Evolution, 56(6), 2002, pp. 1217–1228

HOW FLUCTUATING COMPETITION AND PHENOTYPIC PLASTICITY MEDIATE SPECIES DIVERGENCE

DAVID W. PFENNIG[1] AND PETER J. MURPHY[2]
[1]*Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599-3280*
E-mail: dpfennig@email.unc.edu
[2]*Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901-6501*
E-mail: pjmurphy@siu.edu

Abstract.—Causal evidence linking resource competition to species divergence is scarce. In this study, we coupled field observations with experiments to ask if the degree of character displacement reflects the intensity of competition between two closely related spadefoot toads (*Spea bombifrons* and *S. multiplicata*). Tadpoles of both species develop into either a small-headed omnivorous morph, which feeds mostly on detritus, or a large-headed carnivorous morph, which specializes on and whose phenotype is induced by fairy shrimp. Previously, we found that *S. multiplicata* are inferior competitors for fairy shrimp and are less likely to develop into carnivores in sympatry with *S. bombifrons*. We compared four key trophic characters in *S. multiplicata* across natural ponds where the frequency of *S. bombifrons* varied. We found that *S. multiplicata* became increasingly more omnivore-like as the relative abundance of *S. bombifrons* increased. Moreover, in controlled laboratory populations, *S. multiplicata* became increasingly more omnivore-like and *S. bombifrons* became increasingly more carnivore-like as we increased the relative abundance of the other species. Phenotypic plasticity helped mediate this divergence: *S. multiplicata* became increasingly less likely to eat shrimp and develop into carnivores in the presence of *S. bombifrons*, a superior predator on shrimp. However, divergence also reflected differences in canalized traits: When reared under common conditions, *S. multiplicata* tadpoles became increasingly less likely to produce carnivores as their natal pond decreased in elevation. Presumably, this pattern reflected selection against carnivores in lower-elevation ponds, because *S. bombifrons* became increasingly more common with decreasing elevation. Local genetic adaptation to the presence of *S. bombifrons* was remarkably fine grained, with differences in carnivore production detected between populations a few kilometers apart. Our results suggest that the degree of character displacement potentially reflects the intensity of competition between interacting species and that both phenotypic plasticity and fine-scale genetic differentiation can mediate this response. Moreover, these results provide causal evidence linking resource competition to species divergence.

Key words.—Canalization, character displacement, frequency-dependent natural selection, local adaptation, parapatric speciation, phenotypic plasticity, *Spea*.

Received January 26, 2001. Accepted March 22, 2002.

A central goal of evolutionary biology is to explain why living things are as diverse as they are. A major cause of differences is competition for resources (Darwin 1859; Lack 1947; Brown and Wilson 1956; Roughgarden et al. 1983; Schluter 2000). To understand why, consider that when two previously separated species with similar resource requirements first come together, those individuals most unlike the other species will experience the least competition and will therefore be favored by natural selection. Consequently, the two species may diverge in resource use and in phenotypic features associated with resource use. Such divergent selection stemming from competition may help explain why closely related coexisting species typically differ in phenotype (Brown 1995).

The role of resource competition in promoting phenotypic divergence between interacting species is difficult to demonstrate empirically, however (Conner and Simberloff 1979; Dunham et al. 1979; Schluter and McPhail 1992; Grant 1994; Schluter 1994, 2000; Losos 2000). Experimental tests are generally not feasible because it often takes a long time to observe an evolutionary response to selection imposed by competitors. Thus, most data supporting the competition hypothesis come from correlational studies of character displacement, in which natural populations of closely related species are phenotypically different where they live together but are similar where they live alone (Brown and Wilson 1956; for examples, see Schluter 2000). Yet, because numerous factors can cause interacting species to diverge in phenotype, character displacement is not compelling evidence that competition promotes species divergence (Grant 1972; Endler 1986; Schluter and McPhail 1992; Taper and Case 1992). Indeed, closely related coexisting species may differ in phenotype, not because of a history of evolutionary adjustment by one species to the other, but because of ecological exclusion or extinction of species that are too similar in resource use (Grant 1972; Losos 1990, 1992; Thompson 1994).

Species that respond to competitors through phenotypic plasticity are ideal for evaluating if and how competition promotes phenotypic divergence between interacting species. A causal link can be established between the presence of competitors and character change if, in the presence of a competitor, an individual facultatively expresses an alternative phenotype less like its competitor's phenotype. In essence, phenotypic plasticity provides a setting in which responses to competitors can be measured in developmental time, rather than in evolutionary time.

Moreover, phenotypic plasticity may provide a mechanism whereby the amount of divergence is finely tuned to the intensity of competition between species (e.g., Bourke et al. 1999). Such competitively induced plasticity might even lead to frequency-dependent character displacement (Slatkin 1980), where the magnitude of response depends on the frequency of heterospecific competitors in the population (Fig. 1). Different inherited tendencies to adopt each alternative phenotype might eventually become canalized in different

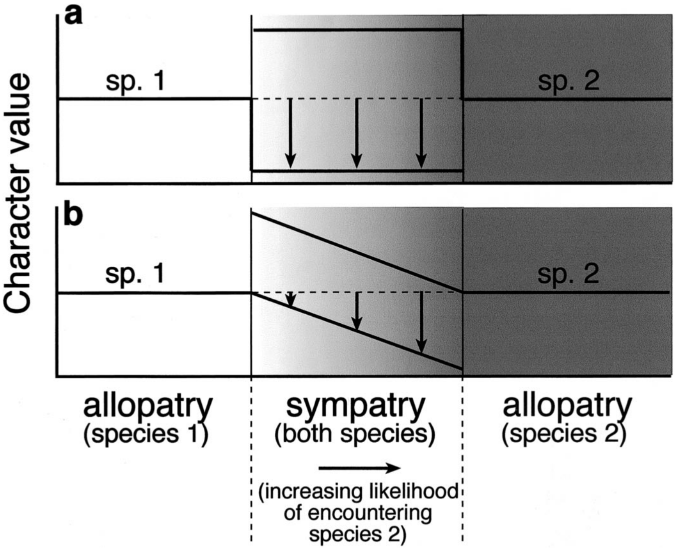

FIG. 1. Two models of character displacement. (a) In the classical model (e.g., Endler 1986), the degree of displacement is constant throughout sympatry, regardless of the relative prevalence of the competitor. For example, the degree of character displacement for species 1 is the same for all populations sampled (compare lengths of the different arrows), despite the fact that species 2 becomes increasingly more common as we travel from left to right through the zone of sympatry (the amount of shading is directly proportional to the prevalence of species 2). (b) In the frequency-dependent model, by contrast, the degree of displacement increases as the likelihood of encountering the competitor increases. Note also that, if both species show a similar response to competitors, the magnitude of divergence between species in sympatry may be less in the frequency-dependent model than in the classical model.

populations that have differed historically in their encounter rate with heterospecifics. Such canalization 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). Finding such fine-scale local adaptation in phenotypic responses to competitors would provide strong support for the competition hypothesis.

Polyphenic tadpoles of the genus *Spea* are excellent for evaluating whether resource competition promotes species diversification. Depending on their diet, tadpoles of plains spadefoot toads (*S. bombifrons*) and New Mexico spadefoot toads (*S. multiplicata*) develop into either a small-headed omnivorous morph, which feeds mostly on detritus, or a large-headed carnivorous morph, which specializes on anostracan fairy shrimp (Fig. 2a; Bragg 1965; Pomeroy 1981; Pfennig 1990, 1992a,b). Tadpoles are born as omnivores, but they may develop into carnivores if they ingest shrimp early in life (Fig. 2b). The two morphs often live within the same pond (Bragg 1965; Pomeroy 1981; Pfennig 1990), and competition is keenest among individuals expressing the same morphotype (Pfennig 1992a). Moreover, because shrimp are limited in most natural ponds (Pfennig 1992a), competition among tadpoles for the more nutritious shrimp prey (D. W. Pfennig 2000) critically affects the probability that any particular tadpole will eat shrimp and thus experience the cue that induces the carnivore morph (Pfennig 1992a; Frankino and Pfennig 2001).

