

ECOLOGICAL OPPORTUNITY AND PHENOTYPIC PLASTICITY INTERACT TO PROMOTE CHARACTER DISPLACEMENT AND SPECIES COEXISTENCE

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Abstract. We investigated the roles of resource availability and phenotypic plasticity in promoting ecological character displacement (i.e., trait evolution stemming from resource competition between species). Because ecological character displacement generates new populations that differ in resource use, this process should only occur when exploitable resources are available. We tested this hypothesis in two species of spadefoot toads (*Spea bombifrons* and *S. multiplicata*) whose tadpoles use phenotypic plasticity to develop into either an omnivore morph, which specializes on detritus, or a physically distinctive carnivore morph, which specializes on shrimp. Both species grow best on shrimp, but when reared together, *S. bombifrons* outcompetes *S. multiplicata* for shrimp and *S. multiplicata* outcompetes *S. bombifrons* for detritus. We found that when each species occurred alone in the field, they produced similar proportions of omnivores and carnivores. When the two species occurred together, however, they underwent ecological character displacement in larval development, with *S. multiplicata* producing mostly omnivores, and *S. bombifrons* producing mostly carnivores. We combined observations of natural populations with experiments to evaluate whether such character displacement was only possible when both shrimp and detritus were relatively abundant. Mixed-species ponds contained abundant detritus and shrimp, in contrast with nearby pure-species ponds, which were deficient in one resource. Experiments revealed that *S. multiplicata* competed poorly when detritus was rare and that *S. bombifrons* competed poorly when shrimp was rare. In nature, when one of these two resources was scarce, one species was missing, perhaps through competitive exclusion by the species that was the superior competitor for the remaining resource. Thus, ecological character displacement and, therefore, coexistence of close competitors, was only possible when diverse resources were available. Finally, even if exploitable resources are available, character displacement is not guaranteed to transpire if species cannot utilize such resources expeditiously. Phenotypic plasticity provides a general and important mechanism for facilitating resource partitioning. Thus, by facilitating shifts in resource use, phenotypic plasticity and ecological opportunity may often interact to promote divergence and coexistence of competitors.

Key words: amphibians; biogeography; competition; competitive exclusion; local adaptation; resource polymorphism.

INTRODUCTION

A central goal of evolutionary ecology is to explain why living things are so diverse and to clarify why species coexist in some situations but not in others. Competition for resources, especially food, has long been considered crucial for explaining both species diversity and coexistence (Darwin 1859, Rosenzweig 1978, Dieckmann and Doebeli 1999, Schluter 2000, Day and Young 2004).

When close competitors come into contact, there are two main evolutionary outcomes. First, one may drive the other locally extinct as predicted by the competitive exclusion principle, which states that no two species can occupy the same niche indefinitely when resources

are limiting (Gause 1934, Park 1948, Hardin 1960, Connell 1961, MacArthur and Levins 1964). Second, competition may lead to ecological character displacement (Brown and Wilson 1956, Slatkin 1980, Losos 2000, Schluter 2001), whereby competition between similar individuals imposes disruptive selection on resource use and associated phenotypic characters, leading to divergence and a reduction in competition (Lack 1947, Hutchinson 1959, MacArthur and Levins 1964, Grant 1972, Schluter 1994, Pritchard and Schluter 2001; reviewed in Robinson and Wilson 1994, Schluter 2000, Day and Young 2004, Dayan and Simberloff 2005). By promoting divergence in resource use, character displacement enables close competitors to coexist.

Models of character displacement typically consider two species that utilize resources along a resource spectrum (reviewed in Taper and Case 1992). The resource

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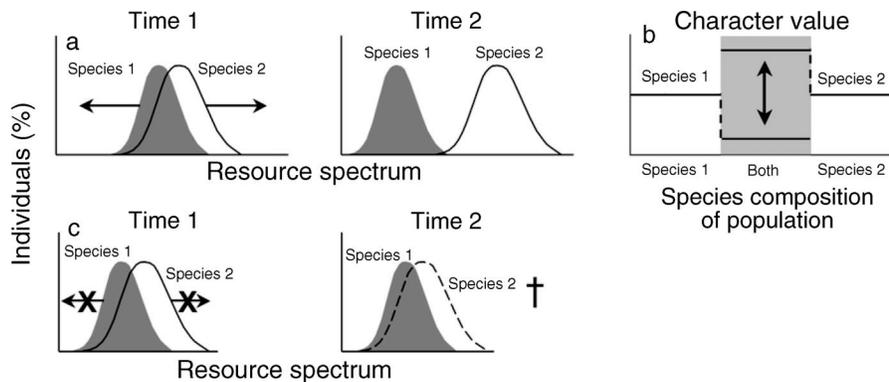


FIG. 1. (a) When species compete over a wide resource spectrum (i.e., a wealth of exploitable resources are available), natural selection can permit them to coexist by causing the species to diverge in resource use and associated features (ecological character displacement). A signature of this process (b) is that competing species should exhibit exaggerated differences in sympatry (where there is selection for divergence), but not in allopatry (where there is no such selection). (c) However, when species compete over a narrow resource spectrum (i.e., exploitable resources are not available, represented here by crossed-out arrows), coexistence may be unlikely. In this case, the species that uses the resource more efficiently (here, species 1) may eventually drive the other species (here, species 2) locally extinct (denoted by the cross).

use of an individual along this spectrum is determined by a single phenotypic trait. The more similar two individuals are in this trait, the more intense the competition. Divergent character displacement occurs as individuals of each species evolve greater ability to utilize less used parts of the resource spectrum (Fig. 1a, b). However, because ecological character displacement generates new populations that differ from the ancestral predisplacement populations in resource use (Fig. 1a, b), exploitable resources must be available for this process to occur; i.e., resources should not already be utilized by another species that is a superior competitor for the resources. In the absence of such exploitable resources, competitive exclusion may result (Fig. 1c).

