used these data and a failure time analysis (with a Wilcoxon comparison between species) to determine if the two species differed in the time that similarly satiated omnivores took to consume a shrimp.

In a second experiment, we tested omnivores of each species for species-specific differences in the tendency to associate with shrimp. We divided a plastic tray (38 × 15 × 5 cm) into three equal sized compartments with vertical 80 μm nylon mesh. A line was drawn down the middle of the center compartment. We flooded the tray with 750 ml of dechlorinated water, placed 20 large fairy shrimp in one end compartment, and waited 2 min before placing a focal tadpole in the middle of the center compartment. After a 2-min acclimation period, we observed the focal tadpole's position continuously for the next 10 min, recording the side of the center compartment in which the tadpole was located. After each tadpole was tested, we rinsed the tray and switched the side in which shrimp were placed. We then used these data and a two-tailed unpaired *t*-test to determine if the two species differed in their associational preferences for shrimp (as estimated by amount of time each species spent on the side of the center compartment closer to the shrimp) and activity level (as estimated by the number of times each species switched sides of the center compartment).

To determine if *S. bombifrons* and *S. multiplicata* differed in length of time spent grazing for food (hypothesis 2 above), we randomly selected 20 similarly sized, two-week-old omnivores of both species as test subjects. We then filled six clear plastic aquaria (34 × 22 × 10 cm) 5 mm deep with bottom detritus from a natural pond. We flooded the aquaria with 6 L of dechlorinated water and waited for the detritus to settle on the bottom. We started each observational trial by placing a single test omnivore into each aquarium. After a 10-min acclimation period, we observed the tadpole in each aquarium for 10 min and categorized its behavior as grazing (feeding on the bottom or surface of the water), swimming (moving through the water column but obviously not feeding), or resting (motionless). The tadpole was then removed from the aquarium, and the above observational procedures were repeated with a heterospecific tadpole. Using a one-way ANOVA on transformed (arcsine-square root) proportion data, we determined if the two species differed in the proportion of time spent in the above three activities.

RESULTS

Field Surveys

The overall proportion of carnivores in the five pure *S. multiplicata* ponds (0.42 ± 0.15 SE) did not differ significantly from that in the four mixed-species ponds (0.39 ± 0.11; $U' = 11$, $P = 0.81$; Fig. 2). We detected no hybrids. However, the proportion of *S. multiplicata* expressing the carnivore morphology in mixed-species ponds (0.03 ± 0.04) was significantly less than the proportion of *S. multiplicata*

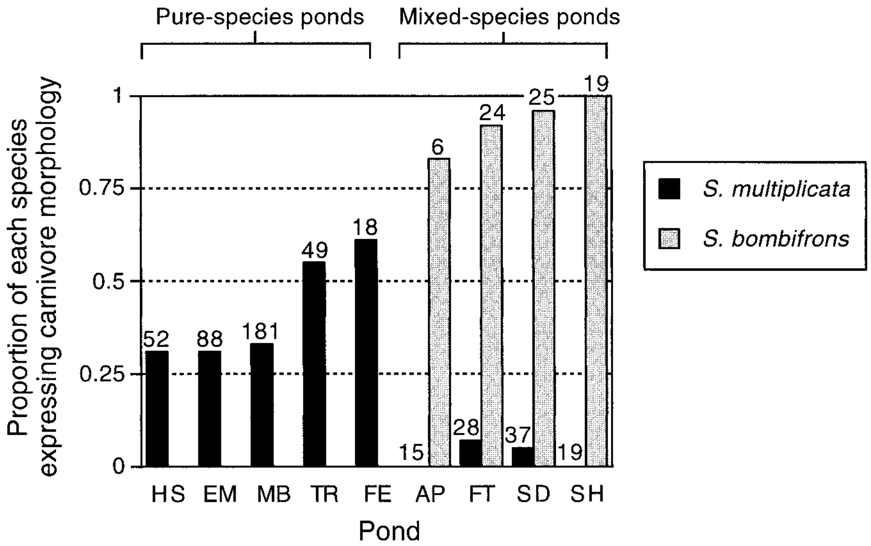

FIG. 2. Proportion of wild-caught tadpoles of each species expressing the carnivore morphology (height of bar) in nine different natural ponds: five pure-species ponds (i.e., ponds where *S. multiplicata* was the only *Spea* species present) and four mixed-species ponds (i.e., ponds were both *S. multiplicata* and *S. bombifrons* were present; there were no *S. multiplicata* carnivores in ponds AP and SH). Number above each bar is the number of tadpoles of each species sampled.