Spea bombifrons and *S. multiplicata* are sympatric in the southwestern United States (Fig. 3a). Recently, we found evidence of character displacement between these two species. In particular, the two species differ more in their tendency to produce carnivores when they live together than when they live alone (Pfennig and Murphy 2000; D. W. Pfennig and P. J. Murphy, unpubl. ms.). This phenotypic divergence reflects, in part, genetically based canalized divergence. Sibships of *S. multiplicata* in sympatry with *S. bombifrons* are less likely than those in allopatry to produce carnivores, even when reared under common conditions from fertilization (Pfennig and Murphy 2000). However, divergence also appears to reflect phenotypic plasticity. In laboratory experiments, we found that *S. multiplicata* facultatively enhances carnivore production in *S. bombifrons* and *S. bombifrons* facultatively suppresses carnivore production in *S. multiplicata* (Pfennig and Murphy 2000). Furthermore, *S. multiplicata* appears to have evolved a reduced propensity to produce carnivores in sympatry with *S. bombifrons*, because *S. multiplicata* are less efficient foragers on shrimp (Pfennig and Murphy 2000).

The ability of *Spea* to respond to competitors through phe-

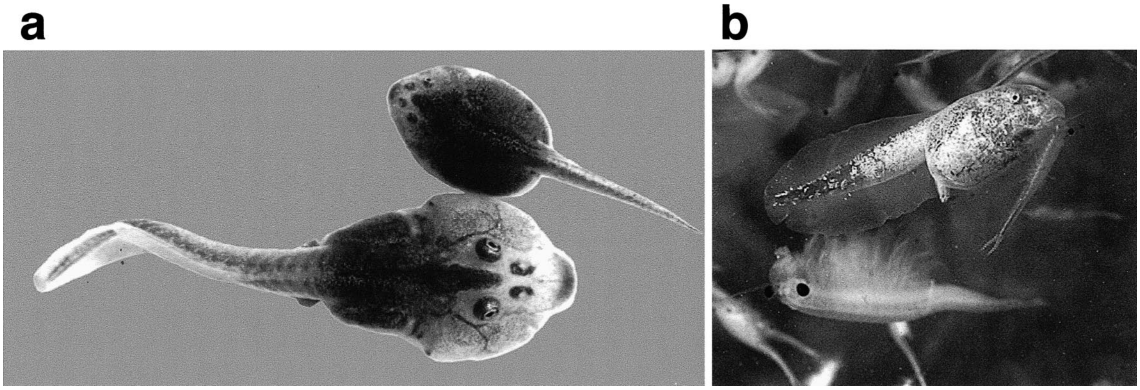

FIG. 2. Polyphenism in spadefoot toad tadpoles (genus *Spea*). (a) *Spea* tadpoles exist either as an omnivore morph (upper tadpole) or as a carnivore morph (lower tadpole). (b) An omnivore morph eating a fairy shrimp. Omnivores develop into carnivores only following ingestion of shrimp or other tadpoles. The enlarged jaw musculature of the carnivore morph enables it to capture and consume shrimp more effectively (photo © David Sanders).

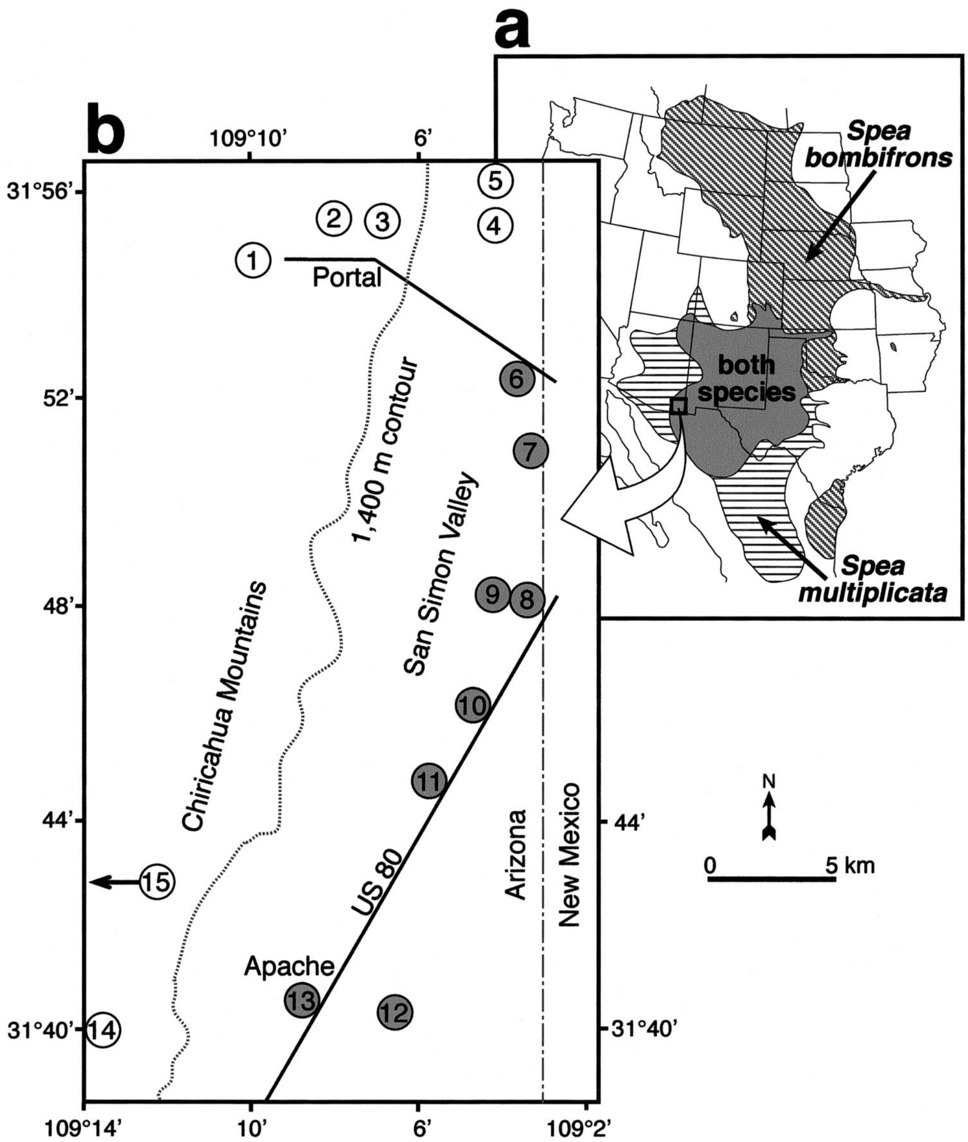

FIG. 3. (a) Distributions of *Spea bombifrons* and *S. multiplicata* in western North American and Mexico (from Conant and Collins 1991). (b) Map of study area, showing locations of ponds used in the analyses (encircled numbers). Gray circles, both *Spea* species present; open circles, only *S. multiplicata* present.

notypic plasticity suggests that the degree of divergence in *Spea* may be fine-tuned to the likelihood of encountering a heterospecific competitor. We tested this hypothesis of competitive divergence and explored its underlying causes in the present study. We addressed two specific questions. First, does the degree of character displacement increase as the intensity of competition between species increases (Fig. 1b)? Second, what is the role of plasticity versus canalized responses in mediating character change?

We addressed the first question by comparing trophic characters of *S. multiplicata* tadpoles collected from ponds containing varying frequencies of *S. bombifrons*. We then used a series of three laboratory experiments to determine whether the magnitude of character displacement does indeed increase as the intensity of competition between species increases and the role of plastic and canalized responses in mediating any such response.

MATERIALS AND METHODS

Field surveys

We used data from natural populations to determine if the degree of character displacement increases as two species' probability of encountering each other increases. We did so by comparing continuous trophic characters in populations of *S. multiplicata* that varied in their probability of contact with *S. bombifrons*. In our prior work (Pfennig and Murphy 2000), we measured divergence as the difference in carnivore production, where carnivores were identified discretely by external gross morphology. Here, we analyzed characters that studies of other tadpole species (DeJongh 1968; Cannatella 1999) suggest may reflect intensity of competition: size of jaw musculature, morphology of keratinized mouthparts, and length of the digestive tract.

We sampled a subset of carnivores and omnivores from

10 ponds near Portal, Arizona, by using methods in Pfennig (1990). Five ponds (ponds 3, 4, 5, 14, 15 in Fig. 3b) were higher-elevation (1380–1500 m) pure-species ponds (i.e., ponds in which *S. multiplicata* was the only species of *Spea* present); the remaining five ponds (ponds 8, 10, 11, 12, 13 in Fig. 3b) were lower-elevation (~1270–1380 m) mixed-species ponds (i.e., ponds in which both species of *Spea* were present). *Spea bombifrons* does not live above about 1400 m elevation in southeastern Arizona (Simovich 1985) and has been present in the mixed-species ponds and absent in the pure-species ponds for at least the past 25 years (Pomeroy 1981; Simovich 1985), or about 12–25 spadefoot toad generations (see Pearson 1955). Other than the presence of *S. bombifrons*, ponds were similar in ecological characteristics (e.g., drying times, fairy shrimp density, tadpole density). Finally, to minimize temporal effects on any possible differences in morphology of tadpoles, allopatric (pure-species) and sympatric (mixed-species) ponds were chosen such that breeding events in each pond type were overlapping and closely contemporaneous (2–9 July 1999).