Here, we address these issues by asking: what role does resource availability play in promoting divergence and coexistence of competitors? Although ecological opportunity, in the form of a wide spectrum of resources with few competitors, has long been viewed as vital in promoting and maintaining species diversity (Simpson 1944, 1953, Lack 1947, Mayr 1963, Heard and Hauser 1994, Robinson and Wilson 1994, Schluter 1996), experimental tests are generally lacking (Schluter 2000; but see Rainey and Travisano 1998). Moreover, because most tests of the ecological opportunity hypothesis focus on the presence or absence of competitors, the role of resource availability per se in promoting divergence and coexistence of competitors is unclear (Schluter 2000).

We combine observations of natural populations with experiments to evaluate whether exploitable resources are necessary for ecological character displacement to occur. We specifically sought to test whether two species of frogs coexist by undergoing ecological character displacement. We then asked if character displacement is only possible when a wide spectrum of

resources is available. Finally, we experimentally manipulated resource availability to determine if character displacement and therefore, coexistence of close competitors, was likely not possible when exploitable resources were rare or unavailable. We conclude by discussing how phenotypic plasticity can facilitate competitively mediated shifts in resource use.

Study system

Plains (*Spea bombifrons*) and Mexican spadefoot toads (*S. multiplicata*) co-occur in the southwestern United States (Stebbins 2003). Their tadpoles develop into either a small, slowly developing tadpole with normal sized jaw muscles used for feeding on detritus at the pond bottom (the “omnivore” morph), or a larger, more rapidly developing tadpole with greatly enlarged jaw muscles used for feeding on anostracan fairy shrimp in open water (the “carnivore” morph; Bragg 1965, Pomeroy 1981, Pfennig 1990, 1992). Shrimp ingestion potentially triggers development of carnivores from omnivores (Pfennig 1990), but different populations vary in propensity to express the carnivore morphology, even when reared under common conditions (Pfennig and Murphy 2000, 2002).

When reared alone, both species grow best on a diet of shrimp (see Pfennig and Murphy 2000: Fig. 4). However, in the absence of competition from the other species, natural populations of each species frequently contain both tadpole phenotypes (Pfennig 1990). Presumably, resource polymorphism within a species is maintained evolutionarily as an adaptation to lessen intraspecific competition for food (Pfennig 1992).

Prior work has documented ecological character displacement in the expression of larval feeding morphology (Pfennig and Murphy 2000, 2002, 2003). Although both species fare best on a common resource (shrimp), one (*S. multiplicata*) switches exclusively to

a new resource (detritus) in the presence of the other. In allopatry, the two species produce similar proportions of carnivores and omnivores (Pfennig and Murphy 2003). In sympatry, however, *S. bombifrons* switches to producing mostly carnivores, and *S. multiplicata* switches to producing mostly omnivores (Pfennig and Murphy 2003). Indeed, *S. multiplicata* undergoes an evolutionary shift in developmental mechanism: in allopatry, *S. multiplicata* maintain plasticity to produce both carnivores and omnivores, but in sympatry, they lose this plasticity and become canalized to produce mostly omnivores (Pfennig and Murphy 2000, 2002).

The observed divergence between species in morph production in sympatric ponds appears to reflect competitive differences between these two species. *Spea multiplicata* is the superior competitor for detritus, whereas *S. bombifrons* is the superior competitor for shrimp (Pfennig and Murphy 2000). These competitive differences apparently stem from differences between species in foraging behavior. Because they spend more time actively searching 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 bottom and, thus, forage more efficiently for detritus (Pfennig and Murphy 2000).

Controlled lab experiments reveal that these shifts in morph production are likely to have evolved because of resource competition imposed by the other species. When each species is reared alone under common conditions (i.e., with both shrimp and detritus), they produce similar proportions of carnivores and omnivores (Pfennig and Murphy 2002). When both species are present, however, *S. multiplicata* are less likely to eat shrimp and thereby experience the cue that triggers carnivores (Pfennig and Murphy 2002). As a result, *S. multiplicata* develop mostly into omnivores in the presence of *S. bombifrons*. In contrast, *S. bombifrons* are more likely to eat shrimp and thus develop mostly into carnivores in the presence of *S. multiplicata* (Pfennig and Murphy 2002). Thus, these experimentally demonstrated niche shifts mirror the canalized niche shifts observed in the field, thereby establishing a causal link between the presence of a heterospecific competitor and character change.

METHODS

To test whether exploitable resources are necessary for character displacement, we conducted three studies. First, by undertaking geographical surveys of tadpoles in natural ponds, we examined where the two species co-occurred and whether they always underwent character displacement in these environments. Second, we examined whether character displacement is only possible in ponds in which shrimp and detritus were both relatively abundant. Conversely, we examined whether one species was missing when one resource was rare

or unavailable. We addressed this issue by measuring resource availability in natural ponds and correlating resource availability with each species' abundance. Finally, we asked if character displacement and therefore, coexistence, was likely not possible when a resource was rare or unavailable. We addressed this issue by manipulating the availability of each resource in microcosms containing both species and measuring each species' morphotype and performance (i.e., growth and survival).

Geographical surveys of habitat occupancy and character displacement

We collected tadpoles and adults during the summers of 1995–2004 from 81 natural ponds along a 180-km transect through southeastern Arizona and southwestern New Mexico, USA (Fig. 2). In this region, both species potentially co-occur below 1350 m elevation; above 1350 m only *S. multiplicata* is found (Pfennig and Murphy 2000). Adults and tadpoles were sampled in 35 ponds, only tadpoles were sampled in 38 ponds, and only adults were sampled in eight ponds. Sixteen ponds were sampled in at least two different years. Adults were collected by hand at breeding aggregations. Tadpoles were sampled from randomly selected sites throughout each pond (14–18 d past pond filling) by using a hand-held dip net. We sampled a total of 1780 tadpoles (17–74 per pond).

We classified each individual as a *S. bombifrons* or a *S. multiplicata* using (for adults) external morphology (Stebbins 2003) and (for tadpoles) genetic markers. Within a few hours of collection, we killed the tadpoles by immersion in a 0.1% aqueous solution of tricane methanesulfonate (MS 222) and preserved them in 95% ethanol (in 1999, we first took a tissue sample from each tadpole and froze it at -80°C). In 1999, we used species-specific allozymes (Simovich and Sassaman 1986), and in 2000–2004 we sequenced a 663-base-pair region of the mtDNA genome to classify each tadpole as *S. bombifrons* or *S. multiplicata*. We used these data to determine which ponds contained only a single species of *Spea* and which ponds contained both species.