expressing the carnivore morphology in pure *S. multiplicata* ponds (0.42 ± 0.15; $U' = 20$, $P = 0.01$), even though *S. multiplicata* was more common in all nine ponds (Fig. 2). Thus, these data suggest that carnivore production in *S. multiplicata* is reduced in the presence of *S. bombifrons.*

Experiment 1

The inherent propensity of *S. multiplicata* tadpoles to express the carnivore morphology varied between sites in allopatry and sympatry with *S. bombifrons* (Fig. 3). When reared under common laboratory conditions, the mean proportion of carnivores produced by *S. multiplicata* sibships from sympatric ponds (0.019 ± 0.010) was significantly less than by sibships from allopatric ponds (0.098 ± 0.013; $U' = 18$, $P = 0.020$). Thus, these data suggest that carnivore production in *S. multiplicata* has diverged evolutionarily between sites in sympatry and in allopatry with *S. bombifrons.*

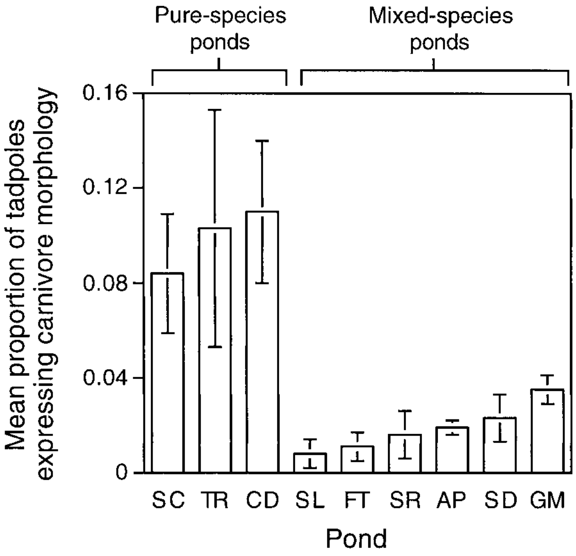

FIG. 3. Mean (± SEM) proportion of *Spea multiplicata* tadpoles from each of nine different ponds expressing the carnivore morphology (height of bar) when reared from fertilization under common conditions. Parents of tadpoles from pure-species ponds were from high-elevation sites where *S. bombifrons* is absent, whereas parents of tadpoles from mixed-species ponds were from low-elevation sites where both *Spea* species co-occur.

Experiment 2

Not only was there evidence of heterospecifics affecting the evolution of different propensities to express carnivores in sympatry and in allopatry, but *Spea* tadpoles also appeared to respond to the presence of heterospecifics facultatively (i.e., through phenotypic plasticity). In particular, carnivore morph tadpoles were significantly more likely to be produced in mixed-species groups than in pure-species groups (Table 1; $\chi^2 = 26.49$, df = 1, $P < 0.0001$). Fifty-one of 60 (85%) of the mixed-species tanks produced a carnivore morph as

TABLE 1. Effect of the presence of heterospecifics on expression of carnivore morphs of spadefoot toad tadpoles in aquaria with equal larval densities.

Composition of aquarium population	Carnivore developed in tank	No carnivore developed in tank	Total tanks
Spea multiplicata only	10 (17%)	50 (83%)	60
S. bombifrons only	43 (72%)	17 (28%)	60
Both species			
Observed	51 (85%)*	9 (15%)	60
Expected[1]	31 (52%)	29 (48%)	60

[1] Expected values in mixed-species tanks were derived from observed values in pure-species tanks (see Methods).

* Significantly more carnivores were produced in mixed-species aquaria than expected (chi-square goodness of fit test: ($\chi^2 = 26.49$, df = 1, $P < 0.0001$).

TABLE 2. Number of carnivores produced by each two species of spadefoot toads when reared in mixed-species tanks.

Species	Carnivore developed in tank	No carnivore developed in tank	Total tanks
Spea multiplicata			
Observed	1 (2%)*	59 (98%)	60
Expected[1]	5.23 (9%)	54.77 (91%)	60
S. bombifrons			
Observed	50 (83%)**	10 (17%)	60
Expected[1]	28.06 (47%)	31.94 (53%)	60

[1] Expected values were derived from observed values in pure-species tanks (see Methods).

* Significantly fewer *S. multiplicata* carnivores were produced in mixed-species aquaria than expected (chi-square goodness of fit test: $\chi^2 = 3.75$, df = 1, $P = 0.05$).