Within a few hours of collection, we killed the tadpoles by immersion in a 0.1% aqueous solution of tricane methanesulfonate (MS 222), placed each tadpole in an individually labeled plastic bag, and froze them at −80°C. 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 on tail tissue to classify tadpoles as *S. bombifrons*, *S. multiplicata*, or F_1 hybrids (Simovich and Sassaman 1986). The remaining tadpole body was then transferred to 95% ethanol.

For morphometric analyses, we used the following four characters (Fig. 4): (1) width of the orbitohyoideus (OH) muscle; (2) width of the interhyoideus (IH) muscle; (3) shape of the keratinized mouthparts (MP); and (4) gut length (GL). The OH muscle is the primary buccal cavity abductor, responsible for opening the mouth cavity; conversely, the IH muscle closes the buccal cavity and forces cavity contents back to the pharynx (Wassersug and Hoff 1979; Cannatella 1999). A relatively large OH increases the tadpole's ability to create inward suction and thereby capture and subdue larger prey, such as fairy shrimp (Ruibal and Thomas 1988; Pfennig 1992b). A relatively large IH increases the force at which food particles are moved rearward in the digestive system, potentially decreasing handling time for large prey (Satel and Wassersug 1981). The MP of carnivore-morph *Spea* are often serrated, suggesting that such serration permits tadpoles to trap, subdue, and cut larger prey efficiently (Turner 1952; Altig and Johnston 1989; Altig and McDiarmid 1999). Increasing GL correlates directly with a tadpole's ability to absorb nutrients from plant food (Alford 1999). Moreover, tadpoles fed primarily on plant matter develop longer intestines than those fed a carnivorous diet (Horiuchi and Koshida 1989; Nodzenski et al. 1989). Overall, we expected carnivorous tadpoles to have relatively larger OH and IH muscles, MP with prominent serration, and shorter GL for a given body size. Conversely, tadpoles specializing on detritus were expected to display relatively smaller OH and IH muscles, MP without serration, and relatively longer GL.

Our morphometric study on 398 tadpoles from 10 study ponds (17–71 per pond) proceeded as follows. The developmental stage (GS, Gosner 1960) and size (snout-vent length, SVL) of each tadpole was noted prior to dissection. Next, the OH and IH jaw muscles were exposed by ventral

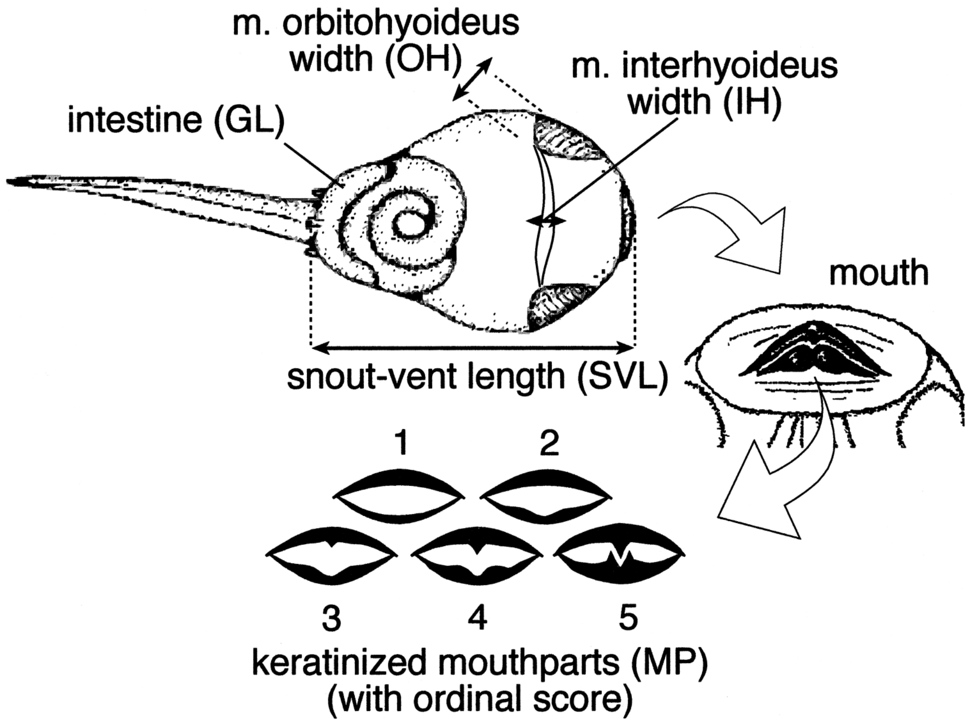

FIG. 4. Diagrammatic representation of a *Spea* tadpole (ventral view), showing characters used in analyses.

dissection and measured using an ocular micrometer, at their widest point perpendicular to the muscle fibers, a distance directly proportional to the force exerted by the muscle (Alexander 1985). For the left and right OH, this point was from the most lateral to most medial insertion point on the posterior ceratohyal (DeJongh 1968; Ruibal and Thomas 1988). For the ribbonlike IH, each measurement was taken halfway between the muscle's midpoint and the lateral insertion points on the right and left medial ceratohyal. Individual tadpole values for OH and IH were determined by taking the mean of left and right measurements. Next, we classified each tadpole's MP into one of five categories, ranging from 1 (least carnivorous) to 5 (most carnivorous; Fig. 4). Finally, the digestive tract was removed and GL determined as the straight-line distance from the anterior manicotto (larval stomach) to cloaca.

Because slight habitat differences impact tadpole growth and development, and carnivores develop more rapidly than omnivores (Pfennig 1990, 1992a), we standardized each character before analysis for body size (SVL) and developmental stage (GS). To perform these standardizations, we combined all populations of both species and then regressed all values of each character (OH, IH, GL, and MP) separately on log(SVL) and log(GS). We compared the mean SVL of *S. multiplicata* among sympatric and allopatric ponds prior to standardization to ensure that standardization was not masking significant tadpole size differences that could confound our morphological analysis. Regression on log(GS) and log(SVL) produced normal residuals (OH and IH were log transformed), which ensured that linear standardization did not introduce bias. We then derived a standardized value for each character and tadpole by adding each tadpole's residual back to the mean value for that character. We used pond means for analyses because tadpoles within a pond compete for shrimp and detritus (Pfennig 1992a). Thus, pondmates are not necessarily morphologically independent. We used these pond-mean standardized values for all statistical comparisons (data presented in Fig. 5 are without log transformation on OH and IH).

We then used these data to examine whether the degree of morphological displacement (i.e., suppression of carnivorous features and enhancement in omnivorous features) in *S. multiplicata* is sensitive to the relative prevalence of *S. bombifrons* and, therefore, the relative intensity of competition with that species. To address this issue, we performed a linear correlation in which the percentage of *S. bombifrons* present in a pond (arcsine square-root transformed) was compared to each morphological character's mean value for that pond.

However, beyond showing that the morphological data fit a linear model, we asked whether this model (i.e., Fig. 1b) explained the morphological data better than a step model (i.e., Fig. 1a). We approximated the step model by fitting an ANOVA with two equal groups (i.e., the allopatric ponds and the sympatric ponds) to the same dataset as the linear model. Both models had equal numbers of estimated parameters, thus comparing their performance was a matter of determining which deviates significantly less often from the actual data (Hilborn and Mangel 1997). Because we only had one dataset for each trait (10 pond means paired with the pond's percentage of *S. bombifrons*), we bootstrapped these data (sampled randomly with replacement) to create 100 replicate datasets for each trait. Next, for each replicate, we calculated the sum of squared deviations (SS) for both the step and linear models, yielding 100 SS per model. Finally, we tested whether the mean SS differed by model using a *t*-test (paired by bootstrap replicate). For each trait, this procedure enabled us to see whether a frequency-dependent model better explained the morphological variation of *S. multiplicata* in response to *S. bombifrons.*

Experiment 1: Does the degree of character displacement increase with increasing intensity of competition?

Next, we sought to test in the laboratory the hypothesis arising from our current field observations. Specifically, does the degree of character displacement increase as the intensity of competition between species increases? We addressed this question by experimentally exposing tadpoles to varying intensities of interspecific competition and noting their morphological responses. We also used these data to evaluate the role of phenotypic plasticity in mediating interspecific resource competition by measuring the morphological responses of individual tadpoles.