Next, we asked if tadpoles of the two species express similar trophic morphologies in allopatry but different morphologies in sympatry, as would be expected if the two species had undergone character displacement in larval development (Pfennig and Murphy 2000, 2002, 2003). We addressed this question in two ways.

First, we classified each tadpole as a carnivore or an omnivore based on a visual inspection of the relative size of the jaw musculature and the shape of the mouthparts (Pfennig 1992). Morph assignments were unambiguous and made without a priori knowledge of each tadpole's species or birthplace.

Second, for 1378 tadpoles from 54 ponds (11–73 per pond), we measured three diagnostic characters using methods outlined in Pfennig and Murphy (2002): (1)

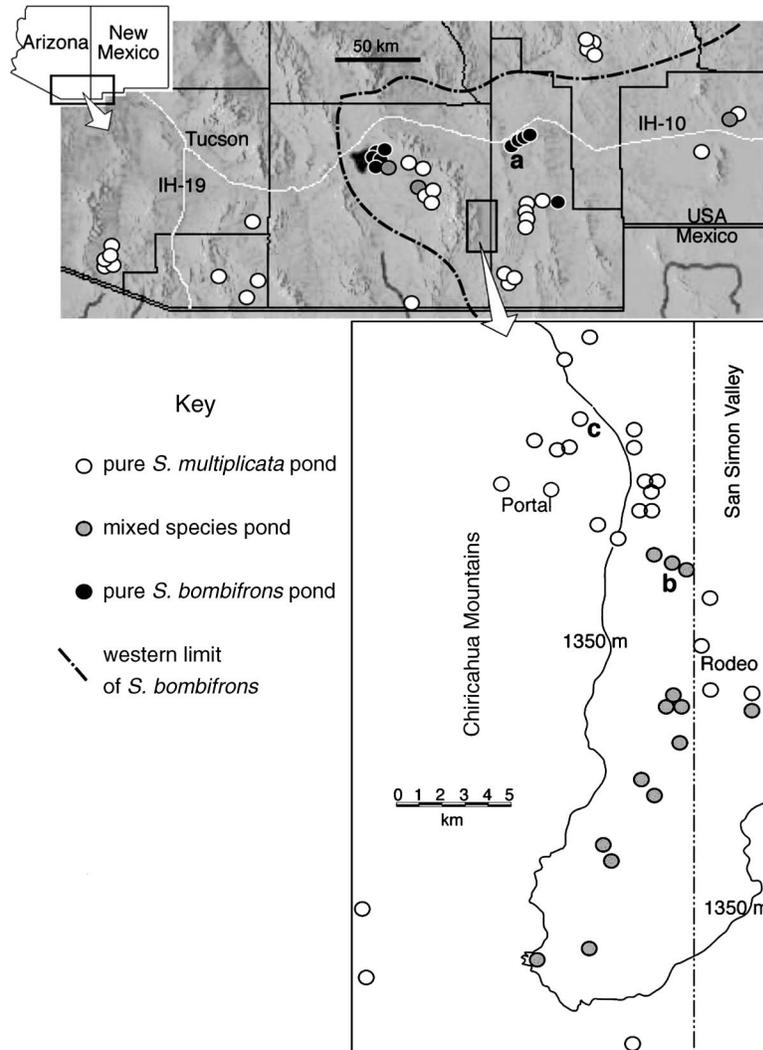


FIG. 2. Map of study area, showing locations of ponds. Boldface letters a–c denote the locations of ponds pictured in Fig. 4, which differed in species composition: pure *Spea multiplicata*, *S. bombifrons*, or a mixture.

width of the orbitohyoideus (OH) muscle, (2) width of the interhyoideus (IH) muscle, and (3) shape of the keratinized mouthparts. We standardized OH and IH for body size (snout–vent length, SVL) by combining all populations of both species and log transforming OH and IH. We then regressed all values of OH and IH separately on $\log(\text{SVL})$. Regression on $\log(\text{SVL})$ produced normal residuals. We derived a standardized value for each character and tadpole by adding the residual back to the original character value for that tadpole. Next, we performed a principal component (PC) analysis of the three characters. We used PC1, which explained over 87% of the variance in the three traits. Using pond means, we then grouped PC1 by species and region (i.e., sympatry and allopatry) and performed an ANOVA to test whether this morphological index differed by species and region. In particular, we tested whether the two species were similar in

allopatry (pure-species ponds), but were different in sympatry (mixed-species ponds).

Assessment of resource availability

Although both species grow well on either resource (see Pfennig and Murphy 2000: Fig. 4; see also *Discussion*), earlier competition experiments demonstrated that *S. bombifrons* outcompetes *S. multiplicata* for shrimp and that *S. multiplicata* outcompetes *S. bombifrons* for detritus (Pfennig and Murphy 2000). We therefore hypothesized that *S. multiplicata* would be absent from ponds in which detritus is scarce but shrimp are present, because *S. bombifrons* would outcompete *S. multiplicata* for the available shrimp. We also hypothesized that *S. bombifrons* would be absent from ponds in which shrimp are scarce but detritus is present, because *S. multiplicata* would outcompete *S. bombifrons* for the available detritus. To test each hy-

pothesis, we first had to assess the availability of shrimp and detritus within natural ponds. We then asked whether, when one of these two resources was scarce, one species was missing, perhaps because of competitive exclusion by the superior competitor for the remaining resource.

To quantify the availability of shrimp, we intensively sampled live fairy shrimp in 16 ponds (five of which contained *S. bombifrons* and 11 of which did not) by using the methods in Pfennig (1990). Additionally, for 68 ponds, we estimated shrimp abundance by sweeping a net throughout each pond and categorizing shrimp densities as "high," "moderate," "low," and "none." The latter subjective estimates were made without a priori knowledge of the abundance of each species in each pond and corroborated by the former, more intensive, quantitative sampling.