** Significantly more *S. bombifrons* carnivores were produced in mixed-species aquaria than expected (chi-square goodness of fit test: $\chi^2 = 32.23$, df = 1, $P < 0.0001$).

opposed to 43 of 60 (72%) *S. bombifrons* pure-species tanks and 10 of 60 (17%) *S. multiplicata* pure-species tanks.

When reared together, there was a striking disparity between *S. bombifrons* and *S. multiplicata* in their propensity to produce carnivore morph larvae. In mixed-species tanks, we expected that 28.06 carnivores would be *S. bombifrons* and 5.23 would be *S. multiplicata* (Table 2). Yet, in 50 of the 51 mixed-species tanks (98%), the only carnivores were *S. bombifrons*; only one tank (2%) contained a *S. multiplicata* carnivore (Table 2). Therefore, in mixed-species tanks, contrary to expectations, fewer *S. multiplicata* carnivores were produced ($\chi^2 = 3.75$, df = 1, $P = 0.05$) and more *S. bombifrons* carnivores were produced ($\chi^2 = 32.23$, df = 1, $P < 0.0001$). In sum, when reared together, carnivore production was enhanced in *S. bombifrons* and suppressed in *S. multiplicata*.

Experiment 3

The presence of heterospecifics differentially altered carnivore production and had differential impact on the growth of carnivore and omnivore tadpole morphs of both species. First, in the carnivore competition experiment, *S. bombifrons* carnivores grew significantly more when reared with a heterospecific rather than with a conspecific carnivore ($t_{43} = 3.28$, $P = 0.002$; Fig. 4a). In contrast, *S. multiplicata* carnivores grew significantly less when competing with a heterospecific rather than a conspecific carnivore ($t_{43} = 2.52$, $P = 0.016$; Fig. 4a). Furthermore, *S. bombifrons* carnivores developed into more extreme carnivores in the presence of *S.*

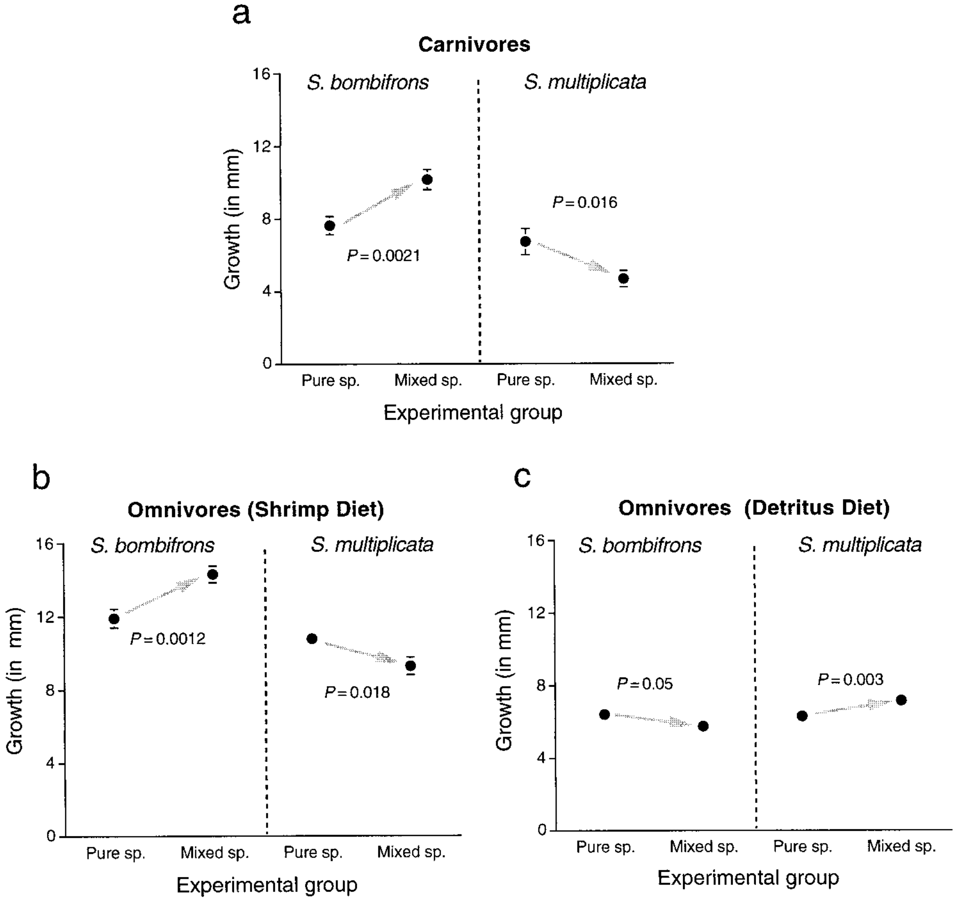

FIG. 4. Evidence of differential competitive abilities of two species (*Spea bombifrons* and *S. multiplicata*) and two morphs (carnivores and omnivores) when reared in the laboratory. Shown is mean (± SD) change in snout-vent length of tadpoles when reared with a conspecific (pure-species group) or a heterospecific (mixed-species group). Carnivores (a) were fed fairy shrimp and detritus; omnivores were fed either fairy shrimp (b) or detritus (c).