Our prior work (Pfennig and Murphy 2000) demonstrated that *S. bombifrons* tadpoles are superior foragers for shrimp, whereas *S. multiplicata* tadpoles are superior foragers for detritus. Based on that result, we varied the proportion of *S. bombifrons* and *S. multiplicata* in laboratory microcosms, thereby changing the intensity of competition for shrimp and detritus, respectively. We then measured the morphological response of tadpoles to determine if *S. multiplicata* became less carnivore-like in morphology as the proportion of *S. bombifrons* in the population increased and if *S. bombifrons* became more carnivore-like as the proportion of *S. multiplicata* increased.

We collected five amplectant pairs each of *S. bombifrons* and *S. multiplicata* from a June 2000 breeding chorus (pond 8 in Fig. 3b). Two days after the tadpoles hatched from spawning boxes, we randomly assigned four similarly sized larvae to the following treatment categories, which varied in the frequency of *S. bombifrons* present: (1) *S. bombifrons* only; (2) three *S. bombifrons* and one *S. multiplicata*; (3) two *S. bombifrons* and two *S. multiplicata*; (4) one *S. bombifrons* and three *S. multiplicata*; and (5) *S. multiplicata* only. Each treatment group was replicated 10 times, producing a total of 50 tanks and 200 tadpoles. Conspecifics in each tank were siblings, and the original five sibships for both species were equally represented across the five treatments.

Rearing tanks (28 × 18 × 10 cm) were filled with 6 L of dechlorinated tap water and placed in the same room. Tanks containing different treatments were interspersed and randomized by location in the rearing room. For the first week of the experiment, each tank received 20 small (total length <10 mm) live fairy shrimp (*Thamnocephalus* and *Streptocephalus* spp.) once a day and 0.05 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 nature (Pfennig et al. 1991). Both diets were restrictive because all shrimp and chow had disappeared from each tank before they were fed again. After one week, when tadpoles increased in size, each tank received about 200 small fairy shrimp daily and 0.1 g of crushed rabbit chow every three days. We ended the experiment after 14 days so tadpoles could be analyzed prior to undergoing the developmental changes of metamorphosis. At this time, tadpoles were killed by immersion in MS 222 and their SVL and the width of the right OH were measured using handheld digital calipers.

Prior to statistical comparisons, data were standardized for body size by regressing OH on SVL. We then regressed the resulting OH residuals against the proportion of competitors in the experimental tank to determine if *S. multiplicata* tadpoles became less carnivore-like (i.e., had a smaller OH) and *S. bombifrons* tadpoles become more carnivore-like as the proportion of competitors in the experimental tank increased.

Experiment 2: What is the proximate mechanism by which S. bombifrons affects expression of carnivores in S. multiplicata?

We sought to elucidate the proximate mechanism by which *S. bombifrons* might suppress expression of carnivores in *S. multiplicata*. We tested the following two hypotheses (Pfennig and Murphy 2000). First, *S. bombifrons* larvae might decrease expression of carnivores through interference competition. In particular, *S. bombifrons* tadpoles may release chemical cues that suppress carnivore production in *S. multiplicata*. 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, *S. bombifrons* larvae might decrease expression of carnivores through exploitative competition. In particular, because *S. bombifrons* are more efficient shrimp foragers than *S. multiplicata* (Pfennig and Murphy 2000), *S. multiplicata* may be less likely to eat shrimp and thus be less likely to become carnivores when *S. bombifrons* are present, because *S. bombifrons* reduces the number of available shrimp.

We simultaneously tested the above two hypotheses by employing a full 2 × 2 factorial design with seven randomized blocks. Four sibships each of *S. multiplicata* and *S. bombifrons* tadpoles were collected as in experiment 1. Two days after hatching, *S. multiplicata* tadpoles were randomly assigned in groups of four (one tadpole per sibship) to one of four treatment groups: (1) *S. bombifrons* tadpoles present, high shrimp level; (2) *S. bombifrons* tadpoles present, low shrimp level; (3) *S. bombifrons* tadpoles absent, high shrimp level; and (4) *S. bombifrons* tadpoles absent, low shrimp level. Each treatment group was replicated seven times, producing a total of 28 tanks and 112 focal *S. multiplicata* tadpoles.

Manipulation of presence or absence of *S. bombifrons* was accomplished by placing focal *S. multiplicata* tadpoles into one compartment of rearing tanks (see experiment 1) that were divided into two equal-sized compartments with vertical 80-μm nylon mesh. The other compartment, the stimulus side of each rearing tank, contained either four *S. bombifrons* larvae or four similarly sized *S. multiplicata* larvae. Again, for each species, each of four sibships was represented. The mesh prevented passage of larvae and shrimp but allowed chemical cues to circulate from one compartment to the other. Thus, this design ensured that *S. multiplicata* were exposed to chemical cues from either *S. bombifrons* (*S. bombifrons* present treatment) or *S. multiplicata* only (*S. bombifrons* absent treatment).

Shrimp level was manipulated by feeding focal *S. multiplicata* tadpoles in the high-shrimp treatment about 200 live shrimp per day and those in the low-shrimp treatment about 40 live shrimp per day. In addition, both treatments received 0.1 g of crushed rabbit chow every three days. In both cases, shrimp levels were restrictive because all shrimp had disappeared from each tank before they were fed again. Tadpoles on the stimulus side were fed rabbit chow only. As in experiment 1, we ended the experiment after 14 days. Again, focal *S. multiplicata* tadpoles were killed by immersion in MS222 and their SVL and OH were measured using handheld digital calipers.

Prior to statistical comparison of *S. multiplicata*'s morphology across treatments, data were standardized for body size by regressing OH on SVL. We then used an ANOVA on the residuals of OH on SVL to determine if *S. multiplicata* became less carnivore-like (i.e., had a smaller OH) when exposed to chemical cues from *S. bombifrons* and/or as their shrimp intake decreased.

Experiment 3: When reared under common conditions, do tadpoles from ponds that have historically differed in exposure to competitors differ in feeding morphology?

We used a common-garden design to determine if populations of *S. multiplicata* that have been exposed historically to higher frequencies of *S. bombifrons* have a lower inherent propensity to express the carnivore morphology. First, we sampled breeding pairs of *S. multiplicata* from nine ponds near Portal, Arizona, that differed in elevation (ponds 1–3, 6–9, 11, 13 in Fig. 3b). Ponds were separated by at least 0.5 km, but no more than 27 km, and 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. 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 fairy shrimp throughout the experiments ad libitum. At two weeks post-hatching, tadpoles were scored as being omnivores or carnivores by characterizing the shape of the head and mouthparts (see Fig. 4). Morph assignments were unambiguous and made without a priori knowledge of pond origin. These experiments involved 2056 *S. multiplicata* tadpoles from 58 sibships.

For the analysis, we first calculated the proportion of tadpoles that developed into carnivores in each tank and then sibship. We then used the values for the different sibship to calculate, for each pond, an overall mean proportion of tadpoles that developed into carnivores. We used a Spearman rank order correlation coefficient to determine if the mean proportion of carnivores produced by *S. multiplicata* in each pond was significantly positively correlated with the elevation of the pond, and, thus, in the likelihood of encountering *S. bombifrons*.

Finally, we used an existing dataset (Simovich 1985) to determine if *S. bombifrons* tadpoles became increasingly more abundant with decreasing pond elevation.

RESULTS

Field surveys

For all four trophic characters that we examined in *S. multiplicata*, the expression of these traits reflected the relative abundance of *S. bombifrons* in the 10 study ponds. No significant differences in SVL of *S. multiplicata* tadpoles among allopatric and sympatric ponds were detected that might confound these analyses ($t_{2,8} = 0.9$, $P = 0.402$). The correlations demonstrated that as the percentage of *S. bombifrons* within ponds increased, the *S. multiplicata* in those ponds became significantly less carnivore-like and more omnivore-like (Fig. 5). Moreover, in three of four cases, the linear (i.e., frequency-dependent) model explained morphological trends better than the ANOVA (step model) based on the data bootstrapped from the natural pond means (OH: $t_{2,99} = 6.5$, $P < 0.0001$; IH: $t_{2,99} = 17.8$, $P < 0.001$; MP: $t_{2,99} = 7.2$, $P < 0.0001$). Only for GL, the trait with the weakest (yet still significant) linear correlation, did the ANOVA model outperform the linear model ($t_{2,99} = 5.1$, $P < 0.0001$).

Experiment 1: Does the degree of character displacement increase with increasing intensity of competition?