To quantify availability of detritus, we compared growth of tadpoles when raised under controlled conditions on substrate from different ponds (on the assumption that tadpoles would exhibit higher growth on pond substrate with greater availability of detritus). We collected substrate from three types of ponds one week after pond filling: (1) a pure *S. bombifrons* pond, (2) a mixed-species pond, and (3) a pure *S. multiplicata* pond. We sampled one of each type of pond in 2003 and 2004, using different ponds each year. Within a few hours of collection, substrate from each pond was poured into a separate wading pool (1.83 m diameter \times 0.3 m tall) filled with dechlorinated tap water. After the substrate settled to a depth of 10 cm, we placed 10 wire mesh cages (20 cm diameter \times 40 cm tall) into each pool such that substrate covered the bottom of each.

We collected six amplexant pairs each of *S. bombifrons* and *S. multiplicata* from a July 2003 breeding chorus near Rodeo, New Mexico (31°48.834' N, 109°3.176' W; elevation 1267 m) and three amplexant pairs each of *S. bombifrons* and *S. multiplicata* from a July 2004 breeding chorus near Portal, Arizona (31°52.688' N, 109°3.687' W; elevation 1275 m). Six days after the tadpoles hatched, we mixed together conspecific tadpoles from different sibships. For each species, we randomly assigned five tadpoles to each of five separate mesh cages in each pool. Thus, each pool held five cages containing five *S. bombifrons* tadpoles and five cages containing five *S. multiplicata* tadpoles (all tadpoles were matched for size at the start of the experiment [approximately 6 mm SVL]). On the fourth day after the experiment began, we moved each cage within each pool to a fresh patch of substrate that had not already been foraged upon. We ended the experiment on the ninth day when we killed the tadpoles by immersion in MS 222. Each tadpole's SVL was measured using hand-held digital calipers. Our response measure was mean size (SVL) of cagemates at the end of the experiment. Because tadpoles in different cages had no opportunity to interact directly or compete, they

were unlikely to have affected each other's growth. Thus, we treated these individuals as replicates for the analysis.

Experimental evidence for the importance of exploitable resources

We found that *S. multiplicata* was absent from ponds in which detritus was scarce, and that *S. bombifrons* was absent from ponds in which shrimp were scarce (see *Results: Assessment of resource availability*). We therefore designed an experiment to establish whether, in the presence of *S. bombifrons*, low levels of detritus lead to poor performance (i.e., survival, growth) among *S. multiplicata* tadpoles. Such evidence might suggest that *S. multiplicata* is competitively excluded by *S. bombifrons* in ponds in which the detritus resource is scarce (as in pure *S. bombifrons* ponds; see *Results: Geographical surveys of habitat occupancy and character displacement*). We also sought to determine whether, in the presence of *S. multiplicata*, low levels of shrimp lead to poor performance among *S. bombifrons* tadpoles. Such evidence might suggest that *S. bombifrons* is competitively excluded by *S. multiplicata* in ponds in which the shrimp resource is scarce (as in pure *S. multiplicata* ponds; see *Results: Geographical surveys of habitat occupancy and character displacement*).

We used *S. bombifrons* and *S. multiplicata* from the July 2003 breeding chorus mentioned previously. Three days after the tadpoles hatched, we randomly assigned two similarly sized larvae (one *S. bombifrons* and one *S. multiplicata* tadpole) to each of the following treatments: (1) a high-shrimp, low-detritus treatment (36 replicate tanks); (2) a high-shrimp, high-detritus treatment (37 replicate tanks); and (3) a low-shrimp, high-detritus treatment (31 replicate tanks; we did not include single species treatments in this experiment, because they were part of a previous study [Pfennig and Murphy 2000], in which both species performed well on both resources). The original six sibships per species were equally represented across treatments. Rearing tanks (28 \times 18 \times 10 cm) were filled with 6 L of dechlorinated tap water. Tanks containing different treatments were interspersed and randomized by location in the same rearing room (maintained at 26°C and on a 14 h light : 10 h dark cycle).

The three diet treatments mimicked the different types of ponds found in our study area. In particular, the high-shrimp, low-detritus treatment resembled a pure *S. bombifrons* pond, where shrimp are relatively abundant but detritus is scarce (see *Results: Assessment of resource availability*). The high-shrimp, high-detritus treatment resembled a mixed-species pond, where both shrimp and detritus are relatively abundant. Finally, the low-shrimp, high-detritus treatment resembled a pure *S. multiplicata* pond, where detritus is relatively abundant, but shrimp are scarce.

Each tank in the low-shrimp treatment received two live fairy shrimp (*Thamnocephalus* or *Streptocephalus*) once a day. The resulting density of shrimp (0.33 shrimp/L) was within the range of densities observed in pure *S. multiplicata* ponds (see *Results: Assessment of resource availability*). In contrast, each tank in the high-shrimp treatment received 20 live fairy shrimp once a day. The resulting density of shrimp (3.33 shrimp/L) was within the range of densities observed in mixed-species and pure *S. bombifrons* ponds (see *Results: Assessment of resource availability*). For detritus, we used crushed fish food (Wardley cichlid floating pellets, 40% protein). The fish food resembled naturally occurring detritus in form and nutrition (Pfennig et al. 1991). Each tank in the low-detritus treatment received 0.025 g of crushed fish food every other day, and each tank in the high-detritus treatment received 0.05 g of crushed fish food every other day. The low-detritus treatment produced growth rates comparable to those found in our detritus bioassays for pure *S. bombifrons* ponds (see *Results: Assessment of resource availability*). The high-detritus treatment produced growth rates comparable to those found in our detritus bioassays for mixed-species and pure *S. multiplicata* ponds (see *Results: Assessment of resource availability*). In all tanks, shrimp and detritus had disappeared before the tadpoles were fed again. Thus, food was a limiting resource in all treatments, reflecting the condition in most natural ponds.

The experiment ended after ten days when tadpoles were killed by immersion in MS 222 and their SVL was measured using hand-held digital calipers. We also categorized each tadpole morphotype using the criteria listed in *Methods: Assessment of resource availability*. Our response measures were survival to, and size (SVL) and morphotype at, the end of the experiment.