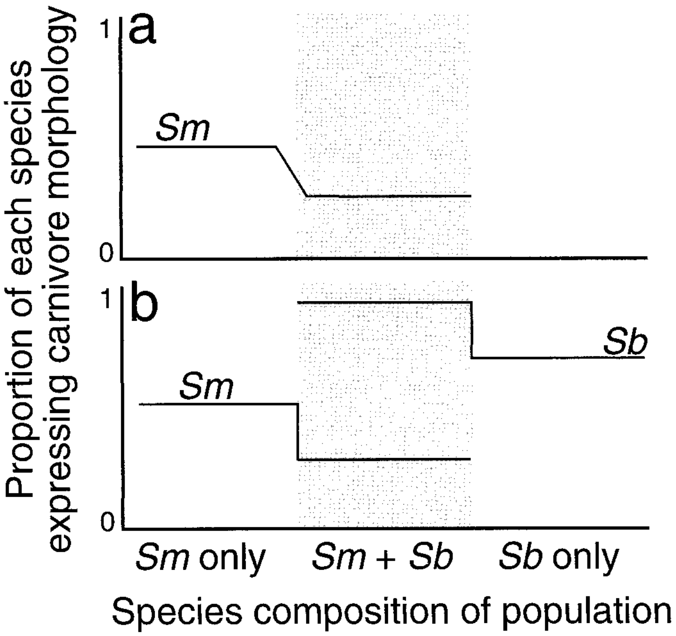

FIG. 5. Two forms of character change observed in our experiments. The proportion of *Spea bombifrons* (*Sb*) and *S. multiplicata* (*Sm*) tadpoles producing the carnivore phenotype varied depending on whether these tadpoles occurred with heterospecifics (gray area where the two species co-occur). This character change was mediated by both (a) character displacement, where *S. multiplicata*'s propensity to produce carnivores varied between sites in sympatry and allopatry, and (b) phenotypic plasticity, where *S. multiplicata* facultatively enhanced carnivore production in *S. bombifrons,* and *S. bombifrons* facultatively suppressed carnivore production in *S. multiplicata.*

multiplicata than in the presence of *S. bombifrons*. The OH:SVL ratio for *S. bombifrons* carnivores reared with a heterospecific (0.16 ± 0.01) was significantly greater than that for carnivores reared with a conspecific (0.15 ± 0.02; $t_{43} = 2.22$, $P = 0.032$). In contrast, *S. multiplicata* carnivores tended to develop into less extreme carnivores in the presence of a *S. bombifrons* carnivore than in the presence of another *S. multiplicata* carnivore, although the differences were not significant ($t_{43} = 1.17$, $P = 0.08$). Thus, *S. bombifrons* carnivores appear to be competitively superior to *S. multiplicata* carnivores.

In the omnivore competition experiment, the presence of heterospecifics also had a pronounced effect on the growth of omnivores, but the type of available food determined which species was superior. When fed shrimp only, *S. bombifrons* omnivores grew more when reared with a *S. multiplicata* omnivore than when reared with another *S. bombifrons* omnivore ($t_{37} = 3.51$, $P = 0.001$; Fig. 4b). In contrast, *S. multiplicata* omnivores grew less when reared with a *S. bombifrons* omnivore than when reared with another *S. multiplicata* omnivore ($t_{37} = 2.49$, $P = 0.018$; Fig. 4b).

When fed on detritus, however, the competitive advantage for *S. bombifrons* omnivores was lost. *Spea bombifrons* omnivores grew less when reared with a *S. multiplicata* omnivore than when reared with another *S. bombifrons* omnivore ($t_{74} = 1.99$, $P = 0.05$; Fig. 4c). In contrast, *S. multiplicata* omnivores grew more when reared with a *S. bombifrons* omnivore than when reared with another *S. multiplicata* omnivore ($t_{74} = 3.08$, $P = 0.003$; Fig. 4c). Thus, *S. multiplicata* omnivores were less efficient shrimp foragers than were *S. bombifrons* omnivores, whereas *S. bombifrons* omnivores were less efficient detritivores than were *S. multiplicata* omnivores.