There was a significant inverse relationship between the percentage of *S. bombifrons* within a tank and the mean mass of individual *S. multiplicata* within that tank ($r^2 = 0.319$, $P < 0.001$). This reduced growth of *S. multiplicata* with increasing frequency of *S. bombifrons* demonstrates that *S. multiplicata* experienced greater competition as the percentage of *S. bombifrons* in a tank increased. By contrast, there was a significant positive relationship between the percentage of *S. multiplicata* within a tank and the mean mass of individual *S. bombifrons* within that tank ($r^2 = 0.167$, $P < 0.012$). This increased growth of *S. bombifrons* with increasing frequency of *S. multiplicata* demonstrates that *S. bombifrons* experienced reduced competition as the percentage of *S. multiplicata* in a tank increased.

As expected, as the percentage of *S. bombifrons* within a tank increased, the *S. multiplicata* in those tanks became significantly less carnivore-like and more omnivore-like (Fig. 6a). By contrast, as the percentage of *S. multiplicata* within a tank increased, the *S. bombifrons* in those tanks became significantly more carnivore-like (Fig. 6b). Moreover, both species showed a similar morphological response to varying frequencies of the other species. The slope of the regression of standardized OH width on the percentage of heterospecific competitors for *S. multiplicata* (0.49) did not differ significantly from that for *S. bombifrons* (0.35; $t_{2,68} = 0.26$, ns). Thus, these data establish a causative link between the frequency of competitors and character change in both species as predicted by the frequency-dependent character displacement model (Fig. 1b).

Experiment 2: What is the proximate mechanism by which S. bombifrons affects expression of carnivores in S. multiplicata?

Spea multiplicata tadpoles in tanks where more shrimp was available developed more carnivorous jaw muscles (Table 1). Conversely, in the presence of potential chemical cues from *S. bombifrons*, there was no significant change in *S. multiplicata* jaw morphology. Furthermore, density of shrimp and the presence of *S. bombifrons* did not interact to impact muscle morphology.

Experiment 3: When reared under common conditions, do tadpoles from ponds that have historically differed in exposure to competitors differ in feeding morphology?

The inherent propensity of *S. multiplicata* tadpoles to express the carnivore morphology varied with elevation. When reared under common conditions beginning just after fertilization, the mean proportion of carnivores produced by *S. multiplicata* sibships was significantly positively correlated with the elevation of their natal ponds (Fig. 7a). We also found, however, that *S. bombifrons* became increasingly more common with decreasing elevation (Fig. 7b). Therefore, *S. multiplicata* became increasingly more likely to encounter *S. bombifrons* with decreasing elevation, and *S. multiplicata* also become increasingly less likely to produce carnivores with decreasing elevation. This pattern indicates that in addition to plasticity, *S. multiplicata* populations have diverged genetically given the degree of historical exposure to *S. bombifrons*.

DISCUSSION

As predicted by the frequency-dependent character displacement model (Fig. 1b), the degree of character displacement increased as the frequency of competitors increased. In particular, when we compared four key trophic characters in *S. multiplicata* across 10 natural ponds where the frequency of *S. bombifrons* varied, we found that *S. multiplicata* became increasingly more omnivore-like as the relative abundance of *S. bombifrons* increased (Fig. 5). Moreover, in controlled laboratory populations, *S. multiplicata* became increasingly more omnivore-like as we increased the relative abundance of *S. bombifrons* (Fig. 6a), whereas *S. bombifrons* became increasingly more carnivore-like as we increased the relative abundance of *S. multiplicata* (Fig. 6b).

By studying species that facultatively express alternative trophic morphs, we were therefore able to establish a causal link between the presence of competitors and character change. In particular, we have shown that in the presence of a competitor tadpoles facultatively expressed a phenotype that was less like their competitor's. More critically, our data suggest that the degree of character displacement reflects the intensity of competition, indicating that competition not only promotes species divergence, but also that the degree of divergence can reflect the intensity of competition between interacting species.

Both *Spea* species responded to the prevalence of competitors through fine-tuned adjustments in their trophic morphology. For *S. multiplicata*, the tendency to become increas-

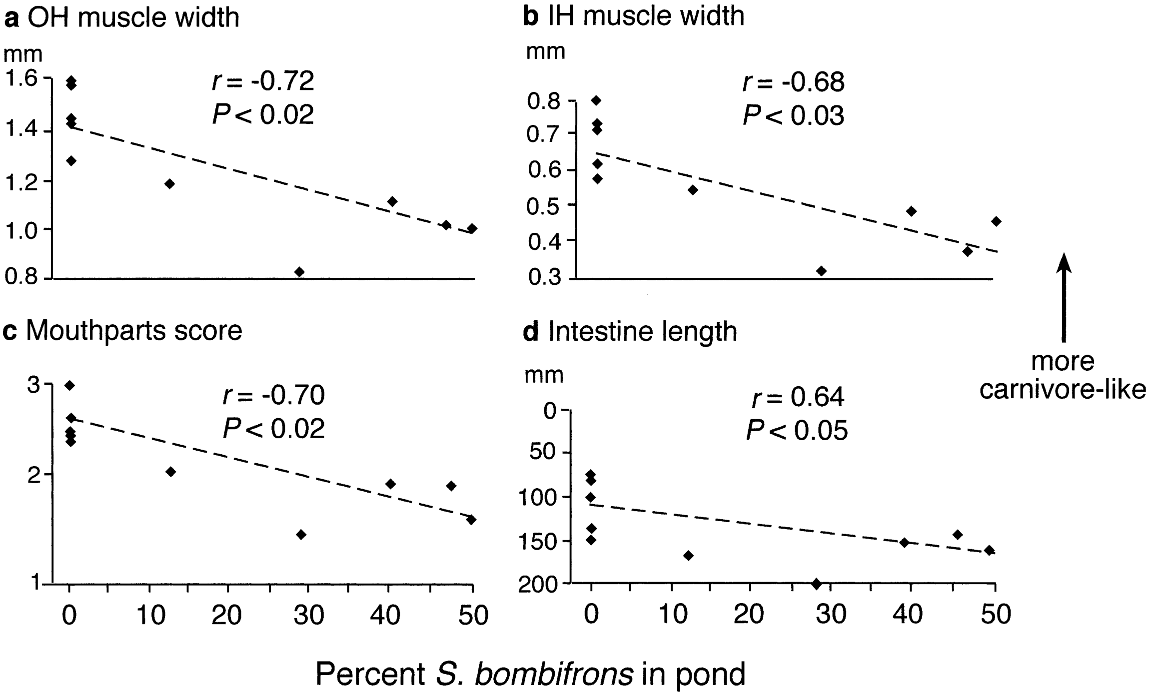

FIG. 5. Linear relationship between percent *Spea bombifrons* present in a pond and the pond mean for *S. multiplicata* for each of four trophic characters. In all cases, linear correlations were computed between transformed percents (arcsine square-root transformed) and trait means, controlling for developmental stage (log Gosner stage) and snout-vent length (log SVL). Each Pearson product moment correlation coefficient (*r*) is followed by its significance level (*P*). The least squares regression (dashed line) is shown for illustrative purposes only.

ingly more omnivore-like as the frequency of *S. bombifrons* increased (Figs. 5, 6a) appears to reflect stronger selection against carnivore-like *S. multiplicata* in ponds where *S. bombifrons* are more common. Conversely, the tendency for *S. bombifrons* to become increasingly more carnivore-like as the frequency of *S. multiplicata* increased (Fig. 6b) appears to reflect stronger selection against omnivore-like *S. bombifrons* in ponds where *S. multiplicata* are more common. *Spea multiplicata* carnivores are competitively inferior to *S. bombifrons* carnivores, whereas *S. bombifrons* omnivores are competitively inferior to *S. multiplicata* omnivores (Pfennig and Murphy 2000). These competitive differences appear to reflect differences between species in their foraging behavior. In particular, because they spend more time actively search-