RESULTS

Geographical surveys of habitat occupancy and character displacement

Spea bombifrons and *S. multiplicata* co-occurred with each other in only 15 of the 81 ponds sampled (18%). Fifty-five ponds (68%) contained only *S. multiplicata*, and 11 ponds (14%) contained only *S. bombifrons* (Fig. 2). Pure *S. multiplicata* ponds tended to occur at higher elevations (Fig. 2). Conversely, pure *S. bombifrons* ponds were found only at the lowest elevations in playa lakes (Fig. 2).

In natural ponds in which they co-occurred, the two species partitioned the shrimp and detritus resources and underwent character displacement in morph production. In mixed-species ponds, *S. bombifrons* developed almost exclusively into carnivores (the phenotype that specializes on shrimp), whereas *S. multiplicata* developed almost exclusively into omnivores (the phenotype that specializes on detritus). In these ponds, the mean (\pm SD) percentage of carnivores produced by *S.*

bombifrons ($95\% \pm 9\%$) was significantly greater than that produced by *S. multiplicata* ($5\% \pm 6\%$; $t = 10.80$, $df = 8$, $P < 0.0001$). By contrast, in pure-species ponds (i.e., ponds containing only a single species of *Spea*), the mean percentage of carnivores produced by *S. bombifrons* ($18\% \pm 15\%$) was not significantly different from that produced by *S. multiplicata* ($21\% \pm 26\%$; $t = 0.17$, $df = 45$, $P > 0.05$). Thus, the two species differed in morph production in sympatry, but not in allopatry.

Further evidence of character displacement comes from an analysis of the morphological index (a continuously varying composite shape variable (first principal component) that included three trophic characters). The two species did not differ significantly in the morphological index in allopatric, pure-species ponds (Fig. 3), but *S. bombifrons* was significantly more carnivore-like and *S. multiplicata* was significantly more omnivore-like in sympatric, mixed-species ponds (Fig. 3; ANOVA, $F_{3,64} = 23.5$, $P < 0.0001$; Tukey-Kramer hsd, $P < 0.05$).

Assessment of resource availability

The nonrandom geographical distributions of the two species within our study area (Fig. 2) reflected a non-random distribution of resources. When we reared tadpoles on detritus sampled from three different types of ponds (mixed-species ponds, pure *S. multiplicata* ponds, and pure *S. bombifrons* ponds; Fig. 4a, b, c), we found that tadpoles of both species experienced lowest growth on detritus from pure *S. bombifrons* ponds (*S. multiplicata*, Fig. 4d; ANOVA, $F_{2,23} = 74.8$, $P < 0.0001$; Tukey-Kramer hsd, $P < 0.05$; *S. bombifrons*, Fig. 4e; ANOVA, $F_{2,24} = 39.3$, $P < 0.0001$; Tukey-Kramer hsd, $P < 0.05$). Thus, detritus was scarcest (or poorest quality) in pure *S. bombifrons* ponds.

Shrimp also were distributed nonrandomly across ponds, and the distribution of *S. bombifrons* was associated with shrimp abundance. Mean (\pm SD) shrimp densities in pure *S. multiplicata* ponds (1.77 ± 2.15 shrimp/L, range = 0–6.4, $n = 11$ ponds) were significantly lower than those in mixed-species ponds (8.40 ± 2.24 shrimp/L, range = 6.3–12.1, $n = 5$ ponds; $t = 5.65$, $df = 14$, $P < 0.0001$). Indeed, both shrimp ($r = -0.75$, $P < 0.0005$) and *S. bombifrons* (Pfennig and Murphy 2000) became increasingly rare at higher elevations. Moreover, subjective estimates of shrimp densities revealed that ponds differing in shrimp density contained significantly different frequencies of *S. bombifrons*, with *S. bombifrons* being most abundant in ponds with the highest densities of shrimp (Fig. 5; ANOVA, $F_{3,64} = 5.1$, $P < 0.003$; Tukey-Kramer hsd, $P < 0.05$ on arcsine-square-root-transformed data).

Experimental evidence for the importance of exploitable resources

When we compared tadpole growth on three different experimental diet treatments, each of which mimicked

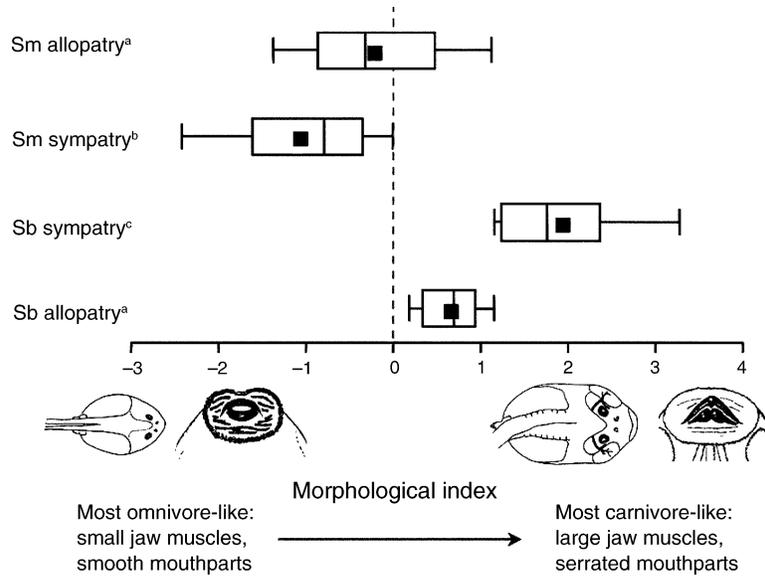


FIG. 3. Character displacement in tadpole morphology. Morphological index (a composite shape variable [first principal component] for three trophic characters) for *S. bombifrons* (Sb) and *S. multiplicata* (Sm) from sympatry (mixed-species ponds) and allopatry (pure-species ponds). Black squares represent means. Box plots show 10th, 25th, 50th (median), 75th, and 90th percentiles. Groups not sharing the same lowercase superscript letter are significantly different ($P < 0.05$). Sample sizes: Sm allopatry, 827 tadpoles from 36 ponds; Sm sympatry, 163 tadpoles from 11 ponds; Sb sympatry, 115 tadpoles from 11 ponds; Sb allopatry, 167 tadpoles from seven ponds. Pond means are reported here and used in the analysis.