Experiment 4

Competitive differences between species for both carnivore and omnivore morphs were at least in part due to species-specific differences in activity and feeding behavior on shrimp and detritus diets. In terms of shrimp handling time, *S. bombifrons* omnivores were more likely to eat a shrimp than were *S. multiplicata* omnivores. The mean time before a satiated *S. bombifrons* omnivore ate a shrimp was 32 ± 24 h, whereas the mean time before similarly satiated *S. multiplicata* omnivore ate a shrimp was 78 ± 33 h (Wilcoxon $\approx \chi^2 = 32.03$, df = 1, $P < 0.0001$). However, omnivores of the two species did not differ in tendency to associate with shrimp: When given a choice in a small test arena of associating with either an area containing shrimp or with an area containing only water, *S. bombifrons* omnivores spent 307 ± 40 sec (of 600 sec) on the side with shrimp, whereas *S. multiplicata* omnivores spent 308 ± 60 sec on the side with shrimp ($t_{41} = 0.07$, $P = 0.94$). Yet, in the presence of shrimp, *S. bombifrons* omnivores were more active than *S. multiplicata* omnivores: during the 10-min test interval, *S. bombifrons* switched sides in the test arena 72 ± 23 times, whereas *S. multiplicata* omnivores switched sides 38 ± 17 times ($t_{41} = 5.46$, $P = 0.0001$). Thus, because they are more active than *S. multiplicata*, *S. bombifrons* may be better foragers on shrimp. Tests on detritus diets revealed additional species differences in omnivores. Omnivores of *S. multiplicata* spent significantly more time grazing on the bottom or the surface of the water than did *S. bombifrons* ($F_{1,31} = 7.70$, $P = 0.009$). Thus, because *S. multiplicata* spend more time grazing than do *S. bombifrons*, *S. multiplicata* may be better foragers on detritus.

DISCUSSION

We used polyphenic tadpoles of the spadefoot toads *S. bombifrons* and *S. multiplicata* to evaluate whether and how resource competition influences production of distinctive carnivorous and omnivorous tadpoles (Fig. 1). When the two species co-occurred, they diverged in tendencies to produce carnivores. Divergence was expressed both as character displacement (where the propensity to express the carnivore phenotype varied between sites in sympatry and in allopatry) and as phenotypic plasticity (where each species facultatively influenced the other's developmental decisions). Below, we consider whether this divergence in carnivore production between conspecifics that did and did not co-occur with heterospecifics reflects selection to minimize competition for food. We also discuss why selection might favor both character displacement and phenotypic plasticity as mechanisms to respond to competitors.

Ideally, six criteria should be met to support the competition hypothesis for the evolution of character displacement (Grant 1972, 1975; Schluter and McPhail 1992): (1) the re-