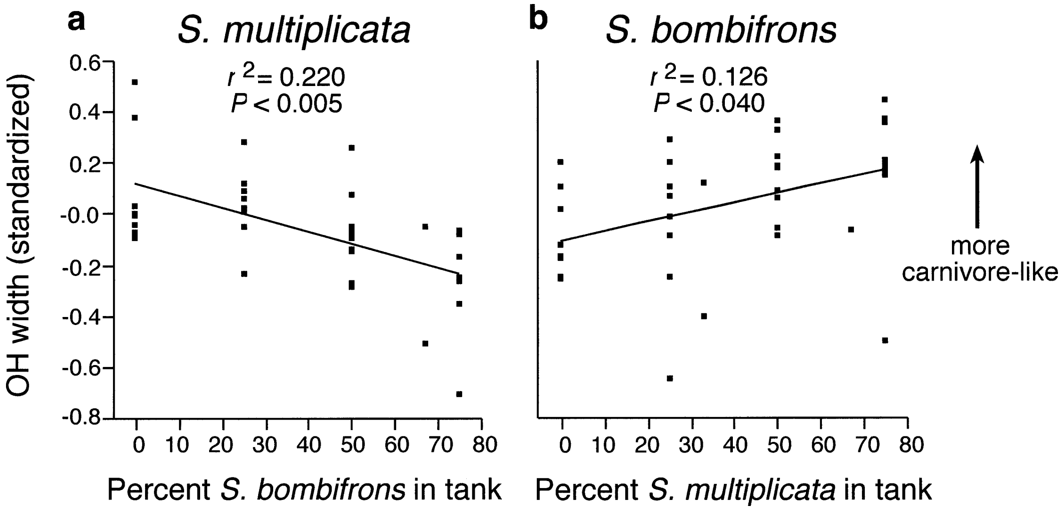

FIG. 6. (a) Linear regression between percent *Spea bombifrons* in laboratory tanks and the tank means for *S. multiplicata* tadpoles in OH width. (b) Linear regression between percent *S. multiplicata* in laboratory tanks and the tank means for *S. bombifrons* tadpoles in OH width. In both cases, we present the residuals of the regression of OH width on snout-vent length (to control for differences among tadpoles in overall body size).

TABLE 1. Two-way ANOVA of shrimp level and presence of *Spea bombifrons* on expression of the carnivore phenotype in spadefoot toad tadpoles, *S. multiplicata*, as measured by the residuals of width of the orbitohyoideus muscle (OH) regressed on overall body size (snout-vent length, SVL). Larger OH values indicate a more carnivore-like tadpole.

Source of variance	Mean residual of OH (regressed on SVL)	df	*F*	*P*
Shrimp level		1	7.199	0.013
High	0.094			
Low	−0.097			
S. bombifrons presence		1	1.737	0.199
S. bombifrons present	0.046			
S. bombifrons absent	−0.048			
Shrimp level × *S. bombifrons* presence	1	2.543	0.124	

ing in the water column, *S. bombifrons* tadpoles forage more efficiently for shrimp (Pfennig and Murphy 2000). In contrast, *S. multiplicata* spend more time grazing on the pool margins and bottoms and, thus, forage more efficiently for detritus (Pfennig and Murphy 2000).

The observed morphological changes among *Spea* tadpoles in response to different frequencies of heterospecific competitors (Fig. 5) stemmed, in part, from phenotypic plasticity. Evidence of plasticity comes from experiment 1, in which we found that individual tadpoles responded to more intense competition by facultatively adjusting their morphology to produce a phenotype more distinct from the superior competitor (Fig. 6). Plasticity was mediated by exploitative competition, in which *S. bombifrons* carnivores limited the amount of fairy shrimp available to *S. multiplicata* tadpoles (Table 1). As more *S. bombifrons* were present, *S. multiplicata* became increasingly less likely to eat shrimp and, thus, experience the cue that triggers carnivores (Fig. 6a). By contrast, as relatively more *S. multiplicata* were present, *S. bombifrons* became increasingly more likely to eat shrimp and thus develop into carnivores (Fig. 6b).

In addition to plasticity, canalized differences among populations in propensity to express the carnivore morphology also mediated fine-scale divergence. We found evidence of different inherited propensities to develop into carnivores at different elevations. In particular, *S. multiplicata* tadpoles became increasingly less likely to produce carnivores with decreasing elevation, even when reared under common conditions from fertilization (Fig. 7a). Presumably, this pattern reflected selection against carnivores in lower-elevation ponds, because *S. bombifrons* became increasingly more common with decreasing elevation (Fig. 7b). Thus, *S. multiplicata* tadpoles from populations that historically have had more contact with *S. bombifrons* possessed an innate tendency to develop into carnivores less frequently. Local genetic adaptation to the presence of *S. bombifrons* was remarkably fine grained, with differences in carnivore production detected between populations a few kilometers apart (Fig. 3). Because this divergence occurred despite gene flow among these populations (Simovich 1985), selection imposed by *S. bombifrons* must be strong.

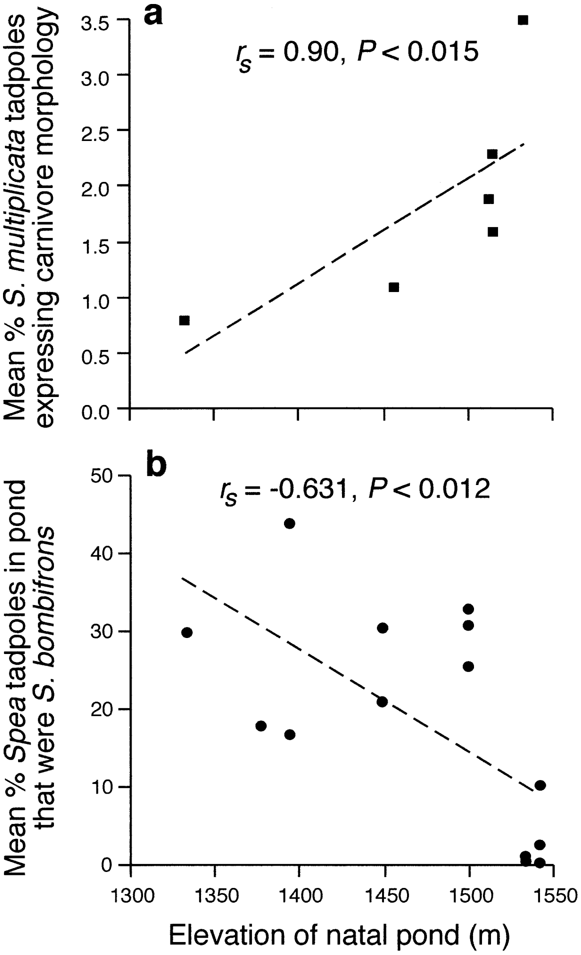

FIG. 7. (a) Mean percent of *Spea multiplicata* tadpoles from six different ponds expressing the carnivore morphology when reared from fertilization under common conditions. Parents of tadpoles were from six different ponds that differed in elevation. (b) Mean percent of *Spea* tadpoles (in 1980–1982) that were *S. bombifrons* as a function of the elevation of their natal pond (data from Simovich 1985). Each Spearman rank-order correlation coefficient (r_s) is followed by its significance level (P). The least squares regression (dashed line) is shown for illustrative purposes only.

Spea multiplicata tadpoles, therefore, responded to competitors through two distinct mechanisms: facultative changes in morphology (Fig. 6) and canalized differences in propensity to adopt the carnivore phenotype (Fig. 7a). Traditionally, competitively mediated plasticity is not considered character displacement (Grant 1972; Endler 1986; Schluter and McPhail 1992; Schluter 2000), because one of the six widely accepted criteria for character displacement is that phenotypic differences between populations and species should have a genetic basis (Grant 1972; Arthur 1982). Yet, the magnitude and direction of a plastic response to the environment (the norm of reaction) is often genetically variable (Schlichting and Pigliucci 1998) and, consequently, subject to natural selection and evolutionary change (West-Eberhard 1989). Moreover, many plant and animal species employ plasticity as a means of responding to competitors adaptively (e.g., Werner and Hall 1979; Sultan 1987; Denno and Roderick 1992; Huber-Sannwald et al. 1996; Passera et al. 1996; Caton et al. 1997; Blanckenhorn 1998; Harvey et al. 2000; see also review in Agrawal 2001).

We therefore propose the terms ''canalized character displacement'' for cases in which phenotypic differences between populations in allopatry and sympatry with competitors are canalized and ''facultative character displacement'' for cases in which plasticity mediates the response to competitors but in which the other five criteria for character displacement are met (see Schluter 2000). Such a dichotomy has the advantage of making clear that both mechanisms, facultative character displacement and canalized character displacement, reflect similar selective pressures and may be employed to respond to competitors adaptively. Moreover, these two mechanisms may actually represent two ends of a continuum, and, as with *S. multiplicata*, both mechanisms may often be used simultaneously.

If organisms can detect competitors and respond appropriately through facultative character displacement, then why would canalized character displacement evolve? Canalized character displacement might often be selectively favored in addition to, or instead of, facultative character displacement. For instance, if assessment of competitor frequency is difficult or costly (DeWitt et al. 1998) and if the fitness cost of expressing an inappropriate phenotype is severe, then canalized responses might be favored over facultative ones, especially if competitors are reliably present (for a similar argument regarding the evolution of canalized versus facultative responses to predators, see Lively 1986). In the present case, because *S. bombifrons* are reliably present in lower-elevation ponds (Fig. 7b), natural selection has presumably favored diminished carnivore production by *S. multiplicata*.