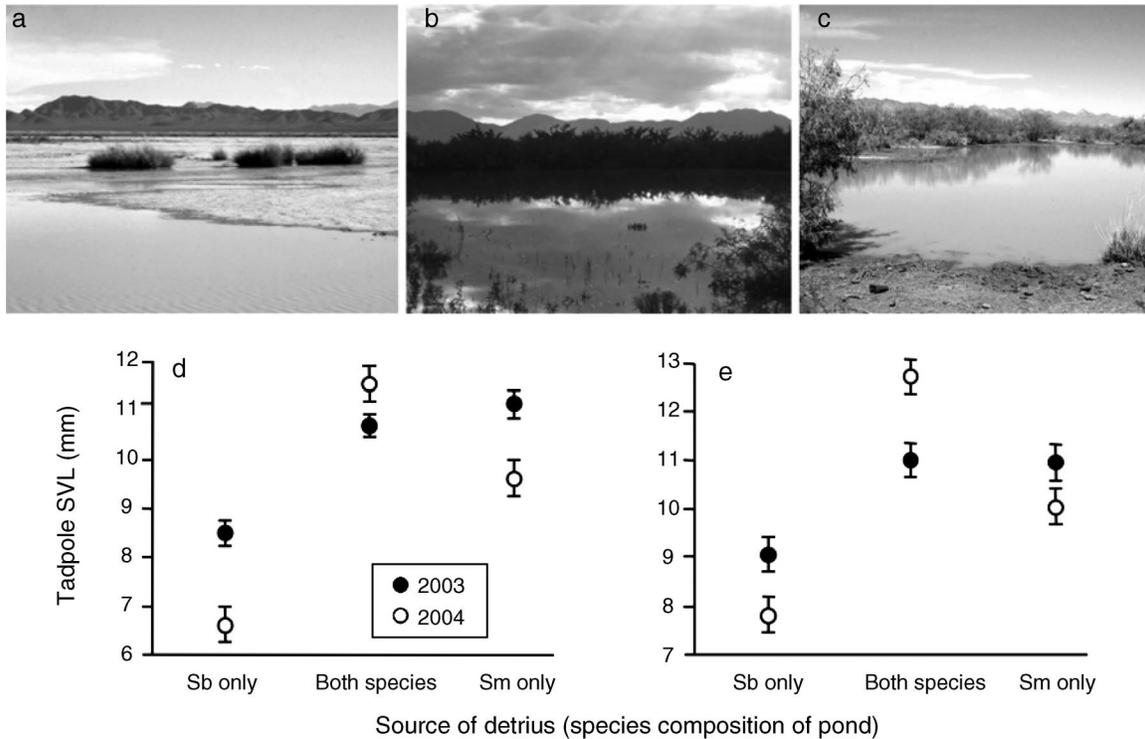


FIG. 4. Photos of a typical (a) pure *S. bombifrons* (Sb) pond (a playa lake), (b) mixed-species pond, and (c) pure *S. multiplicata* (Sm) pond, showing differences in surrounding vegetation (an important source of detritus). Locations of ponds are shown in Fig. 2. Size (snout-vent length, SVL) of (d) *S. multiplicata* and (e) *S. bombifrons* tadpoles when fed detritus from the three types of ponds (a-c) in two different years, 2003 and 2004. Each data point represents the mean size (\pm SE) of tadpoles in five separate cages.

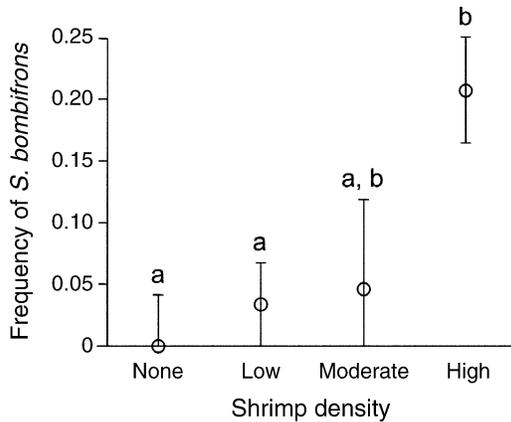


FIG. 5. Frequency (mean \pm SE) of *S. bombifrons* in ponds (proportion of *Spea* tadpoles that were *S. bombifrons*) as a function of estimated pond shrimp density. Pond types not sharing the same lowercase letter are significantly different from one another in the frequency of *S. bombifrons*.

a different type of pond, *S. multiplicata* tadpoles grew the least on the high-shrimp, low-detritus treatment (the treatment that simulated a pure *S. bombifrons* pond; Fig. 6a; ANOVA, $F_{2,101} = 11.3$, $P < 0.0001$; Tukey-Kramer hsd, $P < 0.05$). By contrast, *S. bombifrons* tadpoles grew the least on the low-shrimp, high-detritus treatment (the treatment that simulated a pure *S. multiplicata* pond; Fig. 6b; ANOVA, $F_{2,112} = 68.6$, $P < 0.0001$; Tukey-Kramer hsd, $P < 0.05$). Thus, each species performed the worst on the resource treatment that mimicked the type of pond in which that species was absent in the wild.

Diet treatments also differed in morph production and tadpole mortality. *Spea bombifrons* produced more carnivores in the high-shrimp, high-detritus treatment (which simulated a mixed-species pond) than in the low-shrimp, high-detritus treatment (which simulated a pure *S. multiplicata* pond). In the former treatment, *S. bombifrons* developed into a carnivore in 13 of 37 tanks (35%), whereas in the latter treatment, *S. bombifrons* developed into a carnivore in only 3 of 31 tanks (10%; $\chi^2 = 5.64$, $P < 0.018$). Moreover, *S. multiplicata* experienced significantly higher mortality in the high-shrimp treatments (nine out of 73 died; 12%) than in the low-shrimp treatment (0 out of 31 died; 0%; $\chi^2 = 6.23$, $P < 0.044$). The higher mortality may have been caused, in part, by predation: more *S. bombifrons* developed into carnivores in the high-shrimp than in the low-shrimp treatment, and carnivores tend to be highly predacious (Pfennig and Frankino 1997). Moreover, some of the *S. multiplicata* that died were observed being preyed upon by the *S. bombifrons*.