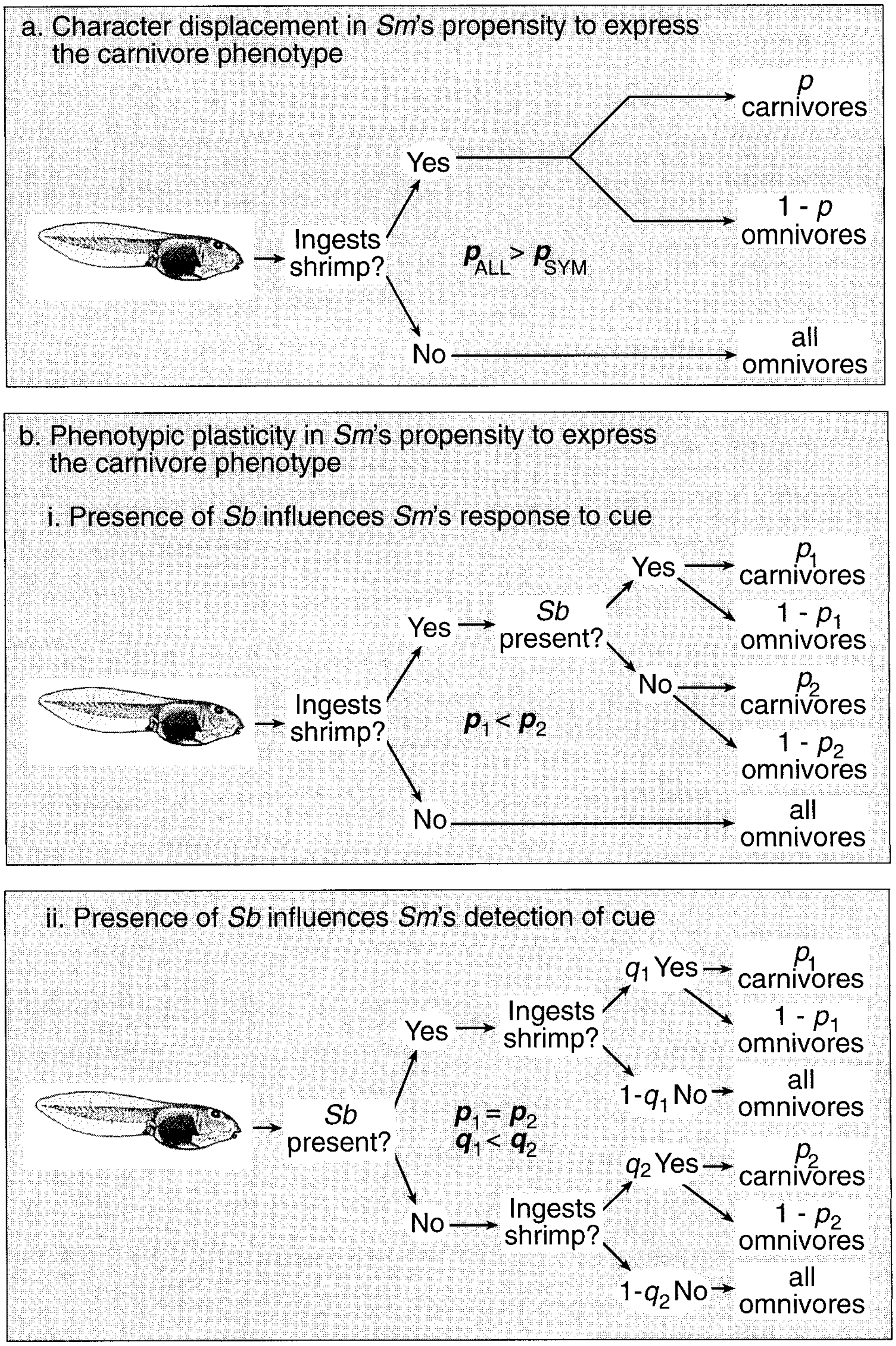

FIG. 6. Alternative proximate mechanisms whereby *Spea bombifrons* (*Sb*) may influence morph determination of *S. multiplicata* (*Sm*). Tadpoles that ingest shrimp have probability p of becoming a carnivore and probability $1 - p$ of expressing the default omnivore morph. However, *S. bombifrons* may modify this developmental switch in *S. multiplicata* through (a) character displacement or (b) phenotypic plasticity. With character displacement (a), individual tadpoles of *S. multiplicata* exhibit a fixed response to the presence of *S. bombifrons*, but this response differs for populations in allopatry (p_{ALL}) and sympatry (p_{SYM}). With phenotypic plasticity (b), individual tadpoles of *S. multiplicata* exhibit a flexible response to the presence of *S. bombifrons*, with the latter either influencing (i) the ability of *S. multiplicata* to respond to the shrimp cue (e.g., through interference competition); or (ii) the ability of *S. multiplicata* to detect to the shrimp cue (e.g., through exploitative competition).

lationship between phenotypic differences and resource use must be demonstrated clearly; (2) chance should be ruled out as an explanation for the divergence of phenotypes; (3) independent evidence of resource competition between similar phenotypes is required; (4) conspecific populations that do and do not co-occur with heterospecifics should be similar ecologically, such that the major difference is the presence and absence of competing species; (5) enhanced differences between co-occurring species should be the outcome of evolutionary shifts, not simply of the inability of similar-sized species to coexist; and (6) phenotypic differences between conspecific populations that do and do not co-occur with heterospecifics should be heritable. Are these six criteria met in polyphenic *Spea* tadpoles?

In addressing the first criterion, there are two lines of evidence to suggest that there is an association between a tadpole's phenotype (carnivore or omnivore) and its diet. First, the two morphs specialize on different diets. Stomach content analyses (Pomeroy 1981) have revealed that, on average, 51% (by volume) of carnivores' contents consist of shrimp and 25% consist of detritus. In contrast, 0% of omnivores' stomach contents consist of shrimp and 91% consist of detritus. Second, only those tadpoles that are fed shrimp develop into carnivores in the first place; those that are fed detritus invariably develop into omnivores (Pfennig 1990). Thus, we conclude that the relationship between phenotypic differences and resource use can be demonstrated clearly, thus satisfying the first criteria.