We might expect to observe both mechanisms of character displacement in the same system if facultative character displacement often precedes the evolution of canalized character displacement. In particular, competitively mediated plasticity might eventually result in alternative phenotypes becoming canalized in different populations that have differed historically in their encounter rate with competitors. Canalization may occur, possibly through genetic assimilation (Schmalhausen 1949; Waddington 1956), for two reasons. First, selection should become increasingly effective at producing a particular phenotype (as opposed to the alternative phenotype[s]) as that phenotype becomes increasingly common in the population (West-Eberhard 1989). Second, as one phenotype is expressed continuously in a population and the alternative phenotype is never expressed, alleles that regulate expression of this hidden phenotype would not be exposed to selection and thus are at risk of chance loss (e.g., through drift or gradual mutation accumulation). For example, sibships in higher-elevation populations of *S. multiplicata* retain the capacity to respond adaptively to the presence of *S. bombifrons* by facultatively producing either omnivores or carnivores (Fig. 7a). By contrast, in lower-elevation populations, where omnivores are almost always expressed (because *S. bombifrons* carnivores are reliably present), some sibships have completely lost the ability to produce carnivores (e.g., see Fig. 7a; see also Pfennig 1999). Thus, *Spea* tadpoles may represent an intermediate stage in the evolution of canalized character displacement.

Additionally, the same ecological conditions that favor alternative morphs might also favor canalized character displacement. Because empty niches enable niche partitioning, character displacement should occur most frequently when vacant niches are available (Smith 1990; Schluter and McPhail 1993), which is the same condition favoring alternative phenotypes (Skúlason and Smith 1995; Maret and Collins 1997). Thus, we might expect to observe canalized character displacement more frequently in species that exist as environmentally triggered alternative morphs (i.e., those that express polyphenism). As *Spea* tadpoles illustrate, when a polyphenic individual is confronted by a competitor, it can occupy the open niche by facultatively expressing an alternative phenotype less like its competitor's phenotype (Fig. 6). In the absence of polyphenism, however, one species might often displace the other before alternative phenotypes that could succeed in the open niche have time to evolve. As expected, character displacement does indeed seem to occur more frequently in species that express alternative morphs or are phenotypically variable (e.g., Milligan 1985; Robinson and Wilson 1994; Schluter 1994; Pfennig and Murphy 2000; Kawano 2002).

The finding of clinal canalized responses to competitors suggests a possible role for competition in promoting speciation. An enduring debate in evolutionary biology has been whether physical isolation is required for populations to diverge or whether natural selection for divergence can overwhelm gene flow and trigger speciation within a continuous population (i.e., parapatric speciation; Mayr 1963; Maynard Smith 1966; Bush 1975; Felsenstein 1981). Theory suggests that populations can diverge even when in contact with each other (Endler 1977; Felsenstein 1981; Rice 1987; Gavrilets et al. 2000). Moreover, there are numerous examples of populations that appear to be diverging, presumably because of differences in habitat or resource use (Pashley 1988; Feder et al. 1989; Brown et al. 1996; Wood and Foote 1996; Carroll et al. 1997; McMillan et al. 1997; Hatfield and Schluter 1999; Lu and Bernatchez 1999; Via 1999).

Different populations of *S. multiplicata* may be undergoing parapatric speciation. Genetically based divergence appears to be occurring along an elevational gradient within a continuous population, owing to strong selection imposed by *S. bombifrons*. Once such populations begin to diverge in tendencies to adopt the carnivore morphology, these populations may become increasingly reproductively isolated from one another, because carnivores and omnivores are adapted to different habitats. In particular, omnivores are favored in longer-lasting ponds because they metamorphose in better condition, whereas carnivores are favored in more ephemeral pools because they develop more rapidly (Pfennig 1992a). Thus, sibships that produce omnivores primarily would be excluded from breeding in ephemeral pools, and those that produce carnivores primarily would be excluded from longer-duration ponds. As evidence that isolation might be taking place, K. Pfennig (2000) found differences in mate preferences between populations of *S. multiplicata* that are sympatric with *S. bombifrons* and those that are allopatric. Future studies are needed to determine if females from different populations (Fig. 3b) prefer to mate assortatively and if, as a result, these populations are becoming differentiated in their genotypes.

Acknowledgments

We thank K. Pfennig, J. Wiens, and two anonymous referees for their detailed comments on the manuscript; K. Pfennig, D. Cycert, and W. Harcombe for laboratory and field assistance; E. Sherbrooke and W. Sherbrooke of the Southwestern Research Station of the American Museum of Natural History for furnishing housing and laboratory facilities; and the Arizona Game and Fish Department for collecting permits. This research was supported by National Science Foundation grants DEB-9873633 and IBN-9808641 to DWP.

Literature Cited

Agrawal, A. A. 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294:321–326.

Alexander, R. M. 1985. Body support, scaling, and allometry. Pp. 26–37 *in* M. Hildebrand, M. Bramble, K. F. Liem, and D. B. Wake, eds. Functional vertebrate morphology. Harvard Univ. Press, Cambridge, MA.

Alford, R. A. 1999. Ecology: resource use, competition, and predation. Pp. 240–278 *in* R. W. McDiarmid and R. Altig, eds. Tadpoles: the biology of anuran larvae. Univ. of Chicago Press, Chicago, IL.

Altig, R., and G. F. Johnston. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. Herp. Mon. 3:81–109.

Altig, R. and R. W. McDiarmid. 1999. Body plan: development and morphology. Pp. 24–51 *in* R. W. McDiarmid and R. Altig, eds. Tadpoles: the biology of anuran larvae. Univ. of Chicago Press, Chicago, IL.

Arthur, W. 1982. The evolutionary consequences of interspecific competition. Adv. Ecol. Res. 12:127–187.

Blanckenhorn, W. U. 1998. Adaptive phenotypic plasticity in growth, development, and body size in the yellow dung fly. Evolution 52:1394–1407.

Bourke, P., P. Magnan, and M. A. Rodríguez. 1999. Phenotypic responses of lacustrine brook char in relation to the intensity of interspecific competition. Evol. Ecol. 13:19–31.

Bragg, A. N. 1965. Gnomes of the night: the spadefoot toads. Univ. of Pennsylvania Press, Philadelphia.

Brown, J. H. 1995. Macroecology. Univ. of Chicago Press, Chicago, IL.

Brown, J. M., W. G. Abrahamson, and P. A. Way. 1996. Mitochondrial DNA phylogeography of host races of the goldenrod gallmaker, *Eurosta solidaginis* (Diptera: Tephritidae). Evolution 50:777–786.

Brown, W. L., and E. O. Wilson. 1956. Character displacement. Syst. Zool. 5:49–64.

Bush, G. L. 1975. Models of animal speciation. Annu. Rev. Ecol. Syst. 6:339–364.

Cannatella, D. 1999. Architecture: cranial and axial musculoskeleton. Pp. 52–91 *in* R. W. McDiarmid and R. Altig, eds. Tadpoles: the biology of anuran larvae. Univ. of Chicago Press, Chicago, IL.

Carroll, S. P., H. Dingle, and S. P. Klassen. 1997. Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. Evolution 51:1182–1188.

Caton, B. P., T. C. Foin, and J. E. Hill. 1997. Phenotypic plasticity of *Ammannia* spp. in competition with rice. Weed Res. 37:33–38.

Conant, R., and J. T. Collins. 1991. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin, Boston, MA.

Conner, D. F., and D. S. Simberloff. 1979. The assembly of species communities: chance or competition? Ecology 60:1132–1140.

Darwin, C. 1859. On the origin of species by means of natural selection. John Murray, London.

DeJongh, H. J. 1968. Functional morphology of the jaw apparatus of larval and metamorphosizing *Rana temporaria* L. Neth. J. Zool. 18:1–103.

Denno, R. F., and G. K. Roderick. 1992. Density-related dispersal in planthoppers: effects of interspecific crowding. Ecology 73: 1323–1334.

DeWitt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. Trend Ecol. Evol. 13:77–81.

Dunham, A. E., G. R. Smith, and J. N. Taylor. 1979. Evidence for ecological character displacement in western American catostomid fishes. Evolution 33:877–896.

Endler, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, NJ.

———. 1986. Natural selection in the wild. Princeton Univ. Press, Princeton, NJ.