DISCUSSION

We used spadefoot toad tadpoles (*Spea bombifrons*, *S. multiplicata*) to test whether exploitable resources are a prerequisite for ecological character displacement

to occur. Because ecological character displacement generates new populations that differ in resource use, we hypothesized that this process should only occur when exploitable resources are available (Fig. 1a, b). In the absence of such resources, competing species should not coexist and competitive exclusion may result (Fig. 1c).

In ponds containing abundant detritus and shrimp, the two species coexisted, and each expressed different trophic phenotypes. *Spea multiplicata* developed primarily into omnivores (the detritus specialists), whereas *S. bombifrons* developed primarily into carnivores (the shrimp specialists). Thus, in mixed-species ponds, the two species partitioned resources (by undergoing character displacement) and thereby coexisted.

In contrast to ponds containing abundant detritus and shrimp, in nearby detritus-poor ponds (Fig. 4), *S. multiplicata* was rare or missing (Fig. 2), whereas in nearby shrimp-poor ponds, *S. bombifrons* was rare or missing

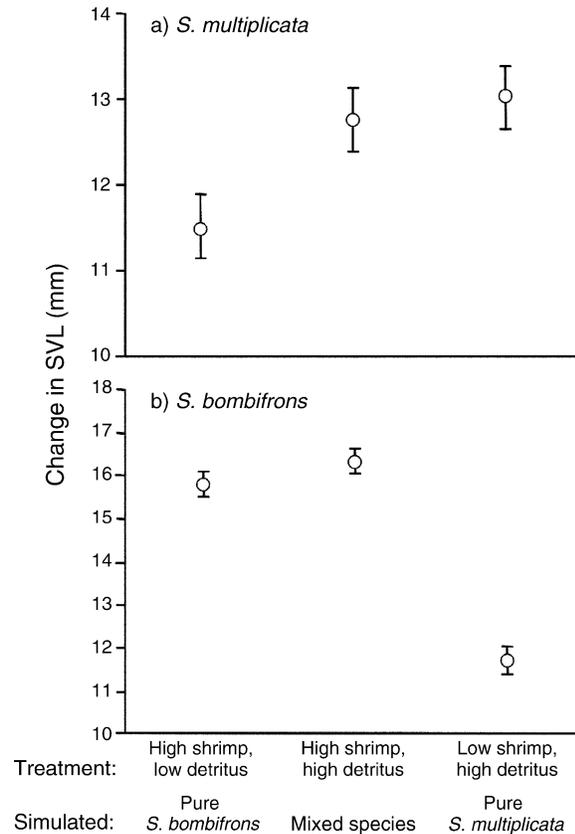


FIG. 6. Size (snout-vent length, mean \pm SE) of (a) *S. multiplicata* tadpoles and (b) *S. bombifrons* tadpoles when each was reared in the presence of the other and fed one of three diet treatments: high shrimp, low detritus (resembling a pure *S. bombifrons* pond); high shrimp, high detritus (resembling a mixed-species pond); and low shrimp, high detritus (resembling a pure *S. multiplicata* pond). Sample sizes: high-shrimp, low-detritus treatment, 36 replicate tanks; high-shrimp, high-detritus treatment, 37 replicate tanks; low-shrimp, high-detritus treatment, 31 replicate tanks.

(Fig. 5). A controlled experiment revealed that each species performed poorly when the resource for which it had a competitive edge was rare. In the presence of *S. bombifrons*, low levels of detritus led to poor growth and survival of *S. multiplicata* tadpoles (Fig. 6a). Similarly, in the presence of *S. multiplicata*, low levels of shrimp led to poor growth of *S. bombifrons* tadpoles (Fig. 6b). Such poor growth would likely diminish fitness in at least two ways. First, low growth rate reduces a tadpoles' chances of metamorphosing from the highly ephemeral ponds in which *Spea* often breed (Bragg 1965, Pomeroy 1981, Pfennig 1990, 1992). Second, low larval growth is associated with low postmetamorphic survival in *Spea* (Pfennig et al. 1991).

We hypothesize that *S. bombifrons* may have been competitively excluded by *S. multiplicata* from high-elevation ponds, and that *S. multiplicata* may have been competitively excluded by *S. bombifrons* from low-elevation playa lakes. High-elevation ponds tended to contain only *S. multiplicata* (Fig. 2). In such ponds, shrimp were scarce (Fig. 5) but detritus was relatively abundant (Fig. 4d, e). Because *S. multiplicata* is better than *S. bombifrons* at exploiting detritus (Pfennig and Murphy 2000), this resource may not have been available to sustain *S. bombifrons* omnivores. At the same time, the relatively small amount of shrimp may have been insufficient for *S. bombifrons* carnivores. Thus, *S. bombifrons* may have been competitively excluded by *S. multiplicata* from high-elevation ponds. By contrast, playa lakes tended to contain only *S. bombifrons* (Fig. 2). In such ponds, detritus was scarce (Fig. 4d, e) but shrimp were relatively abundant (Fig. 5). Because *S. bombifrons* is better than *S. multiplicata* at exploiting shrimp (Pfennig and Murphy 2000), this resource may not have been available to sustain *S. multiplicata* carnivores. At the same time, the relatively small amount of detritus may have been insufficient for *S. multiplicata* omnivores. Thus, *S. multiplicata* may have been competitively excluded by *S. bombifrons* from playa lakes.

Although we cannot say with certainty that competitive exclusion accounts for each species' absence from certain ponds, our data do demonstrate that character displacement only occurred when exploitable resources were available. When such resources were not available, character displacement did not occur, and the species that used the remaining resource less efficiently was missing.