Can chance be ruled out as an explanation for why significantly fewer *S. multiplicata* carnivores were produced from sympatric sites than from allopatric sites? Although there are numerous ways that chance could create enhanced differences between co-occurring species (Robinson and Wilson 1994), such random effects are unlikely to explain our results, for two reasons. First, as noted in the introduction, a causal link can be established between the presence of heterospecific competitors and character change if, by removing (or adding) competitors, a polyphenic species differentiates (or fails to differentiate) into an alternative morph that resembles the competitor. When each species was reared alone, *S. bombifrons* was more likely than *S. multiplicata* to produce carnivores (Table 1; see also Pfennig and Frankino 1997). When reared together, however, *S. multiplicata* facultatively enhanced carnivore production in *S. bombifrons* and *S. bombifrons* facultatively suppressed carnivore production in *S. multiplicata* (Table 2). These findings therefore indicate that in the presence of heterospecifics, polyphenic *Spea* species differentiate into the morph that is more unlike the competitor, thereby establishing a causative link between the presence of heterospecific competitors and character change.

A second reason why random effects are unlikely to explain our results is that we provided a plausible selective explanation for character divergence. In experiment 3, we found that *S. bombifrons* (the species for which carnivore production was enhanced) was the superior competitor for shrimp, and that *S. multiplicata* (the species for which carnivore production was suppressed and omnivore production enhanced) was the superior competitor for detritus (Fig. 4). We also uncovered the likely basis of these competitive differences. *Spea bombifrons* tadpoles spent more time actively searching for food in the water column. This behavior may have made them more efficient shrimp foragers. In contrast, *S. multiplicata* tadpoles spent more time grazing on the bottom of the pool. This behavior may have made them more efficient detritivores. Thus, for the two reasons above, we conclude that random effects are unlikely to explain our results, thereby satisfying the second criterion.

The third criterion, the existence of independent evidence of resource competition between similar phenotypes, also appears to be met in our system. As noted in the introduction, a previous study (Pfennig 1992a) of *S. multiplicata* in natural ponds documented disproportionately severe competition among members of the same morph. Thus, these data provide independent evidence that resource competition between similar phenotypes across species is likely—even under natural conditions—and further substantiate our findings of interspecific resource competition between similar morphs.

To address the fourth criterion, we asked whether sympatric and allopatric sites are similar ecologically, such that the major difference between these populations is the presence and absence of competing species. Two lines of evidence indicate that this criterion is met in our system. First, the pure- and mixed-species ponds used in experiment 1 were similar to each other except for the absence and presence of *S. bombifrons* (see Methods). Even if we allow for undetected ecological differences between pure-species and mixed-species ponds, the more rapidly developing carnivore morph should have been favored in lower-elevation, mixed-species sites because such ponds generally dry faster (e.g., see Pfennig 1990, 1992a). Yet, significantly fewer *S. multiplicata* carnivores were produced from mixed-species ponds (Fig. 4), which was what we had predicted based on the competition hypothesis. Second, in experiment 2, fewer carnivores were produced by *S. multiplicata* when they were reared with *S. bombifrons* than when they were reared alone. Thus, divergence generated by phenotypic plasticity within populations was identical to that observed between sympatric and allopatric sites. This finding suggests that the presence or absence of heterospecifics was sufficient to explain the divergence between sympatry and allopatry. Therefore, the fourth criterion is likely to be met in our system.

The fifth criterion asks whether enhanced differences between co-occurring species are the outcome of evolutionary shifts, not simply the inability of similar-sized species to coexist (e.g., because of competitive exclusion). Enhanced differences in carnivore production between co-occurring *Spea* species is likely not caused by an inability of similar-sized species to coexist. In our study ponds, both *Spea* species frequently co-occur with *Scaphiopus couchii* and *Bufo cognatus* tadpoles, which are similar in size to *Spea* (D. Pfennig, unpubl. data). Thus, this criterion appears to be satisfied for the spadefoot system.

Finally, we address the sixth criterion, that the phenotypic differences between conspecific populations that do and do not co-occur with heterospecifics are heritable. This last criterion is important, because heritable variation is necessary for a trait to evolve in response to natural selection (although a lack of heritable variation for a trait does not preclude the possibility that directional selection has eliminated all such variation from existing populations). A presumed violation of this sixth criterion has led many evolutionary biologists to ignore cases of phenotypic plasticity in studies of character displacement (Arthur 1987). Yet, phenotypic plasticity itself is a trait that can have a heritable basis and that can respond to selection imposed by competitors (Robinson and Wilson 1994).

The available data suggests that the tendency to produce carnivore morphs has a heritable basis and that this character can respond to selection. As mentioned in the introduction, previous common-garden experiments have established that certain families are more likely than are others to produce carnivores (Pfennig 1999). These data suggest that the tendency to produce carnivores has a heritable basis. In addition, the observed divergence in carnivore production between sites in sympatry and in allopatry (Fig. 3) indicates that the tendency to produce carnivores can respond to selection imposed by competitors. Thus, the sixth criterion appears to be fulfilled in our study system.

Based on the above evidence, we conclude that all six criteria necessary to support the competition hypothesis for the evolution of character displacement are met in *Spea*. Thus, character displacement in *Spea* likely has arisen from selection to minimize competition for food. We hypothesize that *S. multiplicata* has evolved a reduced propensity to produce carnivores in sympatry with *S. bombifrons*, because *S. multiplicata* are inferior competitors for the shrimp prey on which the carnivore is specialized.

An important finding to emerge from this study is that both character displacement and phenotypic plasticity may play a role in the mediation of competitive interactions between species (Fig. 5). This finding reinforces an important point concerning studies that fail to establish character displacement (e.g., Grant 1975; Simberloff and Boecklen 1981). Lack of evidence for character displacement between competing species does not necessarily imply that those species have not responded to selection imposed by each other. Selection for character displacement might be mitigated in many species by competitively induced phenotypic plasticity, which may generally provide a more efficient means than character displacement of responding to competitors adaptively.

Given that tadpoles can respond to the presence of heterospecifics through phenotypic plasticity, what proximate cues trigger enhancement/suppression of carnivore production? One possibility is that heterospecifics decrease (or increase) the expression of carnivore morphs through interference competition. In particular, *Spea* tadpoles may use species-specific chemical cues to enhance/suppress carnivore production in the presence of heterospecifics (Fig. 6b, i). Such a mechanism is plausible, given that chemical cues cause carnivores to be produced at different rates in the presence of kin versus nonkin (Pfennig and Frankino 1997). Alternatively, heterospecifics may increase (or decrease) carnivore production through exploitative competition (Fig. 6b, ii). In particular, because *S. bombifrons* are the more efficient shrimp foragers, they may be more likely to eat shrimp in the presence of *S. multiplicata* (and, thus, experience the cue that triggers carnivores; Fig. 1). Conversely, *S. multiplicata* may be less likely to eat shrimp and become carnivores when *S. bombifrons* are present, because *S. bombifrons* reduces the number of shrimp present. In essence, *Spea* tadpoles may respond to heterospecifics indirectly, by evaluating what food is available and modifying their phenotype according to whether shrimp or detritus is more abundant.

If *S. multiplicata* can detect the presence of *S. bombifrons* and respond adaptively by suppressing carnivore production, then why do *S. multiplicata* sibships also show a reduced propensity to express the carnivore phenotype in mixed-species ponds? Such a reduction in the inherited tendency to produce carnivores seems maladaptive, given the potential fitness benefits of becoming a carnivore in a rapidly drying pond (Pfennig 1992a). Perhaps selection has favored redundancy in the mechanism by which heterospecifics influence morph determination because the fitness costs of making a mistake and developing into a carnivore in the presence of *S. bombifrons* are severe. To illustrate the consequences of such errors, consider that when *S. multiplicata* carnivores were reared with *S. bombifrons* carnivores, they experienced a 30% reduction in larval growth rate (Fig. 2a). Given this competitive disadvantage, and given that *S. multiplicata* omnivores are superior to *S. bombifrons* omnivores when competing for detritus (Fig. 2c), a *S. multiplicata* tadpole might realize greater fitness by remaining an omnivore in a mixed-species pond. Thus, we hypothesize that because mistakes in assessment are costly, natural selection may have favored redundant proximate mechanisms—phenotypic plasticity and character displacement—to respond to selection imposed by competitors (Fig. 6).

In sum, our study illustrates how both phenotypic plasticity and character displacement can minimize competition between interacting species. In general, in populations that overlap with close competitors, natural selection might favor both those individuals that are the most unlike the other species as well as those that are the best able to recognize and respond to competitors adaptively through phenotypic plasticity. Understanding how both processes enable organisms to respond to selection imposed by competitors promises to shed new light on character evolution and on the evolutionary and proximate mechanisms that promote diversity among interacting species.

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Corresponding Editor: T. Mousseau