Feder, J. L., C. A. Chilcote, and G. L. Bush. 1989. Are the apple maggot, *Rhagoletis pomonella*, and blueberry maggot, *Rhagoletis mendax*, distinct species? Implications for sympatric speciation. Entomol. Exp. Appl. 51:113–123.

Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? Evolution 35:124–138.

Frankino, W. A., and D. W. Pfennig. 2001. Condition-dependent expression of trophic polyphenism: effects of individual size and competitive ability. Evol. Ecol. Res. 3:939–951.

Gavrilets, S., H. Li, and M. D. Vose. 2000. Patterns of parapatric speciation. Evolution 54:1126–1134.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183–190.

Grant, P. R. 1972. Convergent and divergent character displacement. Biol. J. Linn. Soc. 4:39–68.

———. 1994. Ecological character displacement. Science 266: 746–747.

Harvey, J. A., L. S. Corley, and M. R. Strand. 2000. Competition induces adaptive shifts in caste ratios of a polyembryonic wasp. Nature 406:183–186.

Hatfield, T., and D. Schluter. 1999. Ecological speciation in sticklebacks: environment-dependent hybrid fitness. Evolution 53: 866–873.

Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton Univ. Press, Princeton, NJ.

Horiuchi, S., and Y. Koshida. 1989. Effects of foodstuffs on intestinal length in larvae of *Rhacophorus arboreus* (Anura: Rhacophoridae). Zool. Sci. 6:321–328.

Huber-Sannwald, E., D. A. Pyke, and M. M. Caldwell. 1996. Morphological plasticity following species-specific recognition and competition in two perennial grasses. Am. J. Bot. 83:919–931.

Kawano, K. 2002. Character displacement in giant rhinoceros beetles. Am. Nat. 159:255–271.

Lack, D. 1947. Darwin's finches. Cambridge Univ. Press, Cambridge, U.K.

Lively, C. M. 1986. Canalization versus developmental conversion in a spatially variable environment. Am. Nat. 128:561–572.

Losos, J. B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. Evolution 44:558–569.

———. 1992. The evolution of convergent structure in Caribbean *Anolis* communities. Syst. Biol. 41:403–420.

———. 2000. Commentary: ecological character displacement and the study of adaptation. Proc. Natl. Acad. Sci. USA 97: 5693–5695.

Lu, G. Q., and L. Bernatchez. 1999. Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): support for the ecological speciation hypothesis. Evolution 53:1491–1505.

Maret, T. J., and J. P. Collins. 1997. Ecological origin of morphological diversity: a study of alternative trophic phenotypes in larval salamanders. Evolution 51:898–905.

Maynard Smith, J. 1966. Sympatric speciation. Am. Nat. 100: 637–650.

Mayr, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, MA.

McMillan, W. O., C. D. Jiggins, and J. Mallet. 1997. What initiates speciation in passion-vine butterflies? Proc. Natl. Acad. Sci. USA 94:8628–8633.

Milligan, B. G. 1985. Evolutionary divergence and character displacement in two phenotypically variable, competing species. Evolution 39:1207–1222.

Nodzenski, E. R., R. J. Wassersug, and R. F. Inger. 1989. Developmental differences in visceral morphology of megophrynine pelobatid tadpoles in relation to their body form and mode of life. Biol. J. Linn. Soc. 38:369–388.

Pashley, D. P. 1988. Quantitative genetics, development, and physiological adaptation in host strains of fall armyworm. Evolution 42:93–102.

Passera, L., E. Roncin, B. Kaufmann, and L. Keller. 1996. Increased soldier production in ant colonies exposed to intraspecific competition. Nature 379:630–631.

Pearson, P. G. 1955. Population ecology of the spadefoot toad, *Scaphiopus h. holbrooki* (Harlan). Ecol. Monog. 25:233–267.

Pfennig, D. W. 1990. The adaptive significance of an environmentally cued developmental switch in an anuran tadpole. Oecologia 85:101–107.

———. 1992a. Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionarily stable strategy. Evolution 46:1408–1420.

———. 1992b. Proximate and functional causes of polyphenism in an anuran tadpole. Func. Ecol. 6:167–174.

———. 1999. Cannibalistic tadpoles that pose the greatest threat to kin are most likely to discriminate kin. Proc. R. Soc. Lond. B 266:57–61.

———. 2000. Effect of predator-prey phylogenetic similarity on the fitness consequences of predation: a trade-off between nutrition and disease? Am. Nat. 155:335–345.

Pfennig, D. W., and W. A. Frankino. 1997. Kin mediated morphogenesis in facultatively cannibalistic tadpoles. Evolution 51: 1993–1999.

Pfennig, D. W., and P. J. Murphy. 2000. Character displacement in polyphenic tadpoles. Evolution 54:1738–1749.

Pfennig, D. W., A. Mabry, and D. Orange. 1991. Environmental causes of correlations between age and size at metamorphosis in *Scaphiopus multiplicatus*. Ecology 72:2240–2248.

Pfennig, K. S. 2000. Female spadefoot toads compromise on mate quality to ensure conspecific matings. Behav. Ecol. 11:220–227.

Pomeroy, L. V. 1981. Developmental polymorphism in the tadpoles of the spadefoot toad *Scaphiopus multiplicatus*. Ph.D. diss., University of California, Riverside, CA.

Rice, W. R. 1987. Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. Evol. Ecol. 1:301–314.

Robinson, B. W., and D. S. Wilson. 1994. Character release and displacement in fishes: a neglected literature. Am. Nat. 144: 596–627.

Roughgarden, J., D. Heckel, and E. R. Fuentes. 1983. Coevolutionary theory and the biogeography and community structure of *Anolis*. Pp. 371–410 *in* R. B. Huey, E. R. Pianka, and T. W. Schoener, eds. Lizard ecology: studies of a model organism. Harvard Univ. Press, Cambridge, MA.

Ruibal, R., and E. Thomas. 1988. The obligate carnivorous larvae of the frog *Lepidobatrachus laevis* (Leptodactylidae). Copeia 1988:591–604.

Satel, S. L., and R. J. Wassersug. 1981. On the relative sizes of buccal floor depressor and elevator musculature in tadpoles. Copeia 1981:129–137.

Schlichting, C. D., and M. Pigliucci. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer Associates, Sunderland, MA.

Schluter, D. 1994. Experimental evidence that competition promotes divergence in adaptive radiation. Science 266:798–801.

———. 2000. The ecology of adaptive radiation. Oxford Univ. Press, Oxford, U.K.

Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. Am. Nat. 140:85–108.

———. 1993. Character displacement and replicate adaptive radiation. Trends Ecol. Evol. 8:197–200.

Schmalhausen, I. I. 1949. Factors of evolution: the theory of stabilizing selection. Blakiston, Philadelphia, PA.

Simovich, M. A. 1985. Analysis of a hybrid zone between the spadefoot toads *Scaphiopus multiplicatus* and *Scaphiopus bombifrons*. Ph.D. diss., University of California, Riverside, CA.

Simovich, M. A., and C. A. Sassaman. 1986. Four independent electrophoretic markers in spadefoot toads. J. Hered. 77: 410–414.

Skúlason, S., and T. B. Smith. 1995. Resource polymorphisms in vertebrates. Trend Ecol. Evol. 10:366–370.

Slatkin, M. 1980. Ecological character displacement. Ecology 61: 163–177.

Smith, T. B. 1990. Resource use by bill morphs of an African finch: evidence for intraspecific competition. Ecology 71:1246–1257.

Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. Evol. Biol. 21:127–178.

Taper, M. L., and T. J. Case. 1992. Coevolution among competitors. Oxford Surv. Evol. Biol. 8:63–109.

Thompson, J. N. 1994. The coevolutionary process. Univ. of Chicago Press, Chicago, IL.

Turner, F. B. 1952. The mouth parts of tadpoles of the spadefoot toad, *Scaphiopus hammondii*. Copeia 1952:172–175.

Via, S. 1999. Reproductive isolation between sympatric races of pea aphids. I. Gene flow restriction and habitat choice. Evolution 53:1446–1457.

Waddington, C. H. 1956. Genetic assimilation of the bithorax phenotype. Evolution 10:1–13.

Wassersug, R. J., and K. Hoff. 1979. A comparative study of the buccal pumping mechanism of tadpoles. Biol. J. Linn. Soc. 12: 225–259.

Werner, E. E., and D. L. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60:256–264.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. Annu. Rev. Ecol. Syst. 20:249–278.

Wood, C. C., and C. J. Foote. 1996. Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). Evolution 50:1265–1279.

Corresponding Editor: J. Wiens