It might be contended that predation—not competition—explains each species' absence from certain ponds. Intraguild predation can promote species exclusion, sometimes even mimicking the effects of competition (e.g., Holt 1977). We observed predation of *S. multiplicata* by *S. bombifrons* in our high-shrimp treatments and have observed such predation in the wild. Thus, *S. multiplicata* may be absent from playa lakes (Fig. 2) because of predation by *S. bombifrons*. Intraguild predation and competition may even interact to

explain the absence of *S. multiplicata* from such environments, where the low growth of *S. multiplicata* (Fig. 4d) may render them more vulnerable to both competition and predation (smaller individuals are often targeted as prey). Although we cannot rule out this possibility, it is unclear how intraguild predation could explain the absence of *S. bombifrons* from pure *S. multiplicata* ponds (Fig. 2), where carnivores—and, hence, intraguild predation—are rare (Fig. 3).

It might also be contended that each species was absent from ponds lacking one of the two resources because each was physiologically incapable of utilizing the remaining resource. However, each species can express both morphs in pure-species ponds (Fig. 3), suggesting that neither species is restricted by their physiology from utilizing either resource. Moreover, in each other's absence, each species performs well on both resources (Pfennig and Murphy 2000). Indeed, in the absence of competition from *S. bombifrons*, *S. multiplicata* actually grow better on a diet of shrimp than on a diet of detritus (see Pfennig and Murphy 2000, Fig. 4). Moreover, when reared alone, the two species have similar growth rates on detritus (see Pfennig and Murphy 2000, Fig. 4).

What factors explain the uneven distribution of shrimp and detritus? Shrimp decreased in abundance with elevation (see *Results*). Such a decline may reflect increased predation pressure on shrimp at higher elevations. Because orographic lifting generates greater rainfall, high-elevation ponds tend to receive more runoff and persist longer (Pomeroy 1981, Pfennig 1990). Perhaps as a consequence of their longer duration, high-elevation ponds maintain greater densities and varieties of shrimp predators for a longer period of time (e.g., *Spea* tadpoles remain in such ponds longer; D. Pfennig, *unpublished data*). Why was detritus rare in playa lakes (Fig. 4b)? Playas form in topographic basins, which accumulate high levels of water-soluble salts from marine deposits in the surrounding mountains (especially sodium, calcium, and magnesium sulfates). These high salt concentrations impede buildup of plants (note the absence of vegetation in Fig. 4a). Because most detritus derives from vegetation in and around ponds, playas tend to lack detritus.

If some pure-species ponds can sustain both morphs within a species (Fig. 3), why can these ponds not also enable both species to coexist by partitioning the available resources, as in mixed-species ponds where the two species underwent character displacement? Although pure-species ponds were able to sustain resource polymorphism—presumably because of selection to minimize intraspecific competition (Pfennig 1992) and because an “open niche” was present in such ponds (Smith and Skúlason 1996)—these ponds may not have enabled character displacement and species coexistence, for at least two reasons. First, there may have been insufficient quantities of either resource to sustain an entire population of the other species.

Indeed, compared with mixed-species ponds, pure *S. bombifrons* and pure *S. multiplicata* ponds contained significantly lower levels of detritus and shrimp, respectively (Figs. 4 and 5). Moreover, when we experimentally varied the levels of each resource, each species lost its competitive edge when its resource fell below some critical level (Fig. 6).

A second reason why pure-species ponds may not have been able to sustain both species, even when they were able to sustain both morphs, may be because of the pond's isolation from the missing species' source population. For example, although some high-elevation ponds contained abundant shrimp, ponds deficient in shrimp often surrounded such ponds. In essence, these ponds represented "islands" of suitable habitat surrounded by unsuitable habitat, possibly making them difficult for *S. bombifrons* to colonize.

Finally, we are not suggesting that resource availability explains the allopatric distributions of these species over their entire geographical ranges (e.g., see Stebbins 2003). Indeed, in contrast to what we observed in our study area (Fig. 2), in other areas, pure *S. bombifrons* ponds contain high levels of detritus and low levels of shrimp (e.g., in the Great Plains; D. Pfennig, *personal observation*), and pure *S. multiplicata* ponds contain low levels of detritus and high levels of shrimp (e.g., in central Arizona; D. Pfennig, *personal observation*). Thus, other, as yet unidentified, ecological or historical processes likely explain broader patterns of allopatry in these species.

The role of phenotypic plasticity in promoting character displacement

Even if exploitable resources are available, character displacement is not guaranteed to transpire if species cannot utilize such resources expeditiously. Phenotypic plasticity provides a general and important mechanism for facilitating resource partitioning. Indeed, "facultative character displacement" (sensu Pfennig and Murphy 2002), in which individuals respond to the presence of a competitor by facultatively switching to an alternative, less-used resource, may be more common than the more traditionally studied "canalized character displacement." Moreover, when faced with a superior competitor, animals often adjust their foraging behavior to utilize exploitable resources (e.g., Schoener 1968, 1974, MacArthur 1972). Initially, such a shift may or may not be accompanied by morphological change (Mayr 1963).

Discrete plasticity (i.e., polyphenism) may actually promote shifts in resource use and character displacement. To see how, consider a population that occupies one of two possible peaks on an adaptive landscape (the two peaks might correspond to two morphs). If a superior competitor invades and begins to utilize the same limiting resource, the population would have to cross a fitness valley of maladaptive intermediate forms to climb the alternative peak (and use an alternative

resource), a process normally prevented by natural selection. With polyphenism, however, populations can shift rapidly from one peak to the other without having to pass through the intervening selective valley (Kirkpatrick 1982, Schlichting and Pigliucci 1998, Pál and Miklos 1999). When confronted with a superior competitor, a population displaying polyphenism can express an alternative, selectively favored phenotype that is unlike the competitor's without having to wait many generations for new divergent traits to arise through mutation or recombination (Pfennig and Murphy 2000, 2002). In the absence of such polyphenism, a superior competitor may drive the other species locally extinct before it has time to evolve new canalized traits that lessen competition. In this way, phenotypic plasticity and ecological opportunity may often interact to promote character displacement and species coexistence.